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Internal constraints on energy processing
and their consequences: an integrative
study of behaviour, ornaments
and digestive health in greenfinches

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Internal constraints on energy processing and their consequences: an integrative study of behaviour, ornaments and digestive health in greenfinches

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LIST OF ORIGINAL PAPERS AND MANUSCRIPTS

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2. Lind, M.-A., Hõrak, P., Sepp, T., Meitern, R., 2020. Corticosterone levels correlate in wild-grown and lab-grown feathers in greenfinches (*Carduelis chloris*) and predict behaviour and survival in captivity. Hormones and Behavior 118, 104642.

3. Lind, M.-A., Sepp, T., Štšeglova, K., Hõrak, P., 2021. Antibiotic treatment increases yellowness of carotenoid feather coloration in male greenfinches (*Chloris chloris*). Scientific Reports 11, 13235.

4. Lind, M.-A., 2022. Carotenoids signal gut health through the effects of microbial metabolites on mitochondria. Manuscript.

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Author's contribution to the papers ('*' denotes a moderate contribution, '**' denotes a high contribution, '***' denotes a leading role).

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

1. INTRODUCTION

1.1 Internal constraints on energy processing in animals

Living organisms need to capture energy from the environment and use this energy in physiological processes in order to survive and reproduce. Animals acquire food from the environment, the food is digested and absorbed in the digestive system, and subsequently, chemical energy from nutrients is captured in ATP (adenosine triphosphate) – an energy carrier that can fuel physiological processes in the organism. The majority of ATP is produced via aerobic respiration in mitochondria (Sherwood et al., 2012). However, not all energy stored in the food can be utilised and is available for metabolism due to inefficiencies in the digestive system, which for example, can be caused by parasitic infection (Russell and Ruff, 1978; Sharma and Fernando, 1975). Animals' energy requirements also vary depending on the time of the day, season, life history stage (such as breeding, migration), environmental conditions, parasitic load, injury or disease etc. (McEwen and Wingfield, 2003). Rather than simply maximising ATP production, it is important to match the output of energy of cellular respiration to the need for energy (Hill, 2014). Processes that are not essential for survival are inhibited (e.g., reproduction) when animals' energetic needs exceed the available energy resources. Hormones of the hypothalamo-pituitary-adrenal (HPA) axis, such as corticosterone, are important mediators that regulate organisms' responses to changing energetic needs (McEwen and Wingfield, 2003). Thus, after the food is ingested from the environment, animals experience several internal constraints to energy processing. These include absorption of nutrients in the digestive system, aerobic respiration in mitochondria, and matching energy expenditure to energy input.

Explaining why and how individuals differ in their performance is central to evolutionary and ecological research. Despite unlimited access to energy when *ad libitum* food is provided, substantial variation between individuals can still be observed in captivity. Thus, differences in energy processing between individuals can integrate several seemingly unrelated components that contribute to animals' fitness, such as immune function and parasite resistance, behaviour and ornament expression (Hill, 2014). This highlights the importance of characterising energetic constraints and their effects on individual phenotypic quality in ecological studies. Thus, sensitive, individually consistent and non-invasive biomarkers to assess animals' energetic constraints are needed.

1.2 Glucocorticoid hormones as energy regulators

The energetic needs of an animal and optimal regulation of physiological processes can vastly differ depending on the individual's life history stage and environmental conditions, for example, whether the animal is breeding, migrating or is experiencing unexpectedly harsh weather conditions. Allostasis is a process

through which organisms actively adjust to both predictable and unpredictable events in order to sustain homeostasis, that is, stability of physiological systems to maintain life (McEwen and Wingfield, 2003). Thus, allostasis can be described as maintaining stability through change. Allostatic load describes the cumulative daily and seasonal energetic needs of an animal in order to survive, extra energy needed to migrate, moult, breed, and energy needed to face any additional unpredictable events in the environment. Allostatic overload occurs when energy demand exceeds energy supply, which evokes an emergency life-history stage to restore positive energy balance and physiological responses that help achieve this. Factors like parasite load, injury, body size, and social status can affect individuals' energetic needs and the ability to acquire energy from the environment resulting in higher allostatic load (McEwen and Wingfield, 2003). For example, the energetic needs of an individual with parasitic infection are more likely to exceed available energy resources compared to a healthy individual when unexpected perturbation occurs, such as low temperatures in winter.

Glucocorticoid hormones (GCs) of the hypothalamo-pituitary-adrenal (HPA) axis are important regulators of the stress response (Sapolsky et al., 2000), and it has been suggested that they are also crucial mediators of allostasis (McEwen and Wingfield, 2003). Elevated GCs levels promote gluconeogenesis (generation of glucose from lipids and proteins) (Sapolsky et al., 2000), increase appetite and food-seeking behaviour (Dallman et al., 1993; Sepp et al., 2014), increase locomotor activity (Landys et al., 2006) and inhibit processes that are not essential for survival (McEwen and Wingfield, 2003). Thus, in the short term, elevated GSs levels serve beneficial effects that help to regain positive energy balance and decrease the allostatic load. However, continuously upregulated GC may have deleterious effects, which can lead to disease and even death (Blas, 2015; Landys et al., 2006; McEwen and Wingfield, 2003).

GCs are often referred to as stress hormones, as they are secreted in response to life-threatening and unpredictable stressful events. However, GCs levels also fluctuate in response to circadian rhythms (Dallman et al., 1993), different seasons and life history stages (Landys et al., 2006; McEwen and Wingfield, 2003). It has been shown that GCs also play an important role in the regulation of metabolism, feeding behaviour, and locomotor activity (Landys et al., 2006; McEwen and Wingfield, 2003; Sapolsky et al., 2000) at baseline levels in non-stressful situations, suggesting that GCs are important regulators of allostasis in response to predictable daily and seasonal variations in energetic demands.

Cortisol and corticosterone (CORT) are the most common GCs, and both are expressed in most species. However, most species rely on either one of these – birds, reptiles, amphibians, and some rodents and fish using CORT, while most mammals and marine animals rely on cortisol (Blas, 2015). Measuring CORT has become the main indicator to assess stress in birds (Romero, 2004), but its role as an energy regulator has often been neglected in ecological studies. Most commonly, CORT levels are measured from plasma. Circulating CORT levels can change within minutes in response to a stressor, thus providing a snap-shot view of CORT levels at the time of the measurement (Bortolotti et al., 2008).

Recently, measuring CORT from feathers or faeces has gained popularity, which can provide information about cumulative CORT levels over a longer period of time. However, it remains largely unclear whether CORT levels can reflect some component of an individual's phenotype, such as allostatic load, that is consistent in time.

1.3 Absorption of nutrients in the digestive system

Capability to absorb energy and nutrients from food poses a major internal constraint to energy processing in animals. Due to the inefficiencies in the digestive process, not all food that is eaten can be utilised and is available for metabolism, which may explain why individuals differ in their energy management and allocation decisions (Klasing, 1998). Damage to the intestinal system and malabsorption of nutrients can be caused by intestinal parasites (Russell and Ruff, 1978; Sharma and Fernando, 1975), and the maintenance of digestive organs contributes considerably to individual variations of the metabolic rate due to its high metabolic activity and cell turnover rate (Killpack and Karasov, 2012). The intestinal surface is also a major contact zone between the immune system and microbial antigens. The animal gut is densely populated with microbes. The gut microbiome can provide additional nutrients from food and affect various other host physiological processes (Rosenberg and Zilber-Rosenberg, 2018); thus, it is important to maintain a balanced microbiome.

Studies in poultry have shown that intestinal damage caused by intestinal infection resulted in decreased nutrient absorption (Russell and Ruff, 1978; Sharma and Fernando, 1975). In captive greenfinches (*Chloris chloris*), goldfinches (*Carduelis carduelis*), and Nashville warblers (*Vermivora ruficapilla*) that died in captivity, coccidian infection was linked to thickening of the intestinal wall, which in turn correlated negatively with weight (Gosbell et al., 2020; Swayne et al., 1991). However, methods traditionally used for studying digestive physiology are often not applicable in ecological studies due to the lethality or complexity of the procedure. Therefore, most ecological studies indirectly suggest that parasites cause intestinal damage. For example, experimental infection of greenfinches with coccidian parasites decreased plasma carotenoid and triglycerides, which provides indirect evidence for reduced digestive and absorption capacity (Hõrak et al., 2004). Increased plasma triglycerides are related to the transport of fat to the adipose tissue and energy-consuming organs; thus, they indicate the amount of lipids absorbed and changes in fat stores (Jenni-Eiermann and Jenni, 1994).

Many birds express vivid colours in integument in order to attract a mate. Several pigments that are used for the production of these sexual signals are absorbed from food (Goodwin, 1984; Hill, 2006). For example, carotenoids are fat-soluble red and yellow pigments often used in ornaments that must be acquired from the diet as most animals cannot synthesise carotenoids *de novo* (Blount and McGraw, 2008). Intestinal infections have been shown to affect

carotenoid colouration in wild birds (Baeta et al., 2008; Hõrak et al., 2004), and poultry studies have linked intestinal damage to reduced circulating carotenoids (Ruff and Fuller, 1975; Tyczkowski et al., 1991). Thus, the production of some signals may depend on the integrity of the digestive machinery. However, it remains unclear whether the effect on carotenoid colouration occurs specifically due to parasites' effect on gut integrity or through general condition decline.

The ability to assess digestive efficiency would help to distinguish whether differences between individuals arise from malabsorption or from the efficiency of utilising nutrients. The functioning of the digestive system may also provide information about the animals' capability to resist infections. However, non-invasive methods suitable for ecological studies are currently lacking, and feasible proxies for the assessment of digestive efficiency in wild animals are needed.

1.4 Mitochondrial function and production of condition-dependent signals

Digestive system poses an important constraint for energy acquisition. The amount of body fat and weight has been often associated with the animal's condition – having a large pool of resources available for allocation indicates a better condition. However, condition is not always synonymous with an animal's energy stores. Higher fat stores can hinder flight performance and foraging efficiency and make an animal an easier prey (Witter and Cuthill, 1993). Therefore, fat storage patterns are more likely to depend on the relative cost-benefit ratio of fat storage. It has been suggested that in a healthy organism, energy demand should be matched with energy output rather than maximising energy reserves. Furthermore, condition-based ornaments might signal the capacity to produce energy when needed rather than the availability of the energy per se (Hill, 2014).

After the food is ingested and nutrients are absorbed, the chemical energy in nutrients is captured in ATP or released as heat. The majority of ATP is produced via aerobic respiration in mitochondria (Sherwood et al., 2012). Therefore, the functionality of mitochondria and efficiency of aerobic respiration determines how many ATP molecules can be derived from each unit of food, but also how many reactive oxidative species are created that can be harmful to the organism (Shutt and McBride 2013). Furthermore, glucocorticoid receptors are present in mitochondria, suggesting that the expression of some mitochondrial genes are under the control of glucocorticoids. Thus, glucocorticoid hormones can regulate mitochondrial processes and orchestrate meeting the energy demands of the stress response by increasing the energy production capacity (Lee et al., 2013). Therefore, energy production in the mitochondria is another major site where internal constraints to energy processing might occur. Numerous seemingly unrelated components of condition, such as immune function and parasite resistance, behaviour, ornament expression, and stress response, all seem to be closely related to mitochondrial function (Hill, 2014).

In order to retain honesty, sexual ornaments have to be hard to fake (Zahavi, 1975). It has been often suggested that the production of sexual signals is costly due to trade-offs that arise from the allocation of resources between the production of ornaments and other physiological functions. Alternatively, Hill (2011) proposed that ornament production can be linked to the functionality of the vital cellular processes via shared pathways, known as the shared pathway hypothesis. Accordingly, the expression of condition-dependent traits depends on the capacity to maintain optimal functionality of essential systems within the body (Hill, 2011).

In many species, dietary carotenoids are biotransformed in the organism before they are deposited into ornaments, and it has been suggested that this process takes place in the inner mitochondrial membrane (Hill et al., 2019; Johnson and Hill, 2013; Mundy et al., 2016). This would link carotenoid ornamentation to the functionality of mitochondria via shared pathways, which would make carotenoid ornaments hard to fake, thus reliable indices of individual quality (Hill, 2011; Johnson and Hill, 2013). Therefore, carotenoid-based ornaments could signal an individual's capacity to produce energy.

1.5 Aims of the thesis

The two main aims of this thesis were (1) to explore internal constraints on energy processing and (2) to understand how these constraints impact the survival, behaviour and production of sexually selected ornaments in a passerine bird. Firstly (1), I studied possible mechanisms which might play a role in energy processing and estimated their validity and usefulness in ecological studies (**Paper I and II**). Animals' ability to extract energy and nutrients from food poses major internal constraints to the resources that are available for physiological functions. I set out to develop a method to assess the efficiency of fat digestion for ecological studies based on a method previously used in humans and mice (Sugai et al., 1994; Tran et al., 1994; Van den Neucker et al., 1997) (**Paper I**). Glucocorticoid hormones (GCs) control both stress responses and energy regulation. However, the latter function has received less attention in ecological studies. Therefore, I tested whether corticosterone levels in feathers (fCORT) signal some persistent component of an individual's phenotypic quality (**Paper II**). Secondly (2), I focused on how these constraints on energy processing affect ecologically relevant traits. I tested whether targeting common infections of the digestive system with antimicrobial drugs affects the production of sexually selected carotenoid-based ornaments (**Paper III**) and assessed whether feather corticosterone levels are related to behaviour and survival in captivity (**Paper II**). Finally, I proposed a novel idea that the gut microbiome can significantly affect energy regulation by modifying mitochondrial function, which affects carotenoid colouration (**Paper IV**).

In more detail, I explored whether the acid steatocrit method, which has been validated in human studies, could be used to measure fat content in bird faeces

(**Paper I**). The ability to extract nutrients and energy from food during digestion poses a major constraint on energy acquisition, which can explain why individuals differ in their energy management and allocation decisions (Klasing, 1998). Traditional methods that are used to investigate digestive physiology are mostly unsuitable in ecological studies due to their invasiveness, lethality or complexity of the procedure. Thus, I tested whether the acid steatocrit method enables the detection of between-individual differences in fat absorption that are persistent in time. Secondly, I tested whether this method could be applied in ecophysiological studies as a marker of intestinal health by experimentally manipulating the infection levels by administering antimicrobial drugs or by experimentally infecting the birds with novel coccidian strains originating from multiple hosts. I predicted that the treatment with antimicrobial drugs and experimental infection affect fat content in faeces and that these changes are detectable with the acid steatocrit method. I further predicted that the manipulations of intestinal infections would affect plasma triglycerides and body mass.

In the second study **(Paper II)**, I set out to explore whether corticosterone levels in feathers can convey information about an individual's phenotypic quality. GCs have crucial roles in adequately regulating metabolism, energy mobilisation, immune response, behaviour, reproduction, and other physiological functions (Dallman et al., 1993; Sapolsky et al., 2000). Factors like parasite load, injury, and social status can affect an individual's energetic needs leading to individual differences in baseline and stress-induced GC levels (McEwen and Wingfield, 2003). I predicted that feather corticosterone levels are individually consistent over a longer period of time, signalling persistent components of an individual's phenotypic quality, such as adequate energy regulation and the allostatic load of the animal. I also hypothesised that fCORT levels are related to survival and behaviour.

Precursors of pigments that are used in signalling, such as carotenoids, are absorbed from food (Hill, 2006). Therefore, carotenoid colouration could indicate energetic constraints posed by the integrity of the digestive system. Interestingly, it has also been suggested that biotransformation of dietary carotenoids into pigments that are deposited into ornaments takes place in the mitochondrial membrane, which ties this process to the efficiency of cellular processes (Hill, 2011; Johnson and Hill, 2013). This suggests that carotenoid ornaments might contain information about an organism's overall capacity to produce energy. Therefore I predicted in **Paper III** that if intestinal tract integrity is the key factor linking intestinal parasite infection to carotenoid colouration, carotenoid colouration should be affected by treatment with both antimicrobial drugs – TOLTRA (targets only intestinal coccidian infection) or METRO (a wide spectrum antibiotic that targets several infection and anaerobic bacteria). Alternatively, if the key factor is the overall health of the individual, then birds treated with METRO would show a greater increase in plumage carotenoid colouration.

Intestinal infections have been at the centre of attention in immunobiological research. However, increasing evidence suggests that mutualistic and commensal members of the microbiome also play an important role in individuals' health

(Hanning and Diaz-Sanchez, 2015). Due to the common ancestry (Franco-Obregón and Gilbert, 2017), mitochondria and bacteria share many structural and functional similarities, and growing empirical evidence suggests that bacterial metabolites can affect mitochondrial function (Clark and Mach, 2017). I conducted a literature review (**Paper IV**) and proposed that the intensity of carotenoid ornaments might be related to the gut microbiome via mitochondrial functioning. Thus, the energy regulation of an organism might not only be impaired by the presence of intestinal pathogens but also by the absence of symbiotic microorganisms, with the potential to affect signalling traits.

2. MATERIALS AND METHODS

2.1 Model system

I used wild-caught captive greenfinches as a model organism. Greenfinches can tolerate captivity well and have been used often in ecophysiological research as a model system (Sepp et al., 2010). Using wild animals as opposed to animals grown in captivity makes the results more extrapolatable to natural situations. In addition, captivity enables us to control environmental variables which would not be possible in a natural environment, thus making the model simpler. Carotenoid-based feather colouration in greenfinches makes them a good model species to study constraints to energy processing on signalling traits, including nutrient absorption in the digestive system, biotransformation of carotenoids, and trade-offs between allocating resources to other physiological functions.

Greenfinches are gregarious medium-sized (c. 28 g) seed-eating, sexually dichromatic passerines native to the western Palearctic region. Males are more colourful with yellow, carotenoid-based markings on the sides of the tail feathers, primaries, primary coverts, and breast, while females are more olive-brown and lack full yellow tints in their plumage (Cramp and Perrins, 1994; Stradi et al., 1995). Males with more intense yellow colouration are preferred by the females (Eley, 1991) and have higher lifetime reproductive success (Cantarero et al., 2019). Greenfinches incorporate two main carotenoids, canary xanthophylls A and B, into their feathers to develop yellow colouration (Saks et al., 2003). Canary xanthophylls A and B are metabolically converted inside the organism from dietary lutein and zeaxanthin (McGraw et al., 2002; Stradi, 1998).

Gut parasites can cause damage to the intestinal system and decrease the availability of nutrients, thus decreasing overall energy acquired from food. Green-finches regularly experience outbreaks of digestive tract infections such as coccidiosis (Hõrak et al., 2004) and avian trichomonosis (Lehikoinen et al., 2013). In our study system, the majority of greenfinches are naturally infected with coccidian parasites (Sepp et al., 2012), and occasionally, some birds in the aviary have died with symptoms characteristic of trichomonosis (Männiste and Hõrak, 2014). All the greenfinches in my studies appeared naturally infected by isosporan coccidians (**Papers I and III**). Coccidia are protozoan intracellular parasites, and their asexual and sexual multiplication takes place inside the intestine's epithelial cells (Joyner et al., 1975; Sharma and Fernando, 1975). This can cause extensive damage to the intestinal villi (Pout, 1967), inflammation of the gut surface, reduced digestive efficiency (Russell and Ruff, 1978; Sharma and Fernando, 1975), and malabsorption of carotenoids (Ruff and Fuller, 1975; Tyczkowski et al., 1991) and other nutrients (Joyner et al., 1975; Sharma and Fernando, 1975).

Avian trichomonosis is caused by protozoan *Trichomonas gallinae* and the symptoms include lesions in the upper digestive tract, which in severe cases can block the oesophagus and make the passage of food impossible (Amin et al., 2014). Avian trichomonosis is an emerging disease in greenfinches in Europe that has been reported to cause epidemics with high mortality and a decline in wild greenfinch populations (Chavatte et al., 2019; Robinson et al., 2010).

2.2 Manipulations of intestinal infection

Infection intensity of coccidia is easy to determine from the faeces and the infection status is easy to manipulate with anticoccidial drugs or experimental infection, making it a good parasite-host interaction model to study the effects of intestinal infection on the absorption of nutrients from food. In order to target coccidian infection, I used anticoccidial drugs sulfadimethoxine in **Paper I**, and toltrazuril in **Paper I** and **Paper III**. Toltrazuril is designed specifically for the treatment of coccidiosis and lacks known effects on microbes other than apicomplexans (Hackstein et al., 1995; Sepp et al., 2012). Toltrazuril affects the respiratory mechanism of coccidia by interfering with nuclear division and mitochondrial activity (Krautwald-Junghanns et al., 2009). Sulfadimethoxine is a broad-spectrum sulfonamide drug that is effective against protozoans, including coccidians and also has antibacterial efficacy (Mitrovic and Bauernfeind, 1971).

In **Papers I and III** I targeted trichomonosis and bacterial infections with metronidazole, which is a wide spectrum antibiotic with activity against anaerobic bacteria and protozoans. Metronidazole is widely used for the medication of trichomonosis (Amin et al., 2014; Samuelson, 1999). Metronidazole is only active against bacteria with anaerobic metabolisms and some microaerophiles because aerobic cells lack electron-transport proteins with sufficient negative redox potential (Löfmark et al., 2010).

In **Paper I,** I conducted an experimental infection experiment where birds were inoculated with heterologous coccidian stains from different hosts. Infecting greenfinches with novel coccidian strains originating from multiple hosts has shown to cause a decline in body mass and plasma triglyceride levels (Hõrak et al., 2006), suggesting a variation of virulence of coccidia strains. Excreted oocytes were collected from 20 male birds during 3 days and inocula of sporulated oocytes were prepared as a single stock from all donor individuals as described by Hõrak et al. (2004). A dose of 2000 sporulated oocytes diluted in 1 ml tap water, was administered orally by micropipette to birds in the experimental infection group.

2.3 Acid steatocrit method and corticosterone measurements

Measuring digestive efficiency would help to distinguish general condition decline from decreased nutrient absorption from the gut. However, common methods for studying digestive physiology are mostly unsuitable for ecological studies involving complex invasive procedures or killing the animal. In **Paper I,** I tested the applicability of the acid steatocrit method for use in birds. It is a simple, cheap, and noninvasive technique based on the centrifugation of a faecal sample diluted in the acid medium in a hematocrit capillary tube and quantifying the percentage of fat in faecal matter.

The method was originally developed as a quick technique for diagnosing fat malabsorption in infants (Phuapradit et al., 1981) and after some improvements, the method became known as acid steatocrit (Tran et al., 1994). The method has

been validated and applied in humans and mice to study digestion efficiency (Takahashi et al., 2007; Weidemann et al., 2015). Steatocrit measurements show high correlations with the actual fat concentration of faeces (Amann et al., 1997; Sugai et al., 1994; Tran et al., 1994; Van den Neucker et al., 1997) and faecal energy content (Van den Neucker et al., 1997). Steatocrit method also shows high specificity and sensitivity for diagnosing fat malabsorption (Sugai et al., 1994; Van den Neucker et al., 1997).

Two sheets of A4 paper were placed on the sand bedding of cages 2 h before the lights turned off for the collection of faecal samples for measuring steatocrit. I estimated the fat content in bird faeces based on the acid steatocrit method described by Tran et al. (1994). I diluted and homogenised bird droppings (1:3) with deionised water. After that, I added five molar perchloric acid in volume 1:5 to the homogenate and vortexed for 10 s. The homogenate was collected into the hematocrit capillary tube and centrifuged at 13,000 rpm for 15 min. Subsequently, the capillary tubes were photographed (Canon 1100D, 1s, f8, ISO100). The length in pixels was quantified for the upper fat layer (FL) and solid bottom layer (SL) from the photographs (Figure 1.) using ImageJ software. Steatocrit was expressed as a percentage of fat in the nonaqueous matter of the sample: the length of a fat layer (FL) divided by the sum of the lengths of the fat layer (FL) and solid layer (SL).

Figure 1, adapted from Paper I. The upper hematocrit capillary tube shows a bird with severe steatorrhea; the lower capillary tube indicates light steatorrhea. No faecal fat is visible in the middle capillary tube. Non-fatty faecal solids layer (SL), liquid intermediate layer (IL), and fatty layer (FL).

2.4 Measurements of behaviour and carotenoid feather colouration

Tail damage from flapping against the cage bars is a behavioural trait that has been shown to correlate with fCORT and has been suggested to indicate captivity tolerance of wild-caught birds (Sepp et al., 2014; Sild et al., 2011). It has been previously established from the video recordings that birds with damaged tails perform flapping flights against cage walls more frequently than birds with intact tails (Sepp et al., 2014; Sild et al., 2011). We photographed the tails of the birds under standard conditions at the end of the study before the birds were released back into the wild in order to assess tail damage (**Paper II**). 16 observers rated the photographs of the tails on the five-point scale, ranging from 0 (no damage) to 4 (maximum extent of damage among the photos presented, Fig. 2) for assessment of damage to the tail feathers in captivity. Average ratings of 16 observers were used in the analyses. At capture, all the tails of all the birds were in perfect condition and scored 0.
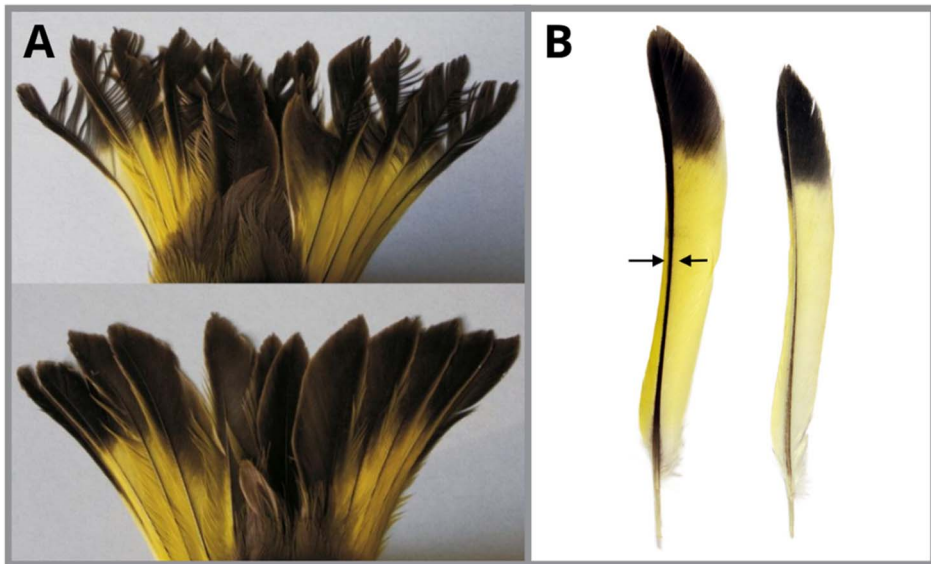

Figure 2, adapted from Papers II and III. (A) Examples of greenfinches with damaged (upper) and intact (bottom) tail feathers. (B) Measurement of feather chroma. The arrows indicate positions where chroma of yellow feather colouration was measured. On the left – a wild-grown feather, and on the right – a lab-grown feather.

In order to measure the carotenoid colouration of feathers, the left and right outermost wild-grown tail feathers (rectrices) were plucked at the beginning (wild-grown feathers) and at the end (lab-grown feathers) of the study (**Paper III**). Collected feathers were stored in a plastic bag in the dark until measurements of chroma of yellow feather parts were carried out. Chroma can be understood as a

measure of the 'purity' or 'saturation' of colour and it has been shown to correlate with the actual carotenoid concentration of feathers in greenfinches (Saks et al., 2003). The locations where chroma was measured are indicated in figure 2. The colour was measured from the feathers placed on a black background, in an area of approximately one mm2, of the visible surface of the feather, using a spectrophotometer (Ocean Optics S2000) and the values of chroma were calculated as described by (Saks et al., 2003).

3. RESULTS AND DISCUSSION

3.1 Assessment of digestive efficiency
with faecal steatocrit method

In my first study (**Paper I**), I tested the reliability and suitability of the acid steatocrit method to assess fat content in the faeces in birds. This method has been validated in humans and mice, but this was the first time when the steatocrit method was applied in birds. Subsequently, I tested whether changes in fat absorption in response to experimental manipulation of intestinal infections are detectable by the acid steatocrit method to confirm its applicability in avian studies. Intestinal parasites can cause damage to the gut wall resulting in decreased absorption of nutrients (Joyner et al., 1975; Ruff and Fuller, 1975; Sharma and Fernando, 1975; Tyczkowski et al., 1991). The digestive system also contributes significantly to individual variations in metabolic rate (Killpack and Karasov, 2012). The vertebrate gut harbours a large microbial community and is a major contact zone between the immune system and microbial antigens. The functioning of the digestive system can thus provide valuable information about animals' physiology and ability to resist infections. However, to study these topics, eco-logists need feasible methods to assess digestive efficiency in wild animals, which are currently lacking.

I used 70 male and 41 female greenfinches in my study that were captured in mist nets and housed indoors in individual cages. Males and females received separate experimental treatments in order to test different types of antimicrobials and to keep the models simple. The males were divided into three groups: treatment with toltrazuril (anticoccidial drug), treatment with metronidazole (wide-spectrum antibiotic) and the third group served as controls. Experimental treatment of females involved medication with sulfadimethoxine (sulphonamide anticoccidial drug), infection with unfamiliar coccidian strains and a control group. It has been previously shown that both toltrazuril (Sepp et al., 2012) and sulfonamide (Hõrak et al., 2004) decrease coccidian infection intensity and sulfonamide increases plasma triglycerides (a marker of nutritional state) compared to infected birds (Hõrak et al., 2004). Experimentally infecting birds with novel coccidian strains has been shown to decrease body mass and circu-lating triglycerides (Hõrak et al., 2006). Faecal samples were collected for assess-ment of coccidian infection and for steatocrit measurements prior to the treat-ment, twice in males and once in females after the treatment. The birds were blood sampled twice, before and after the treatment, in order to determine plasma triglyceride levels. Birds were weighed at several time points throughout the experiments.

I detected that the values of steatocrit showed significant individual con-sistency at least over 20 days in males and over 11 days in females, indicating its reliability to identify persistent individual differences in fat digestion between indi-viduals. Males treated with toltrazuril showed a decreased intensity of coccidian

infection and reduced steatocrit values 8 days after the end of treatment. Metronidazole did not have a significant effect on coccidian infection intensity nor on steatocrit. In females, treatment with sulfadimethoxine significantly reduced the intensity of coccidiosis but did not affect steatocrit. Steatocrit increased in all females that were experimentally infected with heterologous coccidian strains. Interestingly, steatocrit did not decline immediately in males after the end of the medication period, despite a significant reduction of coccidian infection intensity, which suggests that damage to the intestinal surface takes at least a week to repair in greenfinches. This might also explain why we didn't see a decrease of steatocrit in females that were medicated with sulfadimethoxine as samples for steatocrit measures were collected 6 days after the treatment ended.

Interestingly, in females, infection with heterologous parasite strains increased steatocrit levels in all the birds, but I did not detect any significant effects of experimental infection on infection intensity, body mass, or plasma triglycerides. Previous studies in greenfinches have shown that coccidian strains that are unfamiliar to the host appear to be more virulent (Hõrak et al., 2006). Strains with higher virulence might impose more intestinal damage without an observed increase in infection intensity (Ruff et al., 1981). It is also possible that some parasite-induced host response was responsible for the impaired fat absorption rather than damage directly caused by the parasite (Fernando and McCraw, 1973; Russell and Ruff, 1978). Thus, steatocrit appeared more sensitive to experimental manipulation of infection in order to detect parasite-caused malabsorption in the gut than plasma triglyceride levels and body mass.

None of the treatments affected body mass changes or plasma triglycerides levels, contrary to previous studies in greenfinches (Hõrak et al., 2004; Sepp et al., 2012). However, positive correlations occurred between the intensity of coccidian infection on all measurement occasions and steatocrit levels measured after the treatments ceased. Steatocrit before the treatment predicted subsequent body mass loss, Birds whose plasma triglyceride levels declined had increased steatocrit levels. These correlations support the idea that the capability to digest fat is reduced in individuals who suffer from more intense coccidian infection and that individual variation in fat absorption capacity eventually affects circulating triglyceride levels and body mass.

Therefore, I was able to confirm that the steatocrit method could be applied to assess individual variations in fat digestion efficiency that are consistent in time. Experimental manipulations of intestinal infections affected fat absorption capacity, which was detectable with the acid steatocrit method. Detection of differences in digestive efficiency makes it possible to distinguish between the effects of infection on malabsorption and the overall increased energy requirements of the organism. Thus, I suggest that this method has broad applicability in avian studies in order to study the effects of intestinal health on fitness-related outcomes.

3.2 Feather corticosterone is related to the phenotypic quality of the individual and predicts behaviour and survival

Corticosterone is the predominant glucocorticoid hormone in birds and corticosterone levels are often used in order to assess stress levels in birds (Romero, 2004). CORT is secreted in response to stressful and unpredictable environmental perturbations (Blas, 2015; McEwen and Wingfield, 2003). Elevated CORT levels regulate physiological responses that help the animal to cope with stress, such as energy mobilisation and metabolism, immune system, and inhibit growth and reproduction (Romero and Butler, 2007; Sapolsky et al., 2000). In non-stressful situations, baseline levels of CORT are crucial for regulating metabolism and various physiological functions (Dallman et al., 1993; Sapolsky et al., 2000). Fluctuations in baseline levels can be explained by circadian rhythms (Dallman et al., 1993), predictable seasonal changes and life-history states (such as breeding) (Landys et al., 2006). Individual differences in baseline and stress-induced CORT levels might arise from factors like parasite load, injury, body size and social status, which affect animals' energetic needs and thus their allostatic load (McEwen and Wingfield, 2003). However, the current knowledge about individual differences in CORT levels and their impact on survival and behaviour is limited.

CORT levels can be measured from plasma, which has so far been the most popular choice. However, non-invasive methods such as measuring CORT from feathers (Bortolotti et al., 2008) and faeces (Millspaugh and Washburn, 2004) are gaining popularity in ecological studies. CORT is deposited into the feathers during the period of feather growth (Bortolotti et al., 2008). Feather CORT (fCORT) is informative about the cumulative effect of stressors and baseline levels on an individual's CORT levels over a longer period of time, while plasma CORT levels are more fluctuating and can rapidly change in response to an acute stressor (Romero and Fairhurst, 2016). In my second study (**Paper II**), I tested whether CORT levels are individually persistent and reflect individual differences over a longer period and whether these differences are associated with survival and behaviour.

Sixty-two male wild-caught captive greenfinches were used in my second study. CORT levels were measured from plasma, from feathers grown in the wild, and from lab-grown replacement feathers. Plasma CORT measurements collected 7 days apart intercorrelated positively, but no correlations between plasma CORT and fCORT were found, which was expected as plasma CORT levels are more sensitive to acute environmental stressors. fCORT levels correlated positively between wild-grown and lab-grown feathers – birds who deposited more CORT into the feathers in one situation did it also in the other. Environmental conditions are very different during autumnal moult in the wild and during induced moult in captivity during winter. Animals can experience vastly different conditions in the wild, such as predation risk, food availability, and temperature fluctuations, as opposed to the controlled environment in the lab. Thus, despite environmental

and seasonal differences, the fCORT levels indicated some persistent components of individuals' phenotypic quality. However, the environment still had an effect on fCORT levels as fCORT was on average 20% lower in lab-grown feathers.

Persistent inter-individual differences in fCORT might arise from genetic differences (Béziers et al., 2019; Jenkins et al., 2014), epigenetics, early life experiences and other factors that can alter the HPA-axis and from individuals' ability to find and exploit energy resources and its allostatic load (McEwen and Wingfield, 2003), but also the gut microbiome can also affect CORT levels (Burokas et al., 2017; Noguera et al., 2018). Lower fCORT levels in lab-grown feathers might have been caused by the seasonal differences in circulating CORT (Wingfield et al., 1992). It is also possible that the bird experienced fewer stressful events in the lab than in the wild. Alternatively, the lower fCORT levels could be associated with lower energetic demands in the captivity – less physical activity, higher ambient temperature and *ad libitum* food provisioning. It has been suggested that CORT levels might reflect a variation in energy expenditure as in zebra finches (*Taeniopygia guttata*) increase in CORT levels was indistinguishable, whether it was caused by a psychological stressor or by lowering the ambient temperature (Jimeno et al., 2018).

Elevated CORT levels have been related to lower survival (Harms et al., 2015; Kitaysky et al., 2010; Koren et al., 2012; Romero and Wikelski, 2001), but there is also evidence that very low CORT levels increase the risk of death (Brown et al., 2005; Rebolo-Ifrán et al., 2015), suggesting an inverted U-shape relationship between CORT levels and survival. fCORT in wild-grown feathers was significantly higher in four birds that died in the lab. The sample size is small and the results should be interpreted with caution, but at the same time, demonstration of fCORT association to survival in such a small sample might indicate a robust relationship between survival and fCORT.

Variations in the CORT levels can have an effect on the behaviour of the animal. CORT regulates neurobiology, cardiovascular tone and energy mobilisation, which can translate into behavioural choices and facilitate behavioural response to a stressor (McEwen and Wingfield, 2003; Sapolsky et al., 2000). Therefore, I also tested whether fCORT covaries with tail damage from flapping against cage bars. This behaviour has been suggested to indicate captivity tolerance of greenfinches (Meitern et al., 2013; Sild et al., 2011). Higher CORT levels have been usually associated with increased locomotor activity (Landys et al., 2006). Contrary to my prediction, tail damage correlated negatively to fCORT. Previous studies in greenfinches have found a positive relationship between fCORT on tail damage (Meitern et al., 2013) or no significant relationship between these measures (Sild et al., 2011). Therefore, the relationship between tail damage and fCORT levels remains unclear. However, the relationship between activity levels and CORT levels might not be linear, as the greatest locomotive response has been observed at intermediate CORT levels (Breuner et al., 1998).

3.3 Antibiotic treatment increases yellowness of carotenoid feather colouration

Carotenoid ornaments are important sexual signals that play a crucial role in mate choice and females often prefer males with brighter and more intense carotenoid feather colouration (Hill, 1991). In some species, more colourful males live longer and have higher lifetime reproductive success (Cantarero et al., 2019). Intestinal infections such as coccidiosis can decrease the absorption of carotenoids and other nutrients (Ruff and Fuller, 1975; Tyczkowski et al., 1991), which suggests that intestinal integrity could mediate the relationship between carotenoid ornamentation and individual quality. It has also been proposed that the enzyme which is responsible for biotransformation of carotenoids prior to deposition to ornaments resides inside the mitochondrial membrane; thus, carotenoid biotransformation is sensitive to the functionality of mitochondria (Hill et al., 2019). This is one example of the "shared pathway hypothesis", according to which signal honesty could also be maintained when the production of the signal is tied to the functionality of vital cellular processes (Hill, 2011). It was found in a meta-analysis that in species that bioconvert dietary carotenoids prior to depositing them into ornaments, carotenoid colouration was related to parasite resistance and reproductive and parental quality. However, in species that incorporate unchanged carotenoids into ornaments, these relationships were not found (Weaver et al., 2018). In the third study (**Paper III**), I tested whether medicating birds against infections common in nature, coccidiosis and trichomonosis, affects carotenoid feather colouration in greenfinches. My study design set out to differentiate between the direct effects of gut health on carotenoid colouration by treating coccidiosis with an anticoccidial drug and the effects of an overall health state by administration of a wide spectrum antibiotic.

For this study, 70 male greenfinches were captured in mist nets and housed indoors in individual cages. Birds were divided into three groups. The birds received medication treatment with either toltrazuril (TOLTRA) or metronidazole (METRO); the third group served as controls. The birds were weighed at several time points throughout the study and blood samples were drawn before and after the manipulation for measurement of carotenoids and triglycerides in plasma. The left and right outermost wild-grown tail feathers were plucked at the beginning of the experiment (wild-grown feathers) and replacement feathers grown in the lab (lab-grown feathers) were plucked when fully grown and chroma of the yellow parts of the feathers was measured.

Treatment with METRO resulted in significantly higher chroma of yellow parts of the feathers, whereas feather colour in TOLTRA and control group did not differ. Coccidian infection intensity significantly declined in the TOLTRA group, but not in birds who received METRO. It is possible that METRO attenuated the negative effects of trichomonosis, or alternatively, the potential unknown infection of pathogenic bacteria, which could have freed additional energetic resources that could be invested in ornamentation (del Cerro et al.,

2010). On a more speculative note, antibiotic METRO might have induced a change in gut microbiota composition. Some metabolites of microbiota, such as short-chain fatty acids (SCFAs), can affect mitochondrial function (Franco-Obregón and Gilbert, 2017; Saint-Georges-Chaumet and Edeas, 2015). It is possible that although METRO treatment did not result in higher nutrient absorption, it might have elicited a shift in gut microbiota composition that improved the host's cellular processes that also influence the modification and deposition of carotenoids to the feathers (Hill, 2011). Coccidian infection intensity significantly declined in the TOLTRA group, but there was no effect of treatment on yellow feather colouration in the TOLTRA group. One possible explanation could be that the birds might have been naturally infected with mildly virulent strains of coccidia. It has been suggested that wild birds tolerate coccidian parasites well and more serious illness only occurs under stressful conditions (Gill and Paperna, 2008; Swayne et al., 1991), which may increase their allostatic load. However, greenfinches have been shown to tolerate captivity well (Sepp et al., 2010); thus, the captivity stress might not have been severe enough to trigger an exacerbation of the coccidian infection.

There were no significant differences in plasma carotenoids or plasma triglycerides between the experimental groups after the treatment, indicating that the treatment eliminated prior differences in absorption or availability of these nutrients. Yellow feather chroma in lab-grown feathers correlated positively with plasma carotenoids on both blood-sampling dates. However, similar plasma carotenoid and triglyceride levels after the treatment indicate that the more saturated yellow feather colouration of birds that received METRO was not only related to absorption of carotenoids and nutrients in the gut but might have involved a component of increased efficiency in carotenoid modification or deposition, which is consistent with the shared pathway hypothesis. Thus, it is possible that METRO improved the general health state and efficiency of vital cellular processes by targeting trichomonosis or bacterial infections or by altering the gut microbiome. It has been suggested that the microbiome can modulate mitochondrial function. However, specific mechanisms on how the microbiome relates to the production of carotenoid-based ornaments await further investigation.

3.4 Modulation of mitochondrial function by the gut microbiome and its effects on carotenoid colouration

In my fourth paper (**Paper IV**), I set out to further investigate the possible mechanisms that might explain the results from my third study (**Paper III**), where I found that administration of an antibiotic resulted in higher chroma of yellow feathers in greenfinches. I conducted a literature review in which I explored the possibility that the microbiome might modify the mitochondrial function and

whether these alterations in vital cellular processes could affect the production of the carotenoid ornaments, as suggested by the shared pathway hypothesis (Hill, 2011). I also explored whether the microbiome could affect the evolution of host adaptations and the expression of sexual signals.

Maintaining a healthy gut microbiome is crucial for the normal functioning of the organisms and a suboptimal microbiome has been associated with disease and reduced fitness of the animal (Wang et al., 2021). Mitochondria descend from formerly free-living bacteria, (Sagan 1967); thus, mitochondria and bacteria share several structural and biochemical similarities (Boguszewska et al., 2020). Mitochondria often appear as a target to many bacterial pathogens (Lobet et al., 2015), but growing evidence support that mutualistic member of the microbiome can also affect mitochondrial function and regulate energy production (Clark and Mach, 2017; Franco-Obregón and Gilbert, 2017). Interestingly, several microbial metabolites, such as SCFAs, secondary bile acids, 3-Indolepropionic acid, urolithin A and riboflavin, have been shown to affect mitochondria by affecting transcription factors and transcriptional co-activators that regulate mitochondrial function and morphology (Gao et al., 2009; Gnainsky et al., 2021; Kang et al., 2019; Mollica et al., 2017; Owumi et al., 2021; Ryu et al., 2016; Staats et al., 2018). For example, the expression of mitochondrial regulator peroxisome proliferator-activated receptor gamma coactivator (PGC-1α) is affected by the gut microbiome (Gao et al., 2009).

It has been hypothesised that the expression of carotenoids is tied to the mitochondrial function, and therefore carotenoid colouration signals an individual's capacity to produce energy. The enzyme responsible for carotenoid biotransformation is likely located in the inner mitochondrial membrane (Hill et al., 2019; Lopes et al., 2016; Mundy et al., 2016). Positive relationships between carotenoid-based colouration and mitochondrial function have been described in house finches (*Haemorhous mexicanus*) (Hill et al., 2019). Also, experimental manipulation of mitochondria has been shown to affect carotenoid colouration in birds (Cantarero et al., 2020; Cantarero and Alonso-Alvarez, 2017)). Interestingly, a study in house finches showed that elevated PGC-1α expression was associated with duller carotenoid-based colouration (Hill et al., 2019). As the metabolites produced by the symbiotic microbes can regulate the functionality of mitochondria (for example, by affecting PGC-1α levels), it could be possible that these microbial metabolites may subsequently affect the production of ornaments which are tied to mitochondrial function. Therefore, I suggest that the expression of sexually selected ornaments, such as carotenoid colouration, might be substantially affected by the gut microbiome in addition to other factors.

The gut microbiome might also more directly affect carotenoid levels in tissues and ornaments. Carotenoids are lipid-soluble and it has been shown that the availability of the bile acids affects carotenoid absorption in the digestive system (Bohn et al., 2017). Secondary bile acids, which are produced by gut bacteria, can regulate the bile acid pool but also mitochondrial function (Gérard, 2014; Martinot et al., 2017). In some species, carotenoid concentration in muscle tissue has been associated with significant differences in the gut microbiome and some

of the microbial groups that are related to higher carotenoid concentrations have genes for producing carotenoids in their genome (Liu et al., 2020). Also, carotenoids that are produced by an experimentally administered carotenoid-producing bacteria can be detected circulating in the host (Stevens et al., 2021). These examples pose a question of whether some gut microbes may produce carotenoids in the gut. However, it remains unclear whether these examples of possible microbial sources of carotenoid are an exception or whether the potential of the gut microbiome to produce carotenoids have been underestimated in most species.

Few studies have addressed the ecological and evolutionary role of the microbiome as a driver of phenotypic plasticity and adaptation, although possible mechanisms have been proposed on a theoretical level (Henry et al., 2021; Kolodny and Schulenburg, 2020; Shapira, 2016). However, evidence is starting to accumulate that the microbiome can affect local adaptation (Itoh et al., 2018; Wang et al., 2021), mate choice (Sharon et al., 2010), gene frequencies, population dynamics (Rudman et al., 2019) and fitness of the host (Wang et al., 2021). Changes in the host genotype might help tolerate environmentally driven shifts in the microbiome composition (Wang et al., 2021) and the host genome has been described to determine differences in the microbiome composition (Goodrich et al., 2016; Ma et al., 2014; Suzuki et al., 2019), which indicates coevolution between the host and its microbiome. A diverse microbiome might enable the host to outsource some high-cost-low-gain functions as maintaining these pathways would be too costly for the host (Kolodny and Schulenburg, 2020). Beneficial microbes can spread faster in the populations as they can be acquired from the environment and from non-parental individuals.

Therefore, I proposed that the capability to maintain a beneficial and flexible microbiome could be advertised to potential mates. Sexual selection can potentially increase the rate of adaptation when substantial positive covariance between a potential mate's condition and display occurs (Lorch et al., 2003). As an increasing number of pollutants and xenobiotics are released into the environment, the ability to recruit bacteria that can neutralise their toxicity would be highly advantageous. Furthermore, some xenobiotics can cause impairments to mitochondria and to the reproductive system. However, it has been shown that some microbial metabolites can alleviate the negative effect of xenobiotics on mitochondria (Owumi et al., 2021). Therefore, I suggest that carotenoid-based ornaments have a great potential to signal the microbiome-facilitated ability to adjust to the environmental perturbation and sustain organisms' capacity to produce energy.

3.5 Conclusions

One of the central questions in evolutionary ecological research is to understand why and how individuals differ in their performance and how this affects their reproductive success and survival. In this thesis, I explored the internal constraints on energy processing (**Papers I, II**) and how these constraints can impact survival,

behaviour (**Paper II**) and production of sexually selected ornaments in a passerine bird (**Papers III, IV**).

Firstly, I assessed whether two methods, acid steatocrit and measuring feather corticosterone (fCORT), can be applied to characterise individuals' phenotypic quality that is consistent in time and applicability of these methods to study internal constraints to energy processes in ecological research. I was able to demonstrate that the acid steatocrit method can be successfully applied to birds and that differences in individual fat absorption capacity were reliably captured by the steatocrit measure **(Paper I)**. In addition, steatocrit enabled the detection of the effects of experimental manipulations of intestinal infection intensity. Since **Paper I** was published, the steatocrit method has been already applied in several studies in birds in order to study the relationships between fat absorption and carotenoid colouration (Araújo et al., 2022; Madonia et al., 2017) and the effect of light pollution on digestive efficiency (Sepp et al., 2021), which indicates the broad applicability of this method in ecological studies. Feather corticosterone (fCORT) levels in lab-grown feathers and wild-grown feathers were consistent in time, despite vastly different conditions in the wild and lab environment, suggesting that fCORT indicates some persistent component of individuals' phenotypic quality. Furthermore, birds who died in the lab had significantly higher fCORT. My results also support that fCORT could be used to assess allostatic load. However, further studies are needed in order to better understand glucocorticoids' role in energy regulation in an ecological context **(Paper II)**.

Secondly, I investigated how energetic constraints can impact some ecologically relevant traits such as behaviour and production of sexually selected ornaments. Contrary to my prediction, fCORT was negatively correlated with tail damage from flapping against the cage bars (**Paper III**). Previous studies have shown a positive relationship (Meitern et al., 2013) and no relationship (Sild et al., 2011) between tail damage and fCORT. Therefore, it remains unclear whether fCORT is a suitable predictor of behaviour. It may also be possible that tail damage is not a good behavioural measure to estimate captivity stress or that the relationship between fCORT and activity level is nonlinear (Breuner et al., 1998).

Treatment with wide-spectrum antibiotic metronidazole increased the chroma of yellow parts of the feathers in greenfinches. Despite significantly reducing the coccidian infection intensity, an anticoccidial drug had no effect on the yellow feather colour **(Paper III)**. Yellow feather chroma in lab-grown feathers correlated positively with plasma carotenoids, but my results indicate that more saturated yellow colouration was not only related to absorption of carotenoids in the gut but might have involved a component of increased efficiency in carotenoid modification or deposition. In **Paper I**, metronidazole did not affect fat content in faeces as measured by the acid steatocrit method. As carotenoids are fat-soluble, this further supports that rather than alleviating malabsorption caused by intestinal infection, metronidazole might have improved the general health state and efficiency of vital cellular processes that resulted in higher yellow feather chroma **(Paper III)**. One speculative explanation could be that the antibiotic treatment

elicited a shift in the gut microbiome. Antibiotics are usually associated with disruption of the healthy microbiome. However, in some cases, antibiotics can increase the abundance of beneficial bacteria (Ianiro et al., 2016). Also, administering antibiotics as growth promoters have a long history in poultry (Miles et al., 2006).

Due to common ancestry mitochondria and bacteria share several morphological and functional similarities, which makes mitochondria susceptible targets for bacterial metabolites (Lobet et al., 2015). There is growing evidence that bacterial metabolites such as SCFAs, secondary bile acids, Urolithin-A, etc., can affect mitochondrial function (Clark and Mach, 2017) (reviewed in **Paper IV**). Based on that, I proposed in **Paper IV** that the ability to govern a beneficial and flexible community of microbes could be advertised to potential mates via sexual signals. As suggested in **Paper III** production of the carotenoid-based ornaments may be affected by both absorption of dietary carotenoid from the diet but also by the efficiency of vital cellular processes, such as mitochondrial function, which would make carotenoid ornaments a good candidate to convey information about a healthy microbiome (**Paper IV**) and overall capacity of the individual to produce energy. Although I focused on carotenoid-based ornaments, microbial modulation of mitochondrial function can potentially also affect the expression of other condition-dependent traits.
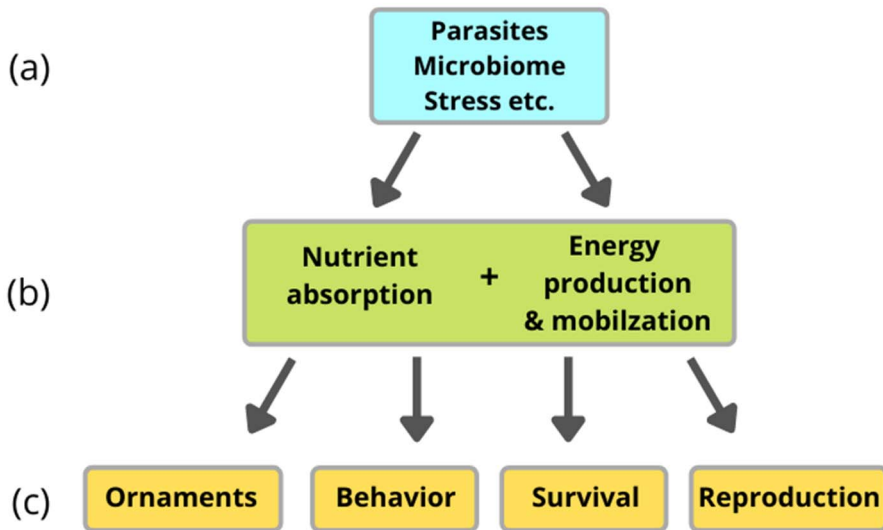

Figure 3. (a) Various factors, such as parasites, environmental perturbations, stress, social status, microbiome etc., can affect animals' allostatic load, that is, energy input required to cover animals' energetic needs. (b) The amount of energy that is available for carrying out physiological processes can be affected by the efficiency of nutrient absorption in the digestive system, but also by the capacity to produce energy in the mitochondria and proper mobilisation of energy reserves. c) The energetic status of the animal can affect its behavioural choices, expression of condition-dependent ornaments and ultimately survival and reproduction.

In conclusion, this thesis provided an integrative overview of constraints to energy processing related to parasitic infection, digestive efficiency, microbiome and how these affect survival, behaviour and carotenoid-based sexual signals (figure 3). An important result of this thesis was the validation of the acid steatocrit method in birds, which has already proven its value in ecological studies. However, understanding the aspects that limit an organism's energy processing is still poorly understood and the mechanisms discussed here are far from exclusive and need further investigation. Also, I came to the conclusion that the role of the microbiome in energy processing and expression of condition-based signals, such as carotenoid ornaments, may be underestimated in ecological studies. The composition of the gut microbiome was not assessed in this thesis, but considering the wide variety of anthropogenic stressors and pollutants, investigation of microbiome facilitated ability to adjust to the environmental perturbation could provide a promising avenue for future research. Overall, I suggest that an integrative view that incorporates animals' energetic needs, internal constraints to energy processing, and traits related to survival and reproductive success (figure 3) is crucial in order to understand why individuals differ in their performance and fitness.

SUMMARY

Explaining the reasons why individuals differ in their performance is a central question in evolutionary and ecological research. Ability to absorb nutrients from the food, produce energy in the mitochondria and energy mobilisation pose major internal constraints to energy processing in the organism, which can affect survival and reproduction. Parasitic infections can reduce nutrient absorption in the digestive system, but several parasites and microbes can also target the mitochondria and affect their functionality. Energetic needs can vastly differ depending on the time of the day, season, individual's life history stage and environmental conditions. Glucocorticoid hormones are important regulators of energy metabolism and stress response. Glucocorticoids are often used to assess stress in animals, but their importance in energy regulation and mobilisation has not received much attention in ecological studies. Rather than maximising the energy stores and mitochondrial ATP output, an organism's energy demands should be matched with energy output. It has been suggested that some condition-based sexual signals, for example, carotenoid colouration, can indicate the capacity to produce energy as their production shares pathways with vital cellular processes. Therefore, energy processing can integrate several seemingly unrelated components that contribute to the performance of an animal, such as stress response, parasite resistance, behaviour and ornament expression. This highlights the importance of characterising energetic constraints and their effects on individual phenotypic quality in ecological studies. In order to do this, sensitive, individually consistent and non-invasive biomarkers to assess animals' energetic constraints are needed.

The main goals of this thesis were to (1) study the internal constraints to energy processing and (2) its impact on survival, behaviour and production of sexually selected ornaments. I used greenfinches as my study subjects because wild greenfinches can tolerate captivity well. This enables to conduct the experiments in a controlled environment, while the results are still relatively well extrapolatable for natural situations. Greenfinches are infected with coccidian and trichomonas parasites in nature, which enables us to study constraints for energy absorption in the gut. Furthermore, male greenfinches have bright yellow sexually selected carotenoid-based feather colouration.

In order to address the goals of my thesis, I firstly focused on studying the mechanisms that can pose constraints to internal energy processing and to how to measure these. Limitations of nutrient absorption in the gut can arise from parasitic infection and its damage to the intestinal wall. The majority of the methods that enable the assessment of digestive efficiency are not suitable for ecological studies due to invasiveness, lethality or complexity of the procedure. Therefore, I explored whether a simple and non-invasive acid steatocrit method that has previously been used in humans and rodents can be applied in ecological studies in birds. The acid steatocrit method enables to measure the relative amount of fat in the faeces and thus providing an estimate of the digestive efficiency of fat. I was able to determine that the values of steatocrit measurements showed significant individual consistency and inter-individual variation confirming the method's

suitability in birds. The acid steatocrit method also enabled to detect the effect of experimental manipulations of intestinal infections on fat absorption capacity.

Corticosterone is a predominant glucocorticoid in birds that has become the main indicator to assess stress levels in birds. Feather corticosterone (fCORT) levels can potentially reflect the cumulative effects of environmental stressors and differences in baseline corticosterone levels. I was able to show that the fCORT in feathers that grew in captivity correlated positively to fCORT levels in feathers grown during moult in the wild, showing individual consistency. Thus, my results indicate that fCORT may contain information about some persistent phenotypic quality of the individual. fCORT levels were on average 20% lower in lab-grown feathers. This might be explained by the lower energy demand in the lab (less physical activity, higher ambient temperature and ad libitum food), as it has been suggested that variation in corticosterone levels can indicate variation in energy expenditure.

Secondly, I investigated how energetic constraints affect ecologically relevant traits such as survival, behaviour and sexual signals. I found that the fCORT levels in wild-grown feathers predicted the survival of the birds in the lab several months after the feathers were grown, further supporting that fCORT can indicate some persistent component of an individual's quality. Variation in corticosterone levels can also affect animals' behaviour. Higher corticosterone is usually associated with a higher locomotive activity. Contrary to my predictions, I found that birds with more damaged tails from flapping against the cage bars had lower fCORT levels, which calls for further research to better understand the relations between fCORT levels and behaviour.

Parasite infections and the gut microbiota can affect nutrient absorption in the digestive system, including the acquisition of carotenoids. Anticoccidial drug toltrazuril significantly reduced the infection intensity of coccidiosis but did not affect carotenoid feather colouration. Administration of wide-spectrum antibiotic metronidazole which targets trichomonas parasites and anaerobic bacteria resulted in significantly higher chroma of yellow parts of the feathers. Similar levels of plasma carotenoids in all groups after the treatment suggests that the feather colouration was not only related to the amount of carotenoids absorbed from food but involved a component of the improved mechanism of carotenoid biotransformation and deposition into ornaments. Therefore, the results indicate that metronidazole might have improved the general health state and efficiency of vital cellular processes, which resulted in more yellow feathers. It is also possible that metronidazole induced a change in gut microbiome composition. Assuming that some microbial metabolites can modulate mitochondrial function, this result is consistent with the shared-pathway hypothesis by which the production of the ornaments shares functional pathways with core life-supporting pathways.

Inspired by the results of the last study, I conducted a literature review in order to explore the possibilities that the gut microbiome could affect carotenoid colouration via modulation of mitochondrial function. Due to common ancestry mitochondria and bacteria share several structural and biochemical similarities, thus making mitochondria more susceptible to bacterial metabolites. There is

evidence that several commensal members of the gut microbiome produce metabolites, such as short-chain fatty acids, secondary bile acids, urolithin-A and riboflavin, that can modulate mitochondrial function. Several studies have shown that microbes can modify traits that are important in mate selection and affect the host's allele frequencies and population dynamics. It has been proposed that the host might outsource high-cost-low gain services from microbes – functions that yield low reward, but the maintenance of the pathways would be too costly for the host. Therefore, I hypothesised that microbial metabolites could affect carotenoid colouration via modulation of mitochondrial function and thus carotenoids might advertise the ability to ensure the presence of a beneficial microbiome to the potential mates

In conclusion, this thesis provided an integrative overview of constraints to energy processing and how these affect survival, behaviour and production of carotenoid-based sexual signals. I was able to demonstrate that the acid steatocrit method, a simple, non-invasive and cheap method for measuring fat content in the faeces, can be used as a proxy for digestive efficiency in birds in ecological studies. This method has wide applicability in ecological research and has already been used in several other studies. I determined that feather corticosterone, which reflects corticosterone levels over a longer period of time, conveys information about an individual's phenotypic quality, which could be potentially related to animals' energy status. The integrity of the digestive system, parasitic infection and microbiome can affect nutrient absorption. However, the gut microbe can also modulate mitochondrial function. I showed that carotenoid colouration was not only related to the circulating plasma carotenoids but involved some improved component of carotenoid modulation or deposition into the feathers. Lastly, I hypothesised that the ability to ensure the presence of a beneficial and diverse microbiome might be advertised to the potential mates through sexual signals. Although carotenoid-based ornaments were in focus, microbial modulation of mitochondrial function can potentially also affect the expression of other condition-dependent traits. Considering the wide variety of anthropogenic stressors and pollutants, investigation of microbiome-facilitated ability to adjust to the environmental perturbation could provide a promising avenue for future research. Overall, I showed in this thesis that an integrative view that incorporates animals' energetic needs, internal constraints to energy processing, and traits related to survival and reproductive success can help to understand why individuals differ in their performance and fitness.

SUMMARY IN ESTONIAN

Sisemised piirangud energiakäitlusele:
integratiivne uuring käitumisest, sugulise valiku
ornamentidest ja seedesüsteemi tervisest rohevintidel

Evolutsioonilise ökoloogia üks peamisi eesmärke on mõista, millest tulenevad isenditevahelised erinevused ning kuidas need erinevused mõjutavad sigimis-edukust ja ellujäämist. Söögist toitainete omastamine, energia tootmine mito-kondrites ja energiavarude mobiliseerimine on protsessid, mis mõjutavad orga-nismi sisemist energiakäitlust. Sooleparasiidid võivad vähendada toitainete imendumist seedesüsteemis ning mitmed infektsioonid võivad avaldada mõju energiatootmise efektiivsusele mitokondrites. Loomade energiavajadus varieerub oluliselt sõltuvalt kellaajast, aastaajast, elukäigu staadiumist (nt migratsioon, paljunemine) ja keskkonnatingimustest. Glükokortikoidhormoonid reguleerivad organismi stressivastust ning energiametabolismi tavasituatsioonis. Glükokorti-koidide taset mõõdetakse tihti selleks, et hinnata loomade stressitaset, kuid glüko-kortikoidide roll energiaregulatsioonis on ökoloogilistes uuringutes jäänud tihti tagaplaanile. Samas pole võimalikult suur ATP-tootmine ja energiavarude kogu-mine enamasti mõistlik. Näiteks võivad rasvavarud suurendada tõenäosust, et loom langeb kiskja saagiks. Seega on olulisem tagada, et energia tootmine vastaks energiavajadustele. Tulenevalt sellest on välja pakutud, et signaalid, mis annavad vastassugupoolele infot isendi kvaliteedist, võivad signaliseerida isendi võimekust energiat toota, kuna nende signaalide avaldumine on seotud samade biokeemiliste radadega kui energiatootmine. Üheks näiteks sellistest signaalidest võivad olla karotenoidsetel pigmentidel põhinevad tunnused, näiteks kollane ja punane sule-või nahavärvus. Selgem arusaamine organismi energiakäitlust piiravatest tegu-ritest võib aidata paremini mõista indiviididevaheliste erinevuste põhjuseid.

Peamisteks eesmärkideks oli (1) uurida sisemisi piiranguid energiakäitlusele ning (2) selgitada välja, kuidas need piirangud mõjutavad ellujäämist, käitumist ja sugulise valiku signaale. Oma uuringus kasutasin mudelorganismina rohevinte. Loodusest püütud rohevindid taluvad hästi vangistust, mis võimaldab katseid läbi viia kontrollitud keskkonnas, samas on tulemused siiski suhteliselt hästi üldis-tatavad looduses esinevatele olukordadele. Vabalt elavad rohevindid on nakatunud koktsidioosi ja trihhomonoosiga, mis võimaldab uurida piiranguid energia omas-tamisele soolestikus. Emased rohevindid eelistavad kollasemaid isaseid, seega sulgede erkkollane karotenoididel põhinev värvus on rohevintidel sugulise valiku tunnus.

Esmalt keskendusin mehhanismide uurimisele, mis võivad mõjutada piiranguid sisemisele energiakäitlusele, ning sellele, kuidas neid mõõta. Parasiitnakkused soolestikus võivad kahjustada seedesüsteemi ning piirata toitainete imendumist. Enamus meetodeid, mis võimaldavad hinnata seedimise efektiivsust, ei sobi öko-loogiliste uuringute jaoks, kuna vajavad looma surmamist. Steatokriti meetod on lihtne, odav ja mitteinvasiivne ning võimaldab mõõta suhtelist rasvasisaldust

väljaheidetes ning anda hinnangu rasvade seedimise efektiivsusele. Varasemalt on seda meetodit kasutatud inimestel ja hiirtel. Oma esimeses uuringus näitasin, et steatokriti meetodit saab kasutada seedeefektiivsuse hindamiseks ka lindudel. Näitasin, et steatokrit võimaldab tuvastada ajas püsivat isenditevahelist varieeruvust. Samuti olid steatokriti meetodi abil tuvastatavad muutused rasvade seedeefektiivsuses pärast rohevintide nakkustaseme eksperimentaalset manipuleerimist.

Kortikosteroon on lindude peamine stressihormoon. Arvatakse, et kortikosterooni tase sulgedes (sKORT) peegeldab sule kasvamise perioodil kumulatiivselt veres ringleva kortikosterooni baastaset ning stressorite mõjul kõrgenenud kortikosterooni taset. Teises uuringus leidsin, et vangistuses kasvanud sulgede sKORT korreleerus positiivselt sKORT tasemega looduses kasvanud sulgedes: lindudel kellel oli kõrgem sKORT looduses oli kõrgem sKORT ka vangistuses. sKORT tase oli ajas püsiv vaatamata sellele, et tingimused vangistuses ja looduses erinevad olulisel määral. Seega võib sKORT anda infot isendi kvaliteedi kohta. Vangistuses kasvanud sulgede sKORT tase oli keskmiselt 20% madalam, mis võib olla tingitud lindude vähenenud energiavajadusest – väiksem kehaline aktiivsus, kõrgem õhutemperatuur ning piiramatus koguses saadaolev toit. Seega võib sKORT anda infot erinevate indiviidide energiavajaduse kohta.

Töö teine peamine eesmärk oli uurida, kuidas energeetilised piirangud mõjutavad ökoloogiliselt olulisi tunnuseid, nagu ellujäämine, käitumine ja suguliste signaalide avaldumine. Leidsin, et sKORT tase looduses kasvanud sulgedes ennustas lindude ellujäämist laboris mitu kuud pärast sulgede kasvatamist, mis kinnitab, et sKORT võib viidata mõnele isendi kvaliteedi püsivale komponendile. Kortikosterooni taseme kõikumine võib samuti mõjutada loomade käitumist ning kõrgemat kortikosteroonitaset seostatakse tavaliselt suurema aktiivsusega. Vastupidiselt ennustustele oli sKORT tase madalam lindudel, kes puurivarbade vastu lendamisest oma sabasuled rohkem sassi ajasid. Kuna minu töö tulemused on vastuolus varem kirjeldatuga, on vajalik läbi viia täiendavaid uuringuid, et mõista kas ja kuidas sKORT tase seostub käitumisega.

Toitainete ja karotenoidide imendumist seedesüsteemis võivad mõjutada parasiitnakkused (nt nakatumine koktsiididega) ja soolestiku mikrobioom. Koktsiidivastane ravim vähendas oluliselt koktsiidinakkuse intensiivsust, kuid ei avaldanud mõju sulestiku kollasele värvusele. Seevastu laia spektriga antibiootikumi manustamine, mis ravib algloomade poolt põhjustatud trihomonoosi ning samuti toimib paljude anaeroobsete bakterite vastu, suurendas sulgede kollase värvi intensiivsust. Karotenoidide tase lindude veres ei erinenud pärast menetlust katsegruppide vahel, mis viitab, et kollast sulevärvi ei mõjutanud mitte ainult karotenoidide imendumine soolestikus, vaid ka isendi üldine tervislik seisund. Arvatakse, et karotenoidide modifitseerimine enne ornamentidesse paigutamist toimub mitokondri membraanis. Seega võis antibiootikumi manustamise tagajärjel paraneda mitokondrite energiatootmise võimekus ning kuna karotenoidide metabolism on seotud mitokondrite funktsionaalsusega, siis peegeldus see intensiivsemas sulevärvis. Antibiootikum võis samuti mõjutada seedesüsteemi mikroobikooslust ning mitmed bakteriaalsed metaboliidid võivad avaldada mõju mitokondrite tööle.

Eelmise uuringu tulemustest inspireerituna koostasin kirjanduse põhjal ülevaate, uurimaks lähemalt võimalust, et mikrobioomi toodetud metaboliidid võivad mitokondrite tööd mõjutades mõjutada karotenoididsete tunnuste värvust. Mitokondrite eellased olid kunagi vabalt elavad bakterid ning seetõttu on mitokondritel ja bakteritel mitmeid struktuurseid ja biokeemilisi sarnasusi, mistõttu on mitokondrid bakteriaalsetest metaboliitidest kergemini mõjutatavad. Uuringutes on näidatud, et mitokondriaalset funktsiooni mõjutavad mitmed kommensaalsete bakterite toodetud metaboliidid, näiteks lühikese ahelaga rasvhapped, sekundaarsed sapphapped ja urolitiin-A. Lisaks on näidatud, et mikrobioom võib mõjutada paarilisevalikut, alleelisagedusi populatsioonis ning populatsioonidünaamikat, mis viitab sellele, et mikrobioom avaldab olulist mõju evolutsioonilistele ja ökoloogilistele protsessidele. Näiteks võib peremeesorganism "allhankida" mikroobidelt funktsioone, mille tulu on liiga väike, et tasuks ära ise vajalikke biokeemilisi radasid töös hoida, kuid mis siiski on teatud situatsioonides ning aegajalt kasulikud. Samuti suudavad mõned mikroobid teha kahjutuks pestitsiide ja muid toksilisi aineid. Sellelt tulenevalt püstitasin hüpoteesi, et mikroobsed metaboliidid võivad mitokondriaalse funktsiooni moduleerides mõjutada karotenoidide värvust ja seega võivad karotenoidsed ornamendid signaliseerida võimet hoida alal mitmekesist mikrobioomi, mis võimaldab muuhulgas peremeesorganismil keskkonnamuutustega paremini toime tulla.

Kokkuvõttes andis doktoritöö ülevaate energiaainevahetusele rakenduvatest piirangutest ning sellest, kuidas need mõjutavad ellujäämist, käitumist ja karotenoidipõhiseid sugulise valiku signaale. Üheks töö olulisemaks tulemuseks on steatokriti meetodi sobilikkuse valideerimine seedeefektiivsuse hindamiseks lindudel. Steatokriti meetodil on lai rakenduspotentsiaal ökoloogiliste uuringutes ning juba praeguseks on seda meetodit kasutatud teiste teadusgruppide poolt. Samuti jõudsin järeldusele, et mikrobioomi mõju on tõenäoliselt evolutsioonilises ökoloogias alahinnatud ning mikrobioomi mõju energiakäitlusele ja keskkonnamuutustega kohamisele pakub paljutõotavaid võimalusi tulevaste uuringute jaoks.

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PUBLICATIONS

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Lind, M.-A., Hõrak, P., Sepp, T., Meitern, R., 2020. Corticosterone levels correlate in wild-grown and lab-grown feathers in greenfinches (*Carduelis chloris*) and predict behaviour and survival in captivity. Hormones and Behavior 118, 104642.

Krasheninnikova, A., Berardi, R., Lind, M.-A., O'Neill, L., von Bayern, A.M., 2019. Primate cognition test battery in parrots. Behaviour 156, 721–761.

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Meitern, R., Sild, E., Lind, M.-A., Männiste, M., Sepp, T., Karu, U., Hõrak, P., 2013. Effects of endotoxin and psychological stress on redox physiology, immunity and feather corticosterone in greenfinches. PLoS One 8, e67545.

Conference theses:

Mari-Ann Lind, Richard Meitern, Peeter Hõrak "Corticosterone levels correlate in wild-grown and lab-grown feathers in greenfinches (Carduelis chloris) and are related to tail damage and survival", 12th European Ornithologists' Union Congress, Cluj Napoca, Romania 2019, oral presentation.

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Lind, M.-A., Sepp, T., Štšeglova, K., Hõrak, P., 2021. Antibiotic treatment increases yellowness of carotenoid feather coloration in male greenfinches (*Chloris chloris*). Scientific Reports 11, 13235.

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Meitern, R., Sild, E., Lind, M.-A., Männiste, M., Sepp, T., Karu, U., Hõrak, P., 2013. Effects of endotoxin and psychological stress on redox physiology, immunity and feather corticosterone in greenfinches. PLoS One 8, e67545.

Konverentsiettekanded:

Mari-Ann Lind, Richard Meitern, Peeter Hõrak "Corticosterone levels correlate in wild-grown and lab-grown feathers in greenfinches (Carduelis chloris) and are related to tail damage and survival", 12th European Ornithologists' Union Congress, Cluj Napoca, Romania 2019, suuline ettekanne.

Muu teadustöö:

Olen retsenseerinud käsikirju ajakirjadele BMC Zoology, Conservation Physiology and Zoology.

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