Czech University of Life Sciences Prague

Faculty of Forestry and Wood Sciences

Department of Game Management and Wildlife Biology

Doctoral Dissertation

Measurement of the stress reaction in free-ranging animals: environmental and anthropogenic disturbance on wild boar

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Ph.D. THESIS ASSIGNMENT

Justine Güldenpfennig

Global Change Forestry

Thesis title

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Objectives of thesis

The main objective of this dissertation is to quantify the stress reactivity of free-ranging wild boars (Sus scrofa) in response to both anthropogenic and natural stressors using complementary physiological and behavioural approaches. The work aims to provide an integrative understanding of how wild boars cope with human disturbance and environmental pressures such as heat.

Specifically, the aims are to:

1. Evaluate physiological stress responses using hormonal analyses of serum cortisol and faecal cortisol metabolites (FCMs) collected from free-ranging wild boars after driven hunts, and to assess the influence of individual traits such as sex and age, as well as methodological differences between assays.
2. Assess behavioural responses to environmental stressors, particularly temperature and precipitation, using acceleration (VeDBA) and GPS data from multi-sensor collars to determine how wild boar activity patterns change under heat stress and prolonged heatwave conditions.
3. Investigate habitat selection and revisitation of sleep sites in relation to human disturbance and environmental conditions, with a focus on how wild boars adjust their resting site selection under heatwave events and in suburban landscapes.

By combining physiological and behavioural data, this thesis aims to highlight the value of multi-indicator approaches in wildlife stress research and to provide insights into the adaptive capacity of wild boars in increasingly human-dominated and climate-challenged environments.

Hypotheses

Study I – Hormonal stress response:

a) Serum cortisol concentrations differ between male and female wild boars depending on the assay used.

b) Blood cortisol levels do not correlate with faecal cortisol metabolites (FCMs).

Study II – Behavioural response to environmental heat:

a) Wild boars reduce their activity in response to higher ambient temperatures.

b) Prolonged periods of heat (heatwaves) further decrease wild boar activity.

c) The effects of heat are mitigated by rainfall, facilitating thermoregulation.

d) Acceleration data (VeDBA) capture more detailed patterns of wild boar activity than GPS-derived step length.

Study III – Sleep site selection and revisitation:

a) Wild boars select sleep sites with a lower likelihood of human disturbance.
b) Under high temperatures, wild boars select sleep sites with favourable microclimatic conditions (thermal shelter).

Methodology

This thesis combines physiological, behavioural, and spatial data to investigate stress responses and adaptive behaviour in free-ranging wild boars (Sus scrofa) across two European study areas. Data were collected before in Germany and will be collected the Czech Republic between 2018 and 2023, encompassing hormonal analyses, GPS and accelerometer tracking, and habitat selection modelling.

Stress hormone analysis:

Serum and faecal samples will be collected from hunted wild boars in both study areas to assess glucocorticoid concentrations as indicators of physiological stress. Blood samples are drawn post-mortem during drive hunts, while faecal samples will be collected from the same individuals when possible. Serum cortisol will be quantified using radioimmunoassay (RIA) in Germany and enzyme immunoassay (EIA) in the Czech Republic, and faecal cortisol metabolites (FCMs) will be analysed using established EIA protocols validated for suids. Generalized Linear Mixed Models (GLMMs) will be employed to examine the effects of sex and age class on hormone levels while accounting for individual variability.

Body motion and travel movement:

To investigate behavioural responses to environmental and climatic stressors, GPS collars equipped with tri-axial accelerometers and magnetometers will be deployed on wild boars in the Czech study area. The vectorial sum of dynamic body acceleration (VeDBA) will be calculated as a proxy for body motion and energy expenditure, while GPS data are used to compute step lengths as indicators of spatial movement. Activity data will be related to ambient temperature, precipitation, and heatwave events using Generalized Additive Mixed Models (GAMMs) and GLMMs, with individual ID included as a random effect. These analyses allow assessment of how behavioural activity varies across diel and seasonal temperature gradients and under thermal stress conditions.

Sleep site selection:

Using fine-scale accelerometer data, sleep phases are identified based on body orientation (pitch and roll) and minimal motion (VeDBA). GPS locations corresponding to the longest daily sleep bouts will be classified as sleep sites and compared to randomly generated points within each individual's home range. Environmental and anthropogenic predictors, including habitat structure, distance to human infrastructure, and microclimatic indices, are extracted in QGIS and analysed in GLMMs. Additional models will evaluate site revisitation rates to assess habitat preference stability and the influence of heatwave conditions on sleep site selection.

Collectively, these methodological approaches integrate endocrinological, behavioural, and spatial analyses to provide a multi-dimensional assessment of wild boar stress ecology under increasing anthropogenic and environmental pressures.

Time schedule

11/2021 – 12/2023 Collection of blood and faecal samples, analysis of hormonal values

11/2021 – 10/2023 Analysis of acceleration and movement

10/2021 – 12/2023 Definition sleep and analysis of sleep locations

01/2022 – 12/2023 Definition of reference values for "normal" and "stress"

01/2022 – 09/2024 Linking behaviour to stress level

05/2021 – 10/2024 Manuscript preparation and submission

The proposed extent of the thesis

100 – 150 pages

Keywords

Activity, biologging, heat, human disturbance, stress reaction, wild boar

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Recommended information sources

Arenas-Montes, A. et al. (2013) 'Blood sampling by puncture in the cavernous sinus from hunted wild boar', European Journal of Wildlife Research, 59(2), pp. 299–303. doi: 10.1007/s10344-013-0701-3.

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2025/26 WS – FFWS – Doctoral Thesis Defense

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Prague on 19. 11. 2025

Declaration

I hereby declare that this dissertation, titled "Measurement of the stress reaction in free-ranging animals: environmental and anthropogenic disturbance on wild boar" is entirely my own work based on consultations and recommendations of the supervisor. All sources used have been appropriately acknowledged and cited. I confirm this dissertation has not been previously submitted for any degree or qualification in any university or other institution. I agree to the publication of the dissertation according to Act No. 111/1998 Coll. on universities as amended, regardless of the outcome of its defence.

Justine Güldenpfennig
PhD student

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Last but not least I want to thank my beloved wild boars – the true protagonists of this work. They reminded me that curiosity, resilience, and adaptability are the best survival skills, in research as in life.

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Foreword

Quantifying the reaction of free ranging animals to disturbances is important yet challenging. Besides invasive methods like hormone measurements, the continuous development of tracking technologies promises non-invasive ways to gain insights into an animal's life. During my PhD study, I aimed to use different methodologies to quantify the stress reaction of wild boars in response to both anthropogenic and natural stressors. This included the measurement of hormones and use of biologging data to determine wild boar behaviour.

This thesis is divided into three sections: (1) stress hormones of wild boars measured after driven hunts, (2) wild boar activity in response to heat, and (3) sleep site selection in a suburban forest. I will discuss the different methodologies used and report the relative results in each section.

I start with a general introduction to stress, followed by the definition and effect of stress, including a description of the Hypothalamic-Pituitary-Adrenal (HPA) axis (*1.1 Stress definition and system*). I then dive deeper into the different ways to validate and quantify the stress reaction (*1.2 Measurement of the stress reaction*) and discuss the use and importance of stress research in wildlife species using an up to date systematic literature research (*1.3 Stress research in wildlife*). I will then finish the introduction with some information on the species of interest of this thesis - the wild boar - describing their biology and reaction to disturbance (*1.4 Biology and ecology of the wild boar*).

Consequently, I will outline the first study, where I used the more traditional method of quantifying the stress reaction of organisms using hormone measurements, namely glucocorticoids (GCs). Important confounding factors when evaluating GC levels include the sex and age of the individual. Although GCs are repeatedly used as stress markers, there is little information about natural effects on GC concentrations. Studies mentioning sex differences in GC concentrations in domestic pigs report conflicting results based on sampling methods and assay. I aimed to define the effect of sex, age, and assay (quantitative measurement of the amount of a substance) used in wild boars and hypothesised that (a) there will be differences in hormone concentrations between male and female wild boars based on assay used and (b) blood cortisol will not correlate with faecal cortisol metabolites (FCMs).

Knowing the complicated interpretation of hormone concentrations, including the inference of the animal handling and individual effects, I aimed to find another way for quantifying the stress reaction, ideally using a non-invasive method. Therefore, in the second study I used

multisensory collars that are combining GPS and biologgers (i.e. accelerator, magnetometer) that can be deployed for several months on the animals. Specifically, acceleration data can be used for quantifying activity of individuals and how it changes in response to disturbances. In the face of climate change, I was especially interested in the change of activity in response to higher ambient temperatures. Suidae are known to be susceptible to heat caused by their lack of sweat glands and adipose tissue, and studies in domestic pigs have reported reduced activity, reduced feed intake and weight gain, as well as a change of lying behaviour exposed to heat (Olsen, Dybkjær and Simonsen, 2001; Huynh *et al.*, 2005; Cross *et al.*, 2020). Whereas in domestic pig productions, it is possible to modify the environment, wild boars are likely dependent on heat loss through behavioural changes and natural water sources. Based off on this, I hypothesised that (a) wild boars will reduce their activity in response to higher ambient temperatures, (b) prolonged periods of heat (heatwaves) will further decrease wild boar activity, (c) these effects will be mitigated by rain, and (d) acceleration data will be able to register more detail in wild boar activity than GPS data.

Finally, in the third study, I kept the topic of climate change and added the effect of human disturbance. Granted that wild boars felt threatened by the presence of humans, I looked at the location and revisitation of sleep sites. At the same time, I checked what environmental traits affected the sleep site selection and if there was a difference between within heatwaves or outside of heatwaves. As described above, I assumed that wild boars would reduce heat stress using thermoregulatory behaviour, including the selection of sleep sites. I hypothesised that (a) wild boars will select sleep sites with less chance of human disturbance and (b) under high temperatures, wild boars will select sleep sites with favourable microclimates (thermal shelter).

In chapter two of the thesis, I will explain the methodologies used in all studies, starting with a description of the study areas and the animal handling (2.1 Study area and animal handling). Then, I elucidate the methodologies used in the different studies, to be exact the measurement of the hormone and its metabolite in the first study (*Hormone measurement*), the use of the collars including the calculation of the energy expenditure (*Body motion and travel movement*) and definitions of sleep and sleep sites (*Sleep sites analysis*).

In the third chapter, I will present the results, followed by the discussion of the results by study in chapter four. I finish with a general conclusion where I debate about the use of different methodologies to measure stress in wildlife, as well as the possible implications of our findings. At the end of the thesis, one can find the list of literature used, as well as an Appendix including a list of publications and keywords used for the literature review.

Table of Contents

1. Introduction

1.1. Stress definition and system

Stress is a widely used term in our society and is often connected to a negative context. While stress is linked to bad performance and discomfort (Romero, 2004), it also has positive effects. To explain this, we must first discuss what is meant with "stress" and how it functions. The first definition of stress (at least in biomedical sciences) by Hans Selye describes stress as "the nonspecific response of the body to any demand of change" (Selye, 1976; Fink, 2010). In this definition, stress is considered a neutral effect. This is also supported by a more general description by Hing and colleagues, who defined it as "a change in psychological, physiological, and physical features of an organism" (Hing *et al.*, 2016). Still, definitions of stress in science remain widely discussed. Generally, all organisms are striving to maintain homeostasis. Stress can be defined as the threat, either real or perceived, to this homeostasis, which may challenge the well-being of an animal (Chrousos, 2009). In response to such threats ("stressors"), whether they are environmental, physical, or psychological, the body activates a complex interaction between the central nervous system and various peripheral systems, including the endocrine, immune, and cardiovascular systems. The main systems are the sympathetic-adreno-medullar (SAM) system, which primarily activates the "fight-flight-or-freeze" response and the Hypothalamic-Pituitary-Adrenal (HPA) axis (Koolhaas *et al.*, 2011). In this work, I will focus on the HPA axis and its end products, glucocorticoids (GCs).

Adkins-Regan (2005) summarised, how external stimuli detected by sensory organs conveying signals to the brain result in the release of GCs and other hormones (Figure 1). In case of neurohormones, the signal can be directly translated in the brain. In case of gonadal and adrenocortical hormones such as GCs, the signal needs to be translated between neuronal and nonneuronal tissue. A central role in this process plays the "hypothalamo-hypophysial portal system", which connects the hypothalamus (neuronal) with the anterior pituitary (nonneuronal). Under a "stressful" situation, the hypothalamus releases peptides like corticotropin-releasing hormone (CRF) into the portal system, which activate the release of adrenocorticotrophic hormone (ACTH) and other hormones upon reaching the anterior pituitary. This stimulates the release of GCs into the blood system from the adrenal glands. The axis is regulating itself with a negative feedback loop. More precisely, rising GC levels inhibit ACTH release resulting in decreasing GC levels, stimulating another HPA pulse (Fulford and Harbuz, 2005). With this, the activity of the HPA axis shows different patterns: basal (both ultradian and circadian) and

stress-induced (Spencer and Deak, 2017). The HPA axis plays a role in maximizing survival in the presence of physical or physiological challenges, and GCs are helpful for short-term survival (Jankord and Herman, 2008).

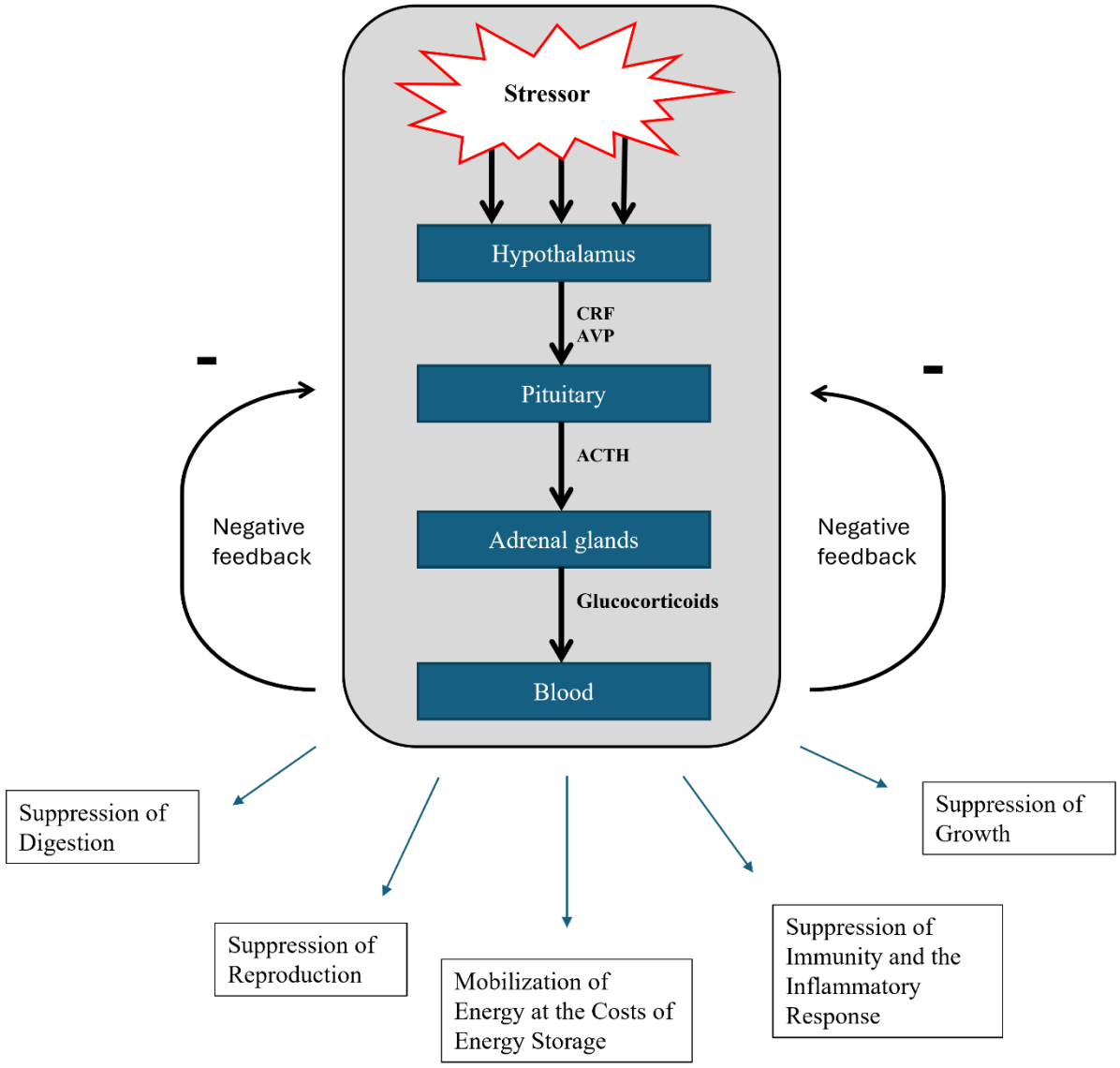

Figure 1: Schematic illustration of the Hypothalamus-Pituitary-Adrenal (HPA) axis and its regulation through a negative feedback loop. (Adapted from Sheriff *et al*., 2011)

The main GC in nearly all mammals is cortisol, which plays a crucial role in energy release, immune and mental activity, development, growth, and reproductive functions (Tryphonopoulos, Letourneau and Azar, 2014; Palme, 2019b). GCs travel through the body bound to corticosteroid-binding globulin (CBG) and are only biologically active in their unbound form (Tryphonopoulos, Letourneau and Azar, 2014). Cortisol is mainly metabolised by the liver and its metabolites are then excreted via the bile or urine (Taylor, 1971). Metabolites in the bile are then further metabolised by enzymes in the intestine and excreted in faeces

(Palme, 2019b). The release underlies a circadian rhythm and peaks right before the activity phase of the daily cycle starts (Ingram, Crockford and Matthews, 1999; Tryphonopoulos, Letourneau and Azar, 2014). Under stress, cortisol modulates the immune system and mobilizes energy stores, making more resources available to respond to specific stressors while suppressing non-essential processes like reproduction and growth (Fulford and Harbuz, 2005; Russell *et al.*, 2012; Palme, 2019b). While GCs benefit short-term survival, enduring/increased release (like during chronic stress) can lead to metabolic, immune, and physiological dysfunction (Jankord and Herman, 2008).

But what counts as stressors and what is chronic stress? Since all living beings are in an environment that is constantly challenging homeostasis, it is essential to differentiate between "acute" or "chronic" stress, as well as the adaptive ("eustress") or maladaptive ("distress") nature of the stress response (Koolhaas *et al.*, 2011). In general, acute stress appears typically after a one-time stressing event and primarily activates the "fight-flight-or-freeze" response. It can help increase performance by activating energy stores and enhancing brain activity (Sapolsky, Romero and Munck, 2000; Tsigos and Chrousos, 2002). For example, the short stress of prey being hunted optimises energy release needed for the escape. These stress responses are adaptive, potentially enhancing the resilience and coping mechanisms to such stressors (Suri and Vaidya, 2015). At the same time, the stress response is also affected by the type of stressor. Here, terms like controllability and predictability become important. Koolhaas et al. (2011) suggest that an animal incurring stress should reach a situation it did not predict (uncontrollability), delaying the recovery of the response (loss of control). This is also true in the physiological part of the stress response. An example of the importance of the context in the response of the hormonal response is an experiment conducted by (WEISS, 1968). They found that the rat (*Rattus norvegicus domestica*) controlling the timing of an electrical shock had a lower GC response than the rat that did not have this control. In contrast, if the situation cannot be solved and the natural behaviour is disturbed for longer, it indicates chronic stress (Wiepkema and Koolhaas, 1993). A previously adaptive stress response can turn into a maladaptive one, depending on timing, intensity, duration, predictability and controllability of the stressor (Suri and Vaidya, 2015). Repeated stress impulses can lead to an over-activation of the HPA axis. In general, there are two primary changes of the stress response to consider: acclimation and facilitation (Romero, 2004). With the repeated occurrence of the same stressor, predictability and controllability might improve, resulting in a reduced stress response (Koolhaas *et al.*, 2011). This would be considered an acclimation to the stressor. In the case of

habituation to a repeated stressor, novel stimuli might result in an altered response (Spencer and Deak, 2017). This is called facilitation.

If and how a situation is perceived as stressful is also affected by the adaptive capacity as well as regulatory range (Koolhaas *et al.*, 2011). Koolhaas et al. (2011) argue that the range of environmental conditions (e.g., temperature, food availability) within which processes do not require adaptive changes can be labelled as the regulatory range of an individual. As per their description, the adaptive capacity is therefore a set of mechanisms at the level of the brain, peripheral physiology and behaviour optimised for a range of environmental conditions (regulatory range). The adaptive capacity can be reduced if an animal struggles to meet conditions within their regulatory range. For example, if an individual cannot maintain their food intake to build adipose tissue, it might struggle with freezing temperatures despite temperatures being within its normal regulatory range (Koolhaas *et al.*, 2011). Under these conditions, freezing temperatures may be perceived as a stressor activating the stress response.

In the past decades, a new more advanced concept has emerged. “Allostasis” refers to the physiological processes by which an organism maintains “stability through change”, adapting to both predictable and unpredictable challenges (Seeley, Proudfoot and Edes, 2022). This concept differs from homeostasis, which refers to the preservation of internal balance by keeping certain variables like pH and body temperature within very narrow, fixed ranges (McEwen, 2004). In contrast, allostasis emphasizes the active adjustment of physiological and behavioural parameters to fluctuate around changing “set points” to meet demand (Seeley, Proudfoot and Edes, 2022). Key mediators of allostasis include hormones of the hypothalamic-pituitary-adrenal axis, catecholamines, and cytokines, which interact in a complex network to create reciprocal effects (McEwen, 2004). Within the concept of allostasis, “allostatic load” represents the “wear and tear” on the body and brain that results from chronic overactivity or inactivity of the physiological systems involved in allostasis (McEwen, 2004; Wu *et al.*, 2025). If such overactivity persists for longer, it can lead to “allostatic overload” (McEwen and Wingfield, 2003). Researchers have identified two types of allostatic overload in animals:

- Type I, which occurs when energy demand surpasses supply, triggering emergency life-history stages (Fight or flight response, proactive and reactive coping styles, sickness behaviour and fever, facultative behavioural and physiological strategies) that direct the animal into survival mode to decrease allostatic load (Wingfield, 2005), and

- Type II, which is characterised by permanent increased energy demand but enough supply to maintain it, not triggering emergency life-history stages. This type can only be reserved by learning or changes in the environment (Wingfield, 2005).

Future research should focus more on how to properly assess allostatic load, e.g., in the form of allostatic load indices, and its association with predictive factors and outcomes (Edes, Wolfe and Crews, 2018). However, first we need to establish standard reference values for future research efforts.

1.2. Measurement of the stress reaction

There are several methodologies to assess the stress reaction and allostatic load in humans and animals. For the purpose of this thesis, this chapter will focus on methodologies I have considered for my research questions and their applicability for research in free-ranging wild boars.

1.2.1. Hormones

The most widely used method to evaluate stress is measuring serum GC concentrations. These values can be measured in blood and saliva, as well as their metabolites in faeces, hair, and other tissues (Sheriff *et al.*, 2011; Palme, 2012). Each of these methods has its own advantages and disadvantages in sample collection, assay, and evaluation. Because of this, it is necessary to be very careful in choosing the right hormone measurement according to one's research question. Thus, while measuring GC levels, or the HPA axis reactivity in general, one has to keep in mind that there are many confounding factors (Millspaugh and Washburn, 2004; Goymann, 2005; Palme et al., 2005; Goymann, 2012). Among all, individuality might be the most important, followed by sex, reproductive state, seasonal variations, diet, and context of the stressor (Romero, 2004; Palme, 2019b). GCs and their metabolites can be measured using radioimmunoassay (RIA) or enzyme immunoassay (EIA).

Measurement of blood cortisol seemed like the main methodology in stress research in the last decades and gives insight into the immediate state of an organism (Sheriff *et al.*, 2011). Cortisol in blood may also be complex to work with. The difficulties start with the sampling process, which in itself can already alter cortisol concentrations. In most animals, blood cortisol concentrations peak only 5-15 minutes after the exposition to a stressor or after handling. Basal concentrations are reobtained after approximately 60-90 minutes (Kanitz *et al.*, 2003; Tryphonopoulos, Letourneau and Azar, 2014; Gentsch, Kjellander and Röken, 2018). After collecting blood samples, for most assays it is possible to have the samples centrifuged to obtain

the serum or plasma, which can then be stored at -20 °C for several years (Stroud *et al.*, 2007). It is important to note, that most assays will measure the total GC concentration, whereas others may measure its free unbound form, which is often the critical measurement (Sheriff *et al.*, 2011). The advantages of measuring blood GCs are that it is relatively easy and, as already mentioned, has the ability to get an immediate snapshot of the HPA axis activation. At the same time, collecting blood samples will also enable the measurement of other indicators of interest, enabling an overall picture of the state of an animal (Sheriff *et al.*, 2011). In wild boars, a large number of blood samples are easy to obtain from dead animals due to the intensive all-year hunting in our study area, although this does not allow the continuous measurement of the same individual.

An alternative to measuring blood GCs is using salivary GC concentrations. These data have to be treated with caution, as saliva contains only biologically free cortisol that does not linearly respond to a challenge (Hellhammer, Wüst and Kudielka, 2009). In addition, collecting saliva might be challenging in free-ranging animal populations. Most common used methods to collect saliva from animals are collecting it directly in a tube or using absorbent materials to chew on. After sample collection, samples are stable under room temperature for one to two days, for a week to 3 months in the refrigerator (5 °C) and frozen at -20 °C and -80 °C up to a year (Garde and Hansen, 2005; Turpeinen and Hämäläinen, 2013). Saliva collection has the advantage that it can be done in a non-invasive way, if one is able to set up an appropriate collection site (Sheriff *et al.*, 2011). In pigs, salivation is induced by chewing, facilitating easy sample collection using absorbent material (Erler, 2010). However, setting up an appropriate mechanism in the field might be difficult. Additionally, we need the individual identification to properly evaluate the measured GCs, which is almost impossible in the field without additional, costly DNA analysis. Another possibility is to collect saliva from dead animals, although there is the possibility of blood contamination, which has to be avoided (Sheriff *et al.*, 2011).

More and more used is the measurement of faecal GC metabolites (FGMs) as it provides non-invasive insight of stress reactivity, although it has to be implemented correctly (Palme, 2019b). As mentioned above, GCs are metabolised first in the bile and then in the intestinal tract, which makes it possible to measure the metabolites. Attention has to be paid to the types of FGMs to be measured, as certain FGMs vary between sexes and are metabolised differently. Faecal samples are relatively easy to collect from trapped animals, but sample collection is getting more challenging in free-ranging populations. FGM concentrations may be influenced by a number of factors, including, but not limited to, environment, age and storage of the sample

(Millspaugh and Washburn, 2004). Additionally, age and sex, as well as other biological factors like reproductive status, are affecting GC secretion (Millspaugh and Washburn, 2004; Sheriff et al., 2011a), which means we at least need information about these factors when collecting the sample. Consequently, a "blind" collection from the field would need some sort of additional identification analysis, like DNA analysis, same as mentioned above with the salivary samples. However, differently from the salivary samples, a large number of faecal samples can be easily collected during standard hunting procedures of wild boars. Important here is that samples have to be frozen as fast as possible, to slow down any microbial or bacterial activity, as well as other processes that can alter FGM concentrations (Millspaugh and Washburn, 2004; Sheriff et al., 2011a).

A much longer record of cortisol levels can be measured using hair, which makes it useful in measuring chronic stress (Sheriff et al., 2011a). This method has become more and more prominent in wildlife stress research. Once the hair growth rate is known, hair can even be divided into consequent parts representing a certain period (in months or even years). Hair samples can be clipped and stored at room temperature without the threat of degradation. Important here is that for measurement of a known period, hair should be cut before the period of interest and then "reclipped" at the same location after (Sheriff et al., 2011b). However, in free-ranging animals, sampling would include trapping and re-trapping of the same individual, which might be nearly impossible in certain study designs. This is also the case in my study with wild boars. Additionally, GC concentrations may also be influenced by environmental influences like solar radiation.

Under consideration of the above-mentioned advantages and disadvantages, I decided to collect blood and faecal samples for this study. Blood cortisol concentrations can be used to see the difference of the HPA activation between age and sex classes, whereas FGM can show the basic differences between age and sex classes without the interference of animal handling. At the same time, both samples can be easily obtained from shot wild boar after driven hunts, in large quantities and from all age and sex classes.

1.2.2. Energy Expenditure and Behaviour

Hormonal measurement may not always be the best method to evaluate stress-related health status. Primarily cortisol levels change quickly based on internal and external stimuli. Therefore, there is a need for alternative stress markers. During stress, the animal's behaviour is altered towards enhanced attention, increased cardiac output and respiration, and higher

catabolism and diverted blood flow to provide total perfusion of the brain, heart, and muscles (Tsigos and Chrousos, 2002). To make more recourses available while responding to a specific stressor, GCs modulate the immune system and mobilize energy stores (Russell *et al.*, 2012; Palme, 2019b). This should be visible in altered energy expenditure. There are several methods to measure physical activity and energy expenditure, with measuring acceleration being one of them (Hills, Mokhtar and Byrne, 2014). Acceleration provides intensity, frequency, and duration of body movement indicators and is easy to use in laboratory and field environments (Dale, Welk and Matthews, 2002). Movement-based power can be calculated using the sum of the acceleration vectors, called dynamic body acceleration (DBA), which is a good proxy of oxygen consumption (Qasem *et al.*, 2012; Wilson *et al.*, 2020). In the literature, two main DBA calculations have been mentioned: the vectorial sum of the dynamic body acceleration (VeDBA) and the overall dynamic body acceleration (ODBA). These two metrics show a very high correlation (Qasem *et al.*, 2012; Wilson *et al.*, 2020). Based on the design of the collars used in this study, I decided to use VeDBA due to possible movements of the collar on the wild boars' neck, which should be avoided when using ODBA (ODBA; Qasem *et al.*, 2012).

A behavioural aspect of the stress response might be a change of standard behaviours, such as sleeping, including the selection of sleep sites. Sleep is essential for health and the well-being of an animal (Manzar, Zannat and Hussain, 2015). It plays a crucial role in enhancing the immune system (Besedovsky, Lange and Haack, 2019), the stress response (Bush *et al.*, 2022), energy conservation, and the regulation of physiological systems (Manzar, Zannat and Hussain, 2015). Sleep may be affected by internal and external factors, e.g., temperature (Harding, Franks and Wisden, 2020), light levels (Reinhardt *et al.*, 2019), and human disturbance (Olejarz *et al.*, 2023). To maintain proper sleep homeostasis, animals tend to select sleeping sites that have optimal protection from predation and other disturbances, as well as optimal habitat properties. However, in a human dominated landscape, this might come with a trade-off between human disturbance and optimal habitat. Animals tend to prefer sleep sites near food resources but avoiding anthropogenic disturbances (Mekonnen *et al.*, 2021). Besides the selection of sleeping sites, human pressure is also influencing the nocturnality of wildlife species. A meta-analysis found that nocturnality increased in areas with high human disturbance as compared to areas with lower human disturbance (Gaynor *et al.*, 2018).

1.3. Stress research in wildlife

Interest in understanding and predicting the effects of stressors on wildlife has increased over the past decades (Baker, Gobush and Vynne, 2013), especially under the aspect of animal

welfare and biodiversity conservation. Both natural stressors (e.g., climate change, predation, disease, insufficient food, water resources) and anthropogenic stressors (e.g., noise, silviculture, agriculture, human disturbance) can cause stress in wildlife (Romano *et al.*, 2010; Atkinson *et al.*, 2015; Hing *et al.*, 2016). With the spread of urbanization, human-wildlife conflicts are increasing (Ditchkoff, Saalfeld and Gibson, 2006). This can cause a new array of stressors, which can furthermore change the behaviour of wildlife adapted to urban and suburban areas, compared to their fellow species in rural areas, changing survival, movement, reproduction, as well as the susceptibility to and the transmission of diseases (Ditchkoff, Saalfeld and Gibson, 2006). The complex relationships between wildlife, disease, and host-parasite equilibrium – a balanced state where host and parasite populations coexist – can significantly impact animal populations, potentially leading to biodiversity loss by altering survival and reproductive success (Hing *et al.*, 2016). At the physiological level, elevated cortisol concentrations have been linked to immune suppression, reduced reproductive success, and compromised fitness. Understanding these dynamics requires careful consideration of various factors crucial for studying stress in wildlife species: age, sex, behaviour (especially social behaviour), population density/dispersal, fitness in general, reproduction, environment, season, and rank (Baker, Gobush and Vynne, 2013; Adcock, Martin and Walsh, 2015).

Further evidence of the importance of wildlife stress research can be seen in anthropogenic cases, such as changes in behaviour in alpine black grouse (*Tetrao tetrix*) exposed to winter recreational activities (Arlettaz *et al.*, 2015), reduced feeding and increased vigilance in elk (*Cervus elaphus*) near roads (Ciuti *et al.*, 2012), or vocal alterations in Brazilian bird species exposed to airport noise (Alquezar and Macedo, 2019). In parallel, global climate change has emerged as another key stressor, with increasing ambient temperatures, altered precipitation, and extreme weather events endangering wildlife and ecosystems (Meehl and Tebaldi, 2004; Calvin *et al.*, 2023).

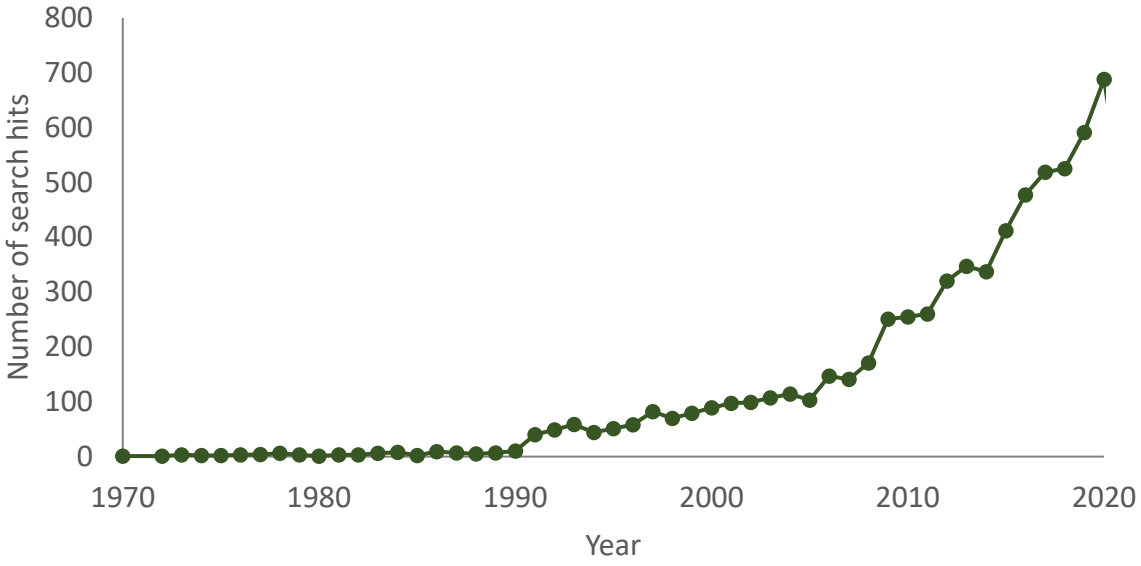

Figure 2: Publications found in Web of Science by year; results of key word search of "stress" and "wildlife". In total, 7137 publications were found (as of 19.09.2021), whereby not all were relevant.

At the beginning of my thesis, a rough search using the keywords "*stress*" and "*wildlife*" illustrated how attention to this topic has grown across past decades (Figure 2). To complement this perspective with recent publications, I performed a more systematic literature review at the end of my thesis. While earlier insights were drawn from a more narrative search, the updated review followed a structured approach using multiple databases.

The systematic search was conducted in three databases (Web of Science, Pubmed, and Scopus), using keywords related to the stress reaction in wildlife (focused on mammals) causing physiological or behavioural changes within the animal. The whole search string can be found in the Appendix. Searches were limited to original research articles and reviews, published between 2020 and 2025, in English or German, and articles with abstract available. This yielded 241 articles in Web of Science, 107 articles in Pubmed, and 443 articles (not filtered for years) in Scopus. After deduplication, 376 articles were selected for further consideration and were screened for eligibility (free-ranging wildlife species reaction to some sort of stressor/disturbance), of which 60 met the criteria. By combining this systematic review with older literature, the following sections provide both historical context and information on recent developments in stress research of wildlife species.

1.3.1. Physiological stress markers and methodological advancements

The analysis of physiological responses to stressors in wildlife is often assessed through GC hormones, which play a central role in regulating the HPA axis. Barukcic et al. (2025) review the use of invasive and non-invasive methods in wild *Cervidae* and *Bovidae* species from

Europe and North America. They report that non-invasive methods, such as collecting faecal, urine, salivary, and hair samples, are increasingly preferred as they minimize stress to wild animals during collection, which can otherwise affect glucocorticoid concentrations. These techniques allow for studying endocrine function in natural populations without capturing or manipulating animals, addressing important questions in ecology, evolution, animal conservation, and welfare (Montgomery et al., 2021). Challenges remain in collecting fresh saliva from wild animals, requiring the development of cost-effective and validated methods for species where it is feasible (Barukcic *et al.*, 2025). As discussed here in chapter 1.2, recent literature agrees that faecal glucocorticoid metabolite levels are often considered a more accurate representation of an animal's endocrine profile than blood samples, as they reflect circulating hormones over a longer period. Hair cortisol concentration has gained significant popularity as a non-invasive method for monitoring medium to long-term physiological stress (Cordeschi *et al.*, 2021; Sandoval-Herrera *et al.*, 2021; Robertson *et al.*, 2023; Santos *et al.*, 2025). Hair cortisol provides an assessment of baseline-levels and short-term peaks over longer periods, reducing sampling bias often associated with acute stress responses during capture (Zenth *et al.*, 2022; Robertson *et al.*, 2023). While the precise pathway of cortisol is still not clear, hair cortisol is considered consistent with integrated salivary cortisol levels and show high intra-individual stability (Kaisin *et al.*, 2025).

Beyond traditional glucocorticoids, new stress markers, including molecular and genetic analyses, offer complementary information on stress responses. Babic et al. (2023) report on an antibody-based protein micro-array to help identify a broader spectrum of stress indicators, including hormones, but also receptors, enzymes, and cell signalling molecules, in samples like skin biopsies of free-ranging bears. They also explore other indicators, like heat-chock proteins and lipids derived from adipose tissue and plasma.

The importance of validation and adherence to methodological practices is evident in all studies mentioning GCs in wildlife research. It is crucial to validate analytical methods and biomarkers for each specific species, and their interpretation is not always straightforward (Pritchard, Palme and Langkilde, 2020; Carlin *et al.*, 2022; Barukcic *et al.*, 2025). Validation confirms that the chosen method is fit for purpose, and the researchers should clearly state the analytical methods used, as commercially available kits can change over time (Barukcic *et al.*, 2025). Factors like sampling protocols, storage, and sample preparation can significantly influence the accuracy of GC analysis. In controlled environments, ACTH challenges (e.g., injecting ACTH to artificially

activate the physiological stress response) can help validate the biological significance and physiological relevance of an assay, though logistical challenges exist for free-ranging animals.

In the end, even while non-invasive methods and innovative biomarkers have greatly improved our ability to evaluate physiological stress in animals, rigorous, species-specific validation is still crucial for accurate interpretation and dependable implementation in ecological and conservation analysis.

1.3.2. Anthropogenic stressors and behavioural ecology

Anthropogenic stressors are known to have a significant effect on wildlife, causing both physiological and behavioural stress. These stressors include urbanization, tourism, noise pollution, habitat disturbance, and human-induced death (Rahman, Hill and MacLarnon, 2025). These factors lead to a rise in interactions between humans and wildlife, posing new problems that can change the survival, migration, reproduction, and susceptibility of animals to illness (Carbillet *et al.*, 2020). Animals in urban environments are often expected to have higher GC levels due to chronic stress from anthropogenic disturbances (Beliniak *et al.*, 2024). For example, black grouse (*Tetrao tetrix*) in human-disturbed areas were found to have higher faecal GC metabolite levels than in undisturbed areas (Arlettaz *et al.*, 2007). A study about chacma baboons (*Papio ursinus*) found higher GC concentrations, increased aggression, and reduced socialising in individuals living within anthropogenic habitats (Chowdhury, Brown and Swedell, 2020). Similarly, Robertson et al. (2023) found that urbanization was one of the main factors driving the physiological stress response. Another study reported that while FGM levels of roe deer (*Capreolus capreolus*) were increased in closer proximity to anthropogenic structures during the day, this effect was mitigated by the availability and use of refuge habitat (Carbillet *et al.*, 2020). It highlights that there are numerous factors, including health, social, and environmental variables that may complicate the relationship between anthropogenic stressors and physiological stress.

Literature showed that noise pollution, particularly from traffic, has become a major anthropogenic stressor and can have severe effects on population dynamics. Additional to the above-mentioned effects on elk and Brazilian bird species, chronic traffic noise was found to reduce the predation risk perception of small mammals, influencing their foraging performance and vigilance in recent literature, which can lead to altered survival of prey species (Giordano, Hunninck and Sheriff, 2022). Likewise, Qu et al. (2022) found altered exploration and metabolism, as well as increased cortisol levels in plateau pikas (*Ochotona curzoniae*).

At the same time, stress responses to anthropogenic disturbances seem to be adaptive. Animals frequently exhibit behavioural adjustments in response to human presence or perceived threats. For instance, giraffes (*Giraffa camelopardalis*) walked further distances and had higher FGM concentrations when humans were present, but this effect decreased with the increase of habituation to the observer (Scheijen *et al.*, 2021). Dheer et al. (2022) investigated how pastoralism affected behaviour and physiological stress response in spotted hyenas (*Crocuta crocuta*). They found no reduction of juvenile recruitments and no elevated FGM levels, discussing this could be due to habituation and social buffering. This highlights the importance of understanding a species' biology, social system, and food availability when attempting to evaluate the stress reaction in response to human disturbances.

1.3.3. Climate change and environmental stressors

Climate change is amongst the most detrimental environmental stressors affecting wildlife. Thus, climate change confronts wildlife species with a new unique set of challenges, including rapidly rising temperatures. In comparison to 1850–1900, the global surface temperature increased by 1.1 °C between 2011 and 2020 due to the rapid increase in greenhouse gas emissions, and more rises are anticipated (Calvin *et al.*, 2023). Along with altered precipitation patterns, this global temperature rise has contributed to an increase in the frequency, intensity, and duration of heatwaves (Meehl and Tebaldi, 2004) and other extreme weather events like wildfires, storms, and floods (Calvin *et al.*, 2023). Furthermore, according to the European Environment Agency (2024), Europe is the quickest warming continent in the world. Ecosystems and their inhabitants are seriously threatened by these changes. According to a meta-analysis evaluating the extinction risk of animal species, 7.9 % of species are expected to become extinct as a result of climate change, and many more species would suffer from habitat loss and heat stress (Urban, 2015). Thermal extremes, including both excessively hot and cold temperatures, represent chronic stressors for mammals, requiring significant energetic expenditure to maintain a constant internal body temperature. These behavioural adjustments, while potentially mitigating immediate thermal stress, may affect energetic costs or alter foraging success, thereby influencing overall fitness (Chowdhury, Brown and Swedell, 2021). Previous studies in wildlife species have reported several spatiotemporal behavioural changes in response to increasing ambient temperatures. These changes include decreased activity in the daytime (moose, Street, Rodgers and Fryxell, 2015; polar bears, Whiteman *et al.*, 2015; Alpine ibex, Semenzato *et al.*, 2021; African antelope, Berry, Dammhahn and Blaum, 2023); increased activity and feeding behaviour in the early or late hours of the day (Alpine ibex, Aublet *et al.*,

2009; moose, Dussault *et al.*, 2016; chamois; Fattorini *et al.*, 2019); overall reductions in feeding time (black wildebeest, Maloney *et al.*, 2005); and the choice of thermally sheltered stands or bedding sites (roe deer, Mysterud, 1996; moose, Verzuh *et al.*, 2023). A more recent study in Chacma baboons (*Papio ursinus*) revealed how seasonal differences in temperature, rainfalls and day length were associated with higher GC levels of females (Chowdhury, Brown and Swedell, 2021). In my own publication, I reported how wild boar change their activity in response to higher ambient temperatures, reducing body motion during the hottest hours of the day when it was dry (Güldenpfennig *et al.*, 2025). Fohringer et al. (2022) investigated the telomer length as an indicator of chronic stress in moose across different ecoregions. Shorter telomers, associated with higher chronic stress were found in regions with more extreme weather conditions in the summer and winter. Another study in the same species reported higher hair cortisol concentrations associated with higher ambient temperatures in the south of Sweden (Spong *et al.*, 2020).

Besides the direct effects of temperature and rainfall, indirect effects caused by climate change affecting wildlife were also reported. Kordosky et al. (2021) investigated the connection between climate change related tree mortality on cortisol levels in fishers (*Pekania pennanti*). Increased tree mortality led to elevated cortisol levels, presumably due to reduced thermoregulatory cover, loss of escape terrain, or decreased prey base. Even more significantly, this study established a link between elevated cortisol levels and reduced female survival, suggesting that ongoing environmental shifts could exacerbate physiological stress and compromise population fitness.

Ultimately, continued research into the physiological effects of climate change, including thermal extremes, is crucial for developing robust frameworks to comprehensively address multiple intrinsic and extrinsic stressors. This may be essential for informing successful conservation and wildlife management strategies in the face of human-induced accelerated climate change. Sensitivity, exposure, resilience, and adaptive capacity are critical factors to consider when assessing an animal's susceptibility to environmental change (Huey et al., 2012). These factors collectively determine how well a species can perceive, respond to, recover from, and ultimately cope with changing environmental conditions.

1.3.4. The role of multiple stressors in Wildlife Health

Stress can increase the influence of infections on animal population sizes (Pedersen and Greives, 2008; Owen *et al.*, 2012). Equally important is the understanding of stress and its effect

on the disease under the aspect of biodiversity conservation and animal welfare. Three main anthropogenic stressors that are directly and indirectly manageable are climate change, habitat disturbance, and wildlife management interventions, including capturing and translocation (Hing *et al.*, 2016).

Wildlife species often face multiple stressors simultaneously (e.g., habitat loss, climate change, human disturbance), and the cumulative effect of these stressors can be greater than the sum of their individual impacts. A collaborative, multiple-stressor approach, as described in Simonis et al. (2025) seems crucial for quantifying the stress reaction and other factors that can indicate compromised health. This approach might help in prioritising conservation efforts and understanding overall health status of populations.

Over the past five years, research on stress in wildlife has advanced significantly, shifting toward more integrative and comprehensive and methodologies that consider both behavioural and physiological reactions to a wide range of stressors. Comprehensive conservation strategies that go beyond single-factor analyses are desperately needed. In order to more accurately predict the long-term effects of environmental change on wildlife populations, future research should maintain focus on validating biomarkers, understanding behavioural cues, comprehending individual variability in stress responses, and creating predictive models. Ultimately, in a world that is becoming increasingly populated by humans and changing quickly, the knowledge gathered from this recent rise in stress research is essential for managing wildlife effectively, advancing animal welfare, and preserving biodiversity.

1.4. Biology and ecology of the wild boar

Wild boars are widely distributed in almost all continents and therefore is one of the most extensively spread species in the world (Lewis *et al.*, 2017; Sales *et al.*, 2017)(Figure 3). They are native to most of Eurasia and North Africa, but considered invasive in the Americas, as well as Oceania (Keuling and Leus, 2019). They are able to occupy a wide range of habitats and are opportunistic feeders, feeding on plant and animal species (Massei and Genov, 2004). Wild boars count as ecosystem engineers, i.e. they turn areas of soil and vegetation while foraging and have a significant impact on biodiversity and landscape. Besides the advantages of wild boar for the forest, the damaging of crops yields high economic losses (Bratton, 1975; Singer, Swank and Clebsh, 1984; Wlazelko and Labudzki, 1992; L Briedermann, 2009). Wild boars also have several effects on wildlife, including predation, habitat and nest destruction that can lead to native species exclusion (Sales *et al.*, 2017).

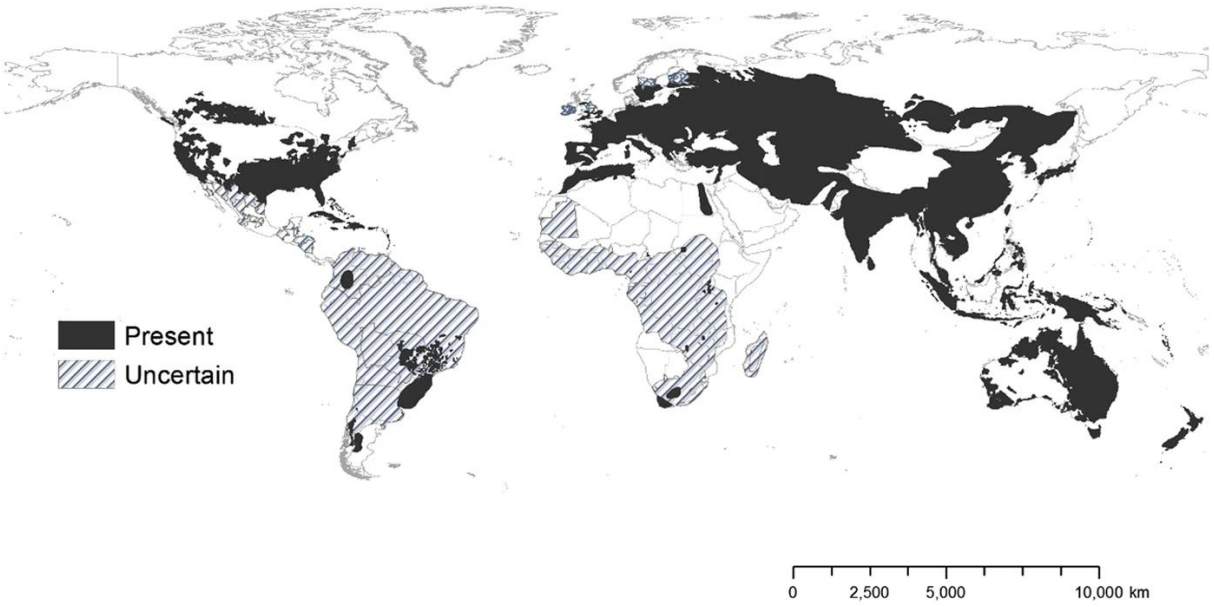

Figure 3: Geographic distribution of wild pig species (Lewis *et al.*, 2017).

Wild boars are gregarious animals. They live in matriarchal groups consisting of adult females and their offspring, although group size and composition changes depending on locality and season (L Briedermann, 2009). I call individuals under one year juvenile, until completion of their second year yearlings and after that adults (Keuling, Stier and Roth, 2008a). Around puberty, male wild boars leave the groups, sometimes forming smaller sounders (L Briedermann, 2009). Adult males live solitary and only join female groups during mating season (Keuling and Leus, 2019). Wild boars have a very high reproduction rate and are able to double their numbers per season. They are seasonal breeders with the main farrowing in spring (L Briedermann, 2009). However, under favourable environmental conditions that favour body condition of young females (e.g., abundant food resources and agreeable weather) multiple births are possible (Mauget, 1982; Gethöffer, Sodeikat and Pohlmeyer, 2007). Females can start to reproduce under the age of one year, dependent on body condition (Bieber and Ruf, 2005; Gethöffer, Sodeikat and Pohlmeyer, 2007). The litter size can vary from one to 12 piglets depending on locality (according to foetus number; (Gethöffer, Sodeikat and Pohlmeyer, 2007; Fonseca *et al.*, 2011; Šprem *et al.*, 2016)).

Due to the high increase of populations, there is an increased risk of wildlife-livestock contact and the transmission of diseases (e.g., brucellosis and pseudorabies, Killian et al., 2006; bovine tuberculosis, Gortázar et al., 2007). Therefore, hunting on wild boars is intensified within the context of risk control measures (currently especially due to ASF). To sufficiently reduce wild boar populations, single hunts are often not enough. In addition to the often-time-consuming practice, studies claim single hunts evoke more stress in wildlife due to the repeated presence

of one or more hunters in the forest (Eisenbarth and Ophoven, 2002; Wölfel, 2003). In contrast, drive hunts, often performed with a big group of hunters, beaters, and hunting dogs concentrated on one or two days in the same area, reduce this hunting-induced stress (Eisenbarth and Ophoven, 2002; Wölfel, 2003; Böhm, 2004).

Because of some characteristics such as opportunistic feeding and habitat diversion, wild boars seem to be not the ideal model organism for stress research, assuming relatively low-stress responses to chronic stress triggers such as food limitation and habitat loss. Still, samples are easy to acquire due to the all-year hunting season in most countries in Europe (e.g., based on the hunting law act n. 449/2001 and veterinary regulation to the eradication of African swine fever, ASF in the Czech Republic; and NML (2019)) and their high density. Behavioural and social structures are well-known, helping to investigate differences between sexes, ages, and social positions. Additionally, researching the stress response of wild boars as organisms living in social groups can help understand the possible effects of this specific social organization on coping behaviour. For example, studies in domestic pigs have shown an effect of the presence of conspecifics on the reaction to a stressor (Reimert *et al.*, 2014).

There are many studies about the behavioural response of wild boars to disturbance. In an area without human disturbance (in the form of hunting), wild boars tend to be nocturnal, showing two activity bouts: one starting before sunset and ending after sunrise, and a smaller one during the day (Russo, Massei and Genov, 1997). In other studies, wild boars showed increased diurnal activity in areas with less hunting pressure (Keuling, Stier and Roth, 2008b). Home ranges increased in areas with combined single and drive hunts and smallest in forest areas with only single hunts (Keuling, Stier and Roth, 2008a). Home ranges did not differ significantly before and after the hunting season if the same group was not hunted repeatedly (Keuling, Stier and Roth, 2008b; Scillitani, Monaco and Toso, 2010). Even if hunted intensively in their central resting area, wild boars, if at all, just moved to the border of their original home range (Sodeikat and Pohlmeyer, 2003). Still, the evasion of wild boars in response to intensive hunting possibly leads to a spread over a wider area, leading to increased crop damage and a greater risk of spreading diseases such as the ASF (Sodeikat and Pohlmeyer, 2003; Thurfjell, Spong and Ericsson, 2013). In response to fleeing, wild boars reduced movement and increased the use of covered habitats (Thurfjell, Spong and Ericsson, 2013). Resting time and the distance between consecutive resting sites were increased after hunts (Scillitani, Monaco and Toso, 2010). The hunting method also influenced wild boar flight or hide behaviour (Thurfjell, Spong and Ericsson, 2013). If not hunted directly (not flushed), wild boars notice hunters but choose to

stay in hiding, reducing the risk of detection (Scillitani, Monaco and Toso, 2010; Thurfjell, Spong and Ericsson, 2013). Wild boars can notice hunters during single (still) hunts even before the first shot was fired and change their behaviour, accordingly, resulting in a lower hunting success (Thurfjell, Spong and Ericsson, 2013). Spatial behaviour of wild boars in response to hunting might not only reflect hunting method and intensity but was also found to reflect habitat types and season and is based on food, shelter, and other resources available (Keuling, Stier and Roth, 2008b, 2008a). Research studying the effects of weather and season on wild boars primarily concentrated on movement analysis (e.g., travel distances, Kay et al. 2017; daily ranges, Johann et al. 2020b, Clontz et al. 2022) or activity scored as a number (activity tracking, Lemel, Truvé and Söderberg, 2003; activity rate, Brivio *et al.*, 2017; binary activity, Johann, Handschuh, Linderoth, Dormann, *et al.*, 2020).

With increasing wild boar populations, hunting (shooting of individuals in single and driven hunts) as a management strategy is often no longer sufficient enough. One additional method includes live-trapping with subsequent relocation or euthanasia, allowing scientific studies (Torres-Blas *et al.*, 2020). This could also be preferred in areas where hunting may be impractical or find opposition from the general public (Conejero *et al.*, 2019). During live-trapping, restraint, and handling, wildlife species are exposed to high stress (Kock *et al.*, 1987; Montané *et al.*, 2003). Several trapping methods were tested in urban and peri-urban areas in Barcelona, Spain, and teleanaesthesia was the least stressful as it did not involve direct physical restraint and handling of wild boars (Torres-Blas *et al.*, 2020).

Obtaining reliable cortisol reference values for free-ranging wild boars remains challenging, as most available data are derived from studies involving trapping or handling, which can itself induce stress (Casas-Díaz et al., 2015). Hence, these values should be consulted and applied with care. Existing studies have reported cortisol concentrations from captive (Weiler *et al.*, 1998), trapped (Casas-Díaz *et al.*, 2015; Esposito *et al.*, 2021) or hunted wild boars (Gentsch, Kjellander and Röken, 2018; Güldenpfennig *et al.*, 2021). However, direct comparisons among these studies are problematic because of differences in analytical methods, assay types, and statistical reporting (e.g, see Table 1). Moreover, several studies observed variation in cortisol levels across age and sex classes (Casas-Díaz *et al.*, 2015; Esposito *et al.*, 2021; Güldenpfennig *et al.*, 2021), consistent with broader evidence that physiological stress responses often differ between males and females (Kudielka and Kirschbaum, 2005; Verma, Balhara and Gupta, 2011).

Table 1: Cortisol values reported in different studies under different conditions. (ELISA – enzyme linked Immunoassay; EIA – enzyme immunoassay; RIA – radioimmunoassay; S.E.M. – standard error of mean; SE – standard error; SD – standard deviation)

	Cortisol	**Assay**	
Captivity	65.0 ± 0.75 (mean ± S.E.M) [ng/ml]	-	Weiler *et al.*, 1998
Trapping	Piglets: 531.03 Juvenile & Adults: 321.28 (median) [nnmol/L]	ELISA	Casas-Díaz *et al.*, 2015
	Male: 29.98 ± 2.73 Female: 27.65 ± 2.87 [µg/dl]	EIA	Esposito *et al.*, 2021
Hunting – single hunts	249.58 ± 36.80 (mean ± SE) [nnmol/L]	RIA	Gentsch, Kjellander and Röken, 2018
Hunting – driven hunts	411.2 ± 242.6 (mean ± SD) [nnmol/L]	RIA	Güldenpfennig *et al.*, 2021
Trauma (including hunting)	775.24 ± 64.66 (mean ± SE) [nnmol/L]	RIA	Gentsch, Kjellander and Röken, 2018

All things considered, the biology, ecology, and behaviour of wild boars show that they are a very resilient and adaptive species that can survive in a variety of settings, including ones that are greatly impacted by human activity. They can adapt to a variety of ecological circumstances and human pressures thanks to their adaptable social structure, omnivorous eating habits, and behavioural plasticity. This flexibility also presents management with more and more difficulties, especially when it comes to disease transmission and population control.

At the same time, this very resilience makes the wild boar an important species for studying the physiological and behavioural mechanisms that allow wildlife to persist under environmental change. Investigating their stress responses in relation to ecological and social factors provides valuable insights into how free-ranging mammals adjust to human disturbance and climatic extremes. Such knowledge not only advances our understanding of wildlife stress ecology but also contributes to more effective and sustainable management strategies in an increasingly human-dominated world.

2. Methodology

2.1. Study area and animal handling

This work includes two study areas with different methodologies used. In the first study area in Germany, I only collected blood samples for hormone analysis. The main part of this thesis was performed in the Czech Republic, including blood and faecal sampling for hormone analysis, as well as GPS and biologger measurement.

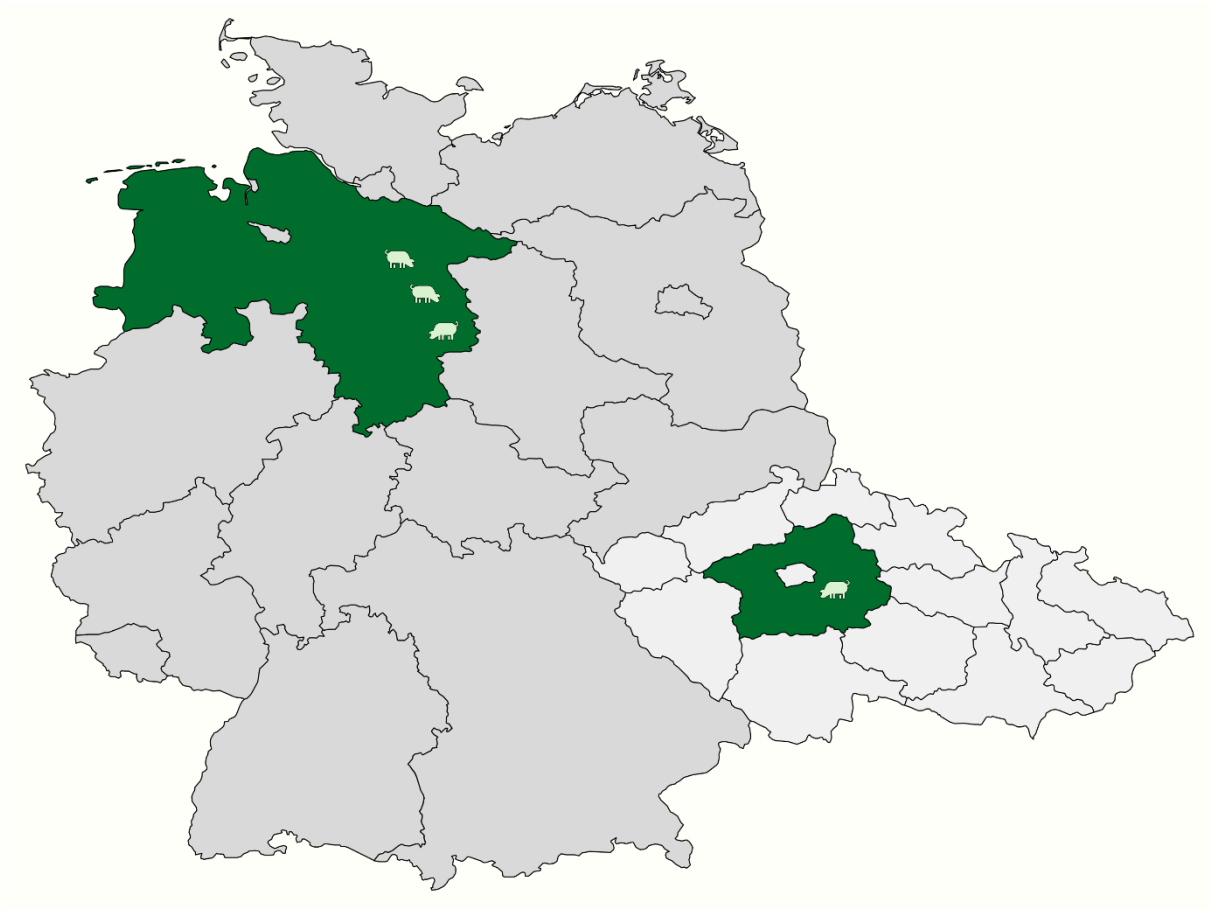

Figure 4: Map of the study areas in Germany and the Czech Republic. The countries and municipalities are outlined in black, while the main sampling locations are marked with pigs.

2.1.1. Germany

The study area was located in the eastern part of the federal state of Lower Saxony (Northern Germany; 52.36°N, 10.35°E, Figure 4). Altitude ranged from 60 to 130 m above sea level with sub continental climates (Gethöffer, 2005). In 2018, the average annual precipitation was 512 mm; the average annual temperature was 10.7 °C (DWD, 2019). The approximately 4900 km^2 study area contained 54.6 % of cultivated fields and 27.6 % forest, buildings and infrastructure claimed the remaining 17.8 % (for detailed description see Frauendorf et al. (2016); Gethöffer, (2005)). In the study area, hunting was usually performed in form of single

hunts or drive hunts. Supplementary feeding was not allowed but baiting as a necessary hunting strategy (Keuling, 2015). Wild boar hunting was especially intensified due to risk control management associated to the African Swine Fever (Gräber, Strauß and Johanshon, 2018).

The blood from the hunting season 2018/2019 was collected in several different hunting areas using 7.5 ml Kabevettes® (Kabe Labortechnik GmbH, Nümbrecht-Elsenroth) during gutting, max. 3 h after death. The samples were first stored in a cooling box and transported back to the university. I centrifuged the blood samples (12 min., 4500 rpm), transferred 1 ml serum to 1.5 ml Eppendorf Tubes® (Eppendorf AG, Hamburg) and stored them at -32° C until assaying. The animals were categorised in age classes based on their tooth eruption (Gethöffer, Sodeikat and Pohlmeyer, 2007). I differentiated animals in j = juvenile < 12 months (piglets), y = yearlings 12 - 23 months and a = adults ≥ 24 months as well as the two sexes f = females and m = males (Keuling, Stier and Roth, 2008a). In total, I chose 115 samples for examination to have similar sample size in all age-sex classes.

2.1.2. Czech Republic

The study area was located 30-55 km east of Prague in the Central Bohemian Region of the Czech Republic, close to the city Kostelec nad Černými Lesy (Figure 4). The forest covers almost 7000 ha, including the Voděradské Bučiny National Nature Reserve. The predominant tree species are Norway spruce and beech, and the dominant forest type is mixed oak (Chytrý, 2013). The forest is framed with farmland and settlements and is a popular area for outdoor recreational activities. Hunting is performed all-year as driven hunts and single hunts. Supplementary feeding during winter is mandatory in the Czech Republic (Bartos, Kotrba and Pintíř, 2010).

Blood and faecal samples in the Czech Republic were collected from dead wild boars after driven hunts in one hunting area across three hunting seasons: 2020/2021, 2021/2022, and 2022/2023. Blood was drawn using intracavernous venipuncture (Arenas-Montes *et al.*, 2013; Jiménez-Ruiz *et al.*, 2016) and stored in 10 ml Vacutainer® tubes (Becton Dickinson Czechia, s.r.o., Prague) which walls were coated with a layer of silicon dioxide to accelerate coagulation. I used the same age and sex classification as in Germany. The samples were stored in a cooling box until transport back to the university. Then, the tubes were centrifuged for 10 min at 1800 g and 20 °C to separate the serum. Approximately 1.5 ml serum was transferred to Eppendorf Tubes® (Eppendorf AG, Hamburg) and stored at -20 °C until assaying. Faeces was collected from the same animals, when applicable, from the rectum and stored in common freezer bags.

In between the drives, the samples were transferred into a -20 °C freezer and stored until assaying. In total, 343 samples were collected, including 193 faecal and 285 blood samples.

To collect data on behaviour and movement, wild boars were trapped using one box cage and several wooden corral traps. After capture they were immobilised using a tranquilliser rifle and darts containing a mixture of Zoletil, Ketamine and Xylazine. After anaesthesia, wild boars were sexed, aged, and equipped with GPS collars (Vectronic Aerospace GmbH) with attached daily diary tags (3-axis accelerometer, 3-axis magnetometer; Wildbyte Technologies Ltd.). Anaesthetised wild boars were left at the capture location and monitored until they regained consciousness.

2.2. Data collection and analysis

2.2.1. Hormone measurement

I commissioned the endocrinological laboratory of the clinic for cattle of the University of Veterinary Medicine Hannover to analyse the blood samples from Germany. The lab conducted the cortisol measurement using radioimmunoassay (Cortisol RIA KIT, Beckmann Coulter, Inc., Krefeld) while following the instructions from the manufacturer. The cortisol concentration was measured in nmol/L.

I performed all hormone measurements of the Czech samples personally under the lead of Prof. Rupert Palme and Dr. Sabine Macho-Maschler at the experimental endocrinology lab of the University of Veterinary Medicine Vienna using standardized protocols. First, I extracted the steroids from the faeces using 80 % methanol and from the blood using diethylether. The extract was then diluted to 1:10 (faeces) and 1:100 (blood) using 7.5 pH Assay Buffer and then stored at -20 °C until assaying. Assays for cortisol (EIA first described: Palme and Mostl (1997)) and cortisol metabolites (Lab code 37e; 5α-pregnane-3ß,11ß,21-triol-20-one; EIA first described: Touma et al. (2003)) were chosen based on suitability and previous verification performed for domestic swine. At the start of the assays, I first created the standard using stepwise 1:2.5 dilutions. Antibody and Label solutions were prepared based on how many microtiter plates (MTP) needed to be measured. The MTPs were previously coated using anti-rabbit IgG. The MTPs were then loaded using assay buffer for nonspecific binding and zero binding, followed by the Standard and the samples. Each was filled in twice. Then, I dispensed biotin-labelled steroid followed by antibody solution in each well. The MTPs were then incubated at 4 °C over night before the first washing. This was followed by the streptavidin reaction, which needed to be incubated for 45 min. at 4 °C. After that, I again washed the plates and started the colour

reaction with another 45 min. at 4 °C incubation period. The colour reaction was then stopped using sulphuric acid. The colour changed from blue to yellow. The hormone concentrations were then calculated using the absorbance measurement using an automatic MTP reader. The detailed protocol was published by Prof. Palme and his team on the website of the veterinary university Vienna (Palme, 2019a). The blood cortisol concentration was measured as ng/ml and the faecal cortisol metabolites (FCM) as ng/g.

All data preparation and statistical tests were performed within the R software (R version 4.2.2), using the packages "mgcv" (Wood, 2017) and "glmmTMB" (Brooks *et al.*, 2017). I visually tested for outliers and confirmed them using the Rosner's generalized extreme Studentized deviate test (Rosner, 1983). Confirmed outliers were then excluded. I built Generalized Linear Mixed Models (GLMMs) with the respective hormone (cortisol or FCM) as the response variables. The age-sex class was added as the predictor variable and animal ID was added as a random effect. I decided to use the Gamma family (log-link) after visually inspecting the residuals using the "DHARMa" package (Hartig, 2022) and calculated marginal and conditional R^2 according to Nakagawa, Johnson and Schielzeth (2017) to assess the model's goodness-of-fit. Since the blood samples were analysed using different assays (RIA vs. EIA), I cannot directly compare the actual values. Therefore, the blood cortisol was modelled in two separate GLMMs. This resulted in three models, $GLM1_{cortGER}$, $GLM2_{cortCZ}$, and $GLM3_{FCMCZ}$. Predictions were calculated using the “predict” function of the "mgcv" package to quantify the percentage increase/decrease between means of interest.

2.2.2. Body motion and travel movement

The collars equipped on the wild boars logged GPS, acceleration, and magnetic heading. GPS fixes were taken every 30 minutes and transmitted to a server, where they could be downloaded at any time. The daily diary tags recorded acceleration and magnetic heading as 10 Hz data (10 points per second), which was stored on a microSD card on the collar. After retrieval of the collar, the data could be read and stored until further processing. The collars were calibrated just before applying them. Calibration was achieved moving the collars in a regular turning motion for five minutes, which can then be seen in the raw data. This is used to set time, date, and orientation of the device. The daily diary is able to record animal movement, behaviour, energy expenditure, and environmental conditions (Wilson, Shepard and Liebsch, 2008).

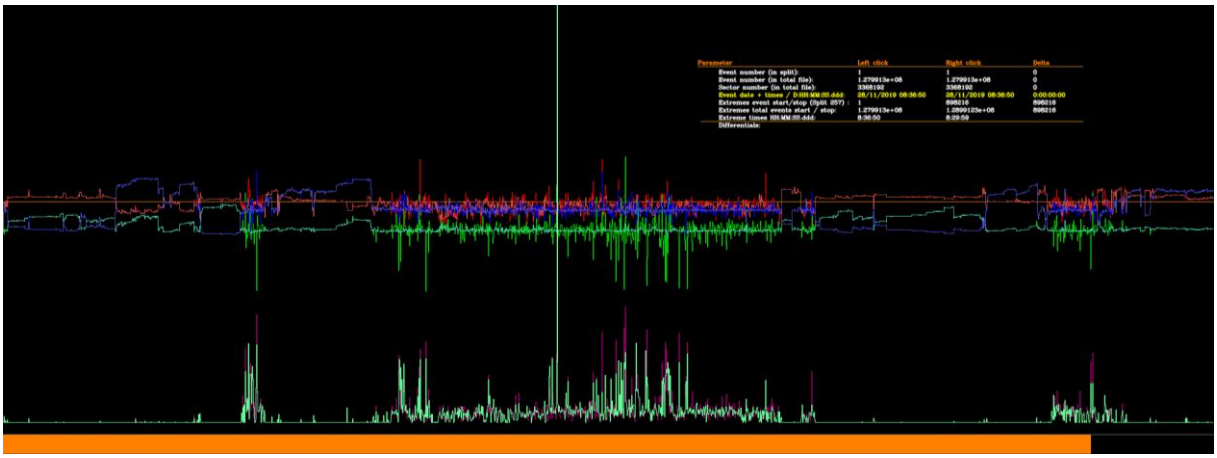

Figure 5: Example of data visualisation within the DDMT software. Triaxial acceleration is visualised as the three lines (red, blue, green) on the top, while the VeDBA (purple) and smoothed VeDBA (light green) can be found in the bottom of the picture.

I used the DDMT software (Wildbyte Technologies Ltd.) to visually inspect and export the data from the daily diary tags (Figure 5). To quantify body motion, I used the vectorial sum of Dynamic Body Acceleration (VeDBA). Dynamic Body Acceleration (DBA) was previously described as a good proxy for energy expenditure in various species, showing a linear relationship (Halsey *et al.*, 2009). Although VeDBA and the Overall Dynamic Body Acceleration (ODBA) show a very high correlation (Qasem et al., 2012; Wilson, Börger, Holton, Scantlebury, Gómez-Laich, et al., 2020), there are several factors influencing the choice of the correct metric (Qasem et al., 2012). In this study, I used VeDBA as I could not guarantee that the loggers are staying in the same position orientated along the major axes of the body, which would be preferred when using ODBA. Within the DDMT software, VeDBA was smoothed using a centred rolling mean over two seconds. I then exported the smoothed VeDBA using 30-minute means and calculated the sum per hour and average per day within the R software. As wild boars are predominantly nocturnal within our study area (Olejarz *et al.*, 2023; Mortlock *et al.*, 2024), I defined one day to start at sunrise on day x and end with the following sunrise on day x+1. This ensures that a full inactive phase during daylight hours (sunrise to sunset) and the full active phase during nighttime hours (sunset to sunrise) are included in one 24 h measurement.

GPS locations were filtered by dilution of precision (DOP) ≥1 and ≤7. I then calculated the step length (SL) using the "amt" package (Signer, 2022). SL was also summarised to hourly sum and daily average. I then added hourly air temperature, daily maximum temperature and precipitation to the data tables. Weather data was acquired using the Visual Crossing Weather Query Builder (Weather Data & Weather API | Visual Crossing, 10.01.2023). For the Kostelec

location, the Query Builder calculated the average of the closest weather stations. Precipitation was converted into a binary factor, with “absence” when the total precipitation over a given period remained 0, and “presence” when the total precipitation was > 0 mm.

The dataset was restricted to observations recorded during the summer months (June to August), spanning 2019 to 2021, and encompassing data from 24 individuals. Ruf et al. (2023) found the summer thermoneutral zone of wild boars to be 6–24°C. According to this, heatwaves were defined as any period 23+ hours with a daily average temperature over 24 °C. I calculated the mean daily average of VeDBA, mean daily average of SL, average daily maximum temperature, and total precipitation during each heatwave sequence. Precipitation was then again categorized as “absent” or “present” as described above.

To compare VeDBA and SL, I first tested the correlation using simple Kendall rank statistic (Kendall’s tau). I used Generalized Additive Mixed Models (GAMMs) and Generalized Linear Mixed Models (GLMMs) to analyse the relationship between the smoothed VeDBA and SL as a proxy for body motion or travel movement and climate variables as described above. I assessed the direct effect of summer temperatures within one day in the first GAMMs, setting the hourly smoothed sum of the VeDBA ($GAM1_{VeDBA}$) and the hourly sum of SL ($GAM1_{SL}$) as the response variables. Hourly temperature, hour and the interaction between temperature and hour were included as fixed effects. In both models, temperature was modelled using default thin plate regression splines and hour was modelled using cyclic cubic spline function to account for its periodicity. To define the tensor product interaction between temperature and hour while including the main effects, I used the "*ti*" function (Wood, 2017). Precipitation was added as a factor-smooth interaction (variable "by" factor) in all smooths and added as a linear main effect. Within the second GAMMs testing the weather effects at the seasonal scale, I used the daily sum of the VeDBA ($GAM2_{VeDBA}$) and the daily mean of SL ($GAM2_{SL}$) as the responses. Daily maximum temperature, day of the year (DOY) and the interaction between them (using the "*ti*" function) were set as the predictors. Both main effects were modelled as thin plate regression splines (no circularity occurs in DOY, since our study period is restricted to summer). As in GAM1, the precipitation was added as a factor smooth interaction and as a linear main effect. I included animal ID as a random effect in all models and used the maximum likelihood estimation while modelling the response variables through Gaussian errors (link = identity). The robustness of the models was tested using the "gam.check" function within the "mgcv" package, confirming the suitability of the chosen models. The results were tested and quantified using the “predict” function of the same package.

To test the effect of heatwave duration on wild boar activity, I used GLMMs including the average daily mean of VeDBA (GLM_{VeDBA}) and SL (GLM_{SL}) during heatwaves as the response variables. I included the interaction between the length of heatwaves in days with precipitation and the interaction between the average maximum temperature and precipitation as fixed effects, together with their main effects. I used the "tweedie" family (link: log) to model response variables and included animal ID as a random effect. Covariates were scaled to improve model convergence. Residual diagnostics of the GLMMs were performed using the "DHARMa" package (Hartig, 2022). I also calculated marginal and conditional R^2 according to Nakagawa, Johnson and Schielzeth (2017) to assess the model's goodness-of-fit.

2.2.3. Sleep sites analysis

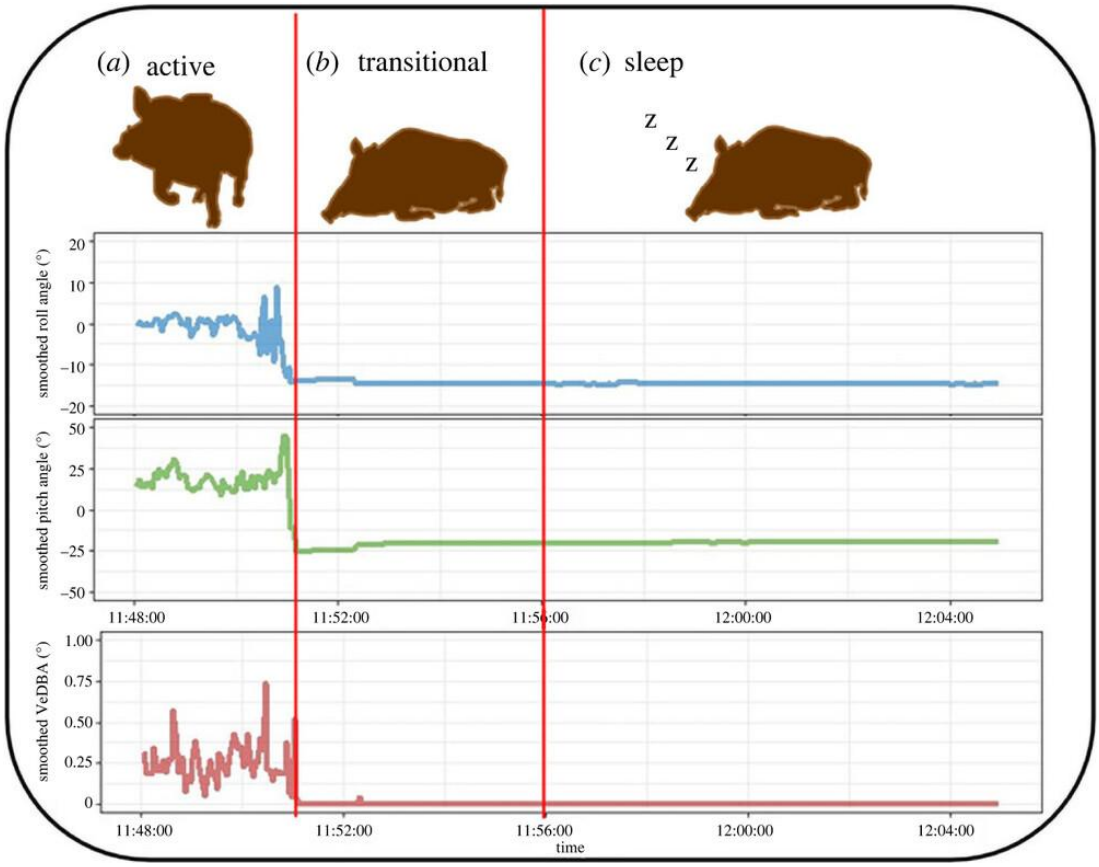

Figure 6: Example of sleep classification using data from the daily diary (Mortlock *et al.*, 2024). The different axes show smoothed roll, pitch, and VeDBA values, explaining the different phases of sleep classification (marked by vertical lines). (a) shows daily diary data corresponding to general behaviours, (b) shows the transitional phase of drowsiness, and (c) the actual sleep pattern after five minutes of the transitional phase.

I defined sleep sites as locations were wild boars had the longest sleeping bout per day. Sleep was defined using stereotypical sleeping positions combined with the absence of body motion as described by Mortlock et al. (2024). The sleep positions were derived from studies in domestic pigs, which state pigs primarily sleep on their belly or on their side (Kuipers and

Whatson, 1979; Lonergan *et al.*, 1998). This body position could be defined using pitch and roll values using the acceleration data. At the same time, body position was combined with a lack of movement using VeDBA data. To account for the transition of wakefulness to sleep, five minutes were discarded from each sleep bout (Mortlock *et al.*, 2024). After marking the longest sleeping bouts per day, I filtered one GPS location per bout as a "used" location. I then generated 100 random points with random dates within the home range of each individual for the whole summer. Each used and random location was mapped in QGIS (QGIS Version 3.2.8.1) and overlaid with multiple raster and polygon files containing information about habitat traits, and microclimatic indices. Habitat traits were dominant tree type (conifers, leaves; ©European Union, Copernicus Land Monitoring Service 2024, European Environment Agency (EEA)), tree stand age (derived from the Forest Management Plan; Sections 24, 26 and 27 of Act No. 289/1995 Coll., on forests and on amendments to certain acts (Forest Act) & Decree No. 84/1996 Coll., on forest management planning, of the Ministry of Agriculture of the Czech Republic), and the distance to roads, paths, buildings (OpenStreetMap contributors, 2017), rivers (Amatulli *et al.*, 2022), and forest edge (using European Union's Copernicus Land Monitoring Service information; https://doi.org/10.2909/960998c1-1870-4e82-8051-6485205ebbac). Indices included were the Heat Load Index (HLI), Topographic Wetness Index (TWI), Solar Radiation Aspect Index (SRAI), and the Tree Cover Density (TCD). The HLI and SRAI were calculated using the "spatialEco" package (Evans and Murphy, 2023) after (McCune and Keon, 2002) (HLI) and (Roberts and Cooper, 1989) (SRAI). HLI and SRAI are ranging from 0 (north-northeast; coolest, wettest) to 1 (south-southwest; hottest, dryer). The TWI was calculated as a function of the local upslope contributing area and slope (Beven and Kirkby, 1979), describing the tendency of an area to accumulate water. Higher values are indicating higher potential of water accumulation – therefore, wetter areas. TCD was downloaded and extracted from the Copernicus Land Monitoring Service using the "Tree Cover Density 2018" raster (©European Union, Copernicus Land Monitoring Service 2024, European Environment Agency (EEA)"). It is a percentage of canopy cover and is ranging from 0 % to 100 %. Heatwaves, as defined above, were added according to dates. In the next step, I tested for the revisitation of the sleep sites. I created clusters using the sleeping locations based on proximity (5 m threshold) and averaged the above parameters by cluster ID and animal ID. Additionally, I counted the number of sleeping locations within each cluster as visitations. For the statistical analysis of the revisitation rate, I transformed the number of visitations by subtracting 1. Sleep sites that were visited only once have a value of 0.

Statistical analysis was performed within the R environment using the "glmmTMB" package. To test our hypotheses, I built two binomial different models. Sleep locations or random points were set as the response variable (1 or 0) and animal ID was added as a random variable for each model. The family was set to binomial (link = logit). Model 1 ($GLM1_{dist}$) included the distance to roads, paths, buildings, and edge of the forest as predictors to examine if wild boars select sleep sites based on the chance of human disturbance. Model 2 ($GLM1_{hab}$) included distance to rivers, HLI, TWI, TCD, SRAI, dominant forest type, and tree stand age as the predictors to test if wild boars chose sleep sites based on microclimatic traits. Heatwave as 1 (within heatwave) and 0 (outside of heatwave) was added as an interaction term to the habitat model. To test the parameters characterising frequently used sleep sites, I built two models using the number of revisitations as the response variable. In Model 3 ($GLM2_{dist}$), I included the human disturbance parameters distance to roads, paths, buildings, and forest edge. In Model 4 ($GLM2_{hab}$), I included the habitat parameters distance to rivers, HLI, TWI, TCD, SRAI, dominant forest type, and tree stand age. Animal ID and cluster ID were set as random parameters to account for repeated observations of the same individual and in the same cluster. The family was set as negative binomial using quadratic parameterization (nbinom2; (Hardin and Hilbe, 2018)). I checked all models for collinearity using the "check_collinearity" within the "performance" package (Lüdecke *et al.*, 2021). Only predictors with low correlation were included in the final models. Additionally, residual diagnostics were performed using the "DHARMa" package. Probabilities of the sleeping location selections were calculated using model predictions.

4. Results

4.1. Hormones

Mean cortisol concentrations in Germany were 411.16 nmol/L with 95 % CI [366.35, 455.96] and ranged from 30.60 nmol/L to 1457.92 nmol/L. In the Czech Republic, mean cortisol concentrations averaged at 8.99 ng/ml with 95 % CI [8.23, 9.76] and ranged from 0.59 ng/ml to 35.95 ng/ml. Faecal cortisol metabolite concentrations were averaged at 114.42 ng/g with 95 % CI [98.19, 130.65] and ranged from 7.66 ng/g to 800.47 ng/g.

Table 2: Detailed results of the generalised linear mixed models used to examine the effect of age and sex on hormonal values. The response values are cortisol [nmol/L] ($GLM1_{cortGER}$), cortisol [ng/ml] ($GLM2_{cortCZ}$) and faecal cortisol metabolites [ng/g] ($GLM3_{FCMCZ}$). Predictors included the age-sex classes (M0 – male juveniles, M1 – male yearlings, F1 – female yearlings, M2 – male adults, F2 – female adults).

	$GLM1_{cortGER}$				**$GLM2_{cortCZ}$**				**$GLM3_{FCMCZ}$**			
Predictors	**Estimates**	**CI**	**p**		**Estimates**	**CI**	**p**		**Estimates**	**CI**	**p**	
(Intercept)	5.94	5.75 – 6.12	**<0.001**	***	1.99	1.83 – 2.15	**<0.001**	***	4.20	4.04 – 4.36	**<0.001**	****
age sex [M0]	0.36	0.07 – 0.64	**0.014**	*	0.05	-0.17 – 0.27	0.659		0.17	-0.04 – 0.39	0.109	
age sex [F1]	0.36	0.04 – 0.69	**0.029**	*	0.49	0.22 – 0.77	**<0.001**	***	0.53	0.24 – 0.83	**<0.001**	***
age sex [M1]	-0.41	-0.70 – -0.11	**0.006**	**	0.09	-0.34 – 0.51	0.692		0.96	0.40 – 1.53	**0.001**	****
age sex [F2]	0.31	-0.01 – 0.63	0.060		0.47	0.25 – 0.70	**<0.001**	***	0.57	0.34 – 0.80	**<0.001**	***
age sex [M2]	-0.31	-0.62 – 0.00	0.051		-0.21	-0.55 – 0.12	0.214		1.78	1.41 – 2.14	**<0.001**	****
Observations		115				273				183		

CI = confidence intervals **Significance codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05**

Marginal R2 / Conditional R2	Marginal R2 / Conditional R2	Marginal R2 / Conditional R2
0.289 / 0.289	/	/

There were significant differences between the age-sex classes in all models (Table 2). In $GLM1_{cortGER}$, male juveniles had 35 % higher cortisol concentration than female juveniles, whereas male yearlings and adults had 73 % and 60 % lower cortisol concentration than female yearlings and adults. In $GLM2_{cortCZ}$ male yearlings and adults had lower cortisol concentrations than females as well (-40 % and -66 %), whereas male juveniles had almost the same cortisol concentration than female juveniles (5 %). FCMs in $GLM3_{FCMCZ}$ showed opposing structures, with male juveniles having 17 % higher FCM concentrations, male yearlings 42 % higher, and male adult 108 % higher FCM concentrations as compared to the respective females.

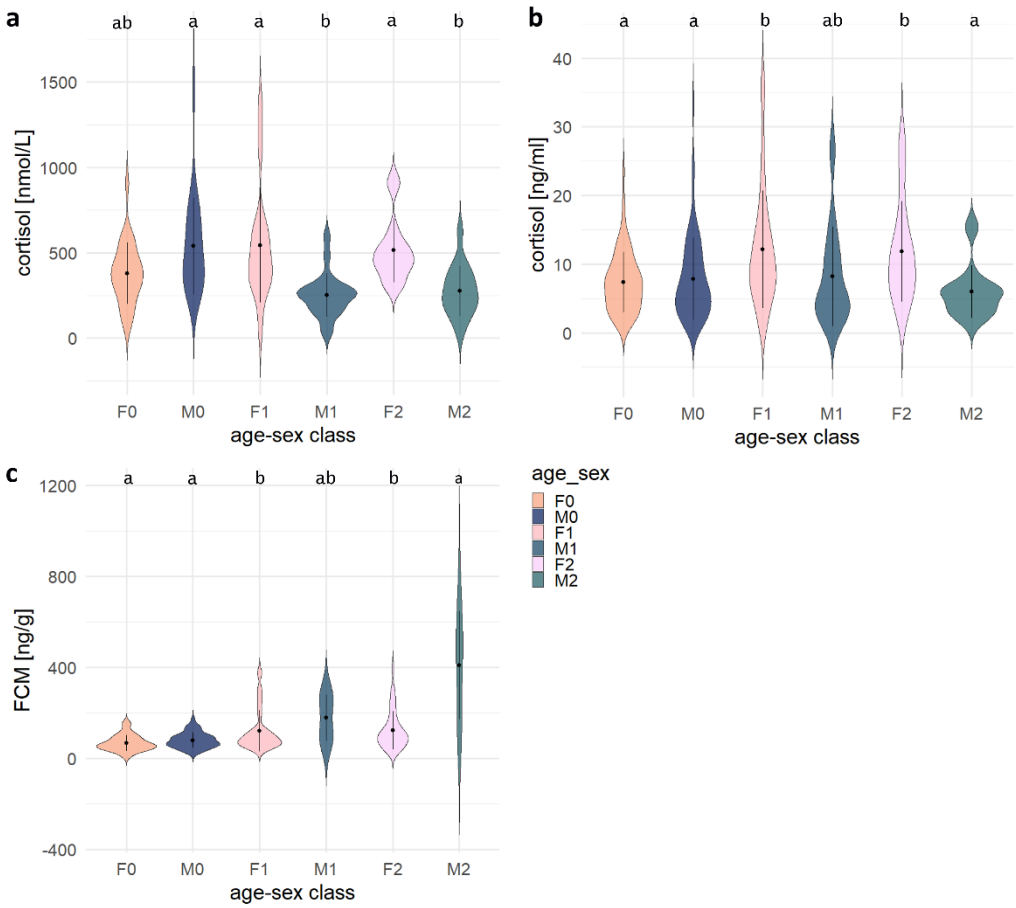

Figure 7: Hormones concentrations from (a) Germany and (b&c) Czech Republic.

4.2. Effects of heat on wild boar activity

The average annual summer temperature (June–August) in our study area was 19.6°C during the 2019–2021 study period. While 2020 and 2021 saw average temperatures of 19.1°C (8.1–33.2°C, average daily maximum of 24.0°C) and 19.0°C (5.5–32.0°C, average daily maximum of 23.4°C), respectively, 2019 had the hottest year with an average summer temperature of 20.8°C (9.3–36.7°C; average daily maximum of 26.3°C). While August was the hottest month in 2020, June was the hottest month in 2019 and 2021. The average daytime temperature during the entire study period was 20.9°C, while the average nighttime temperature was 17.1°C. In comparison to 2019 (total precipitation 174.94 mm, mean precipitation 0.08 mm, and 47 days with precipitation) and 2021 (total precipitation 269.20 mm, mean precipitation 0.13 mm, and 55 days with precipitation), 2020 had the most precipitation (288.27 mm, mean precipitation 0.14 mm, and 58 days with precipitation). Seven of the 14 heatwave sequences that we recorded during the study period lasted longer than a day. In 2019, the average heatwave lasted 1.88 days (1–4 days, n = 8); in 2020, it lasted 1.25 days (1–2 days, n = 4); and in 2021, it lasted 3.00 days

(1–5 days, n = 2). VeDBA and SL showed a significant correlation, but with a weak correlation coefficient (tau = 0.273, p-value < 2.2^{e-16}).

4.2.1. Daily activity and step length patterns

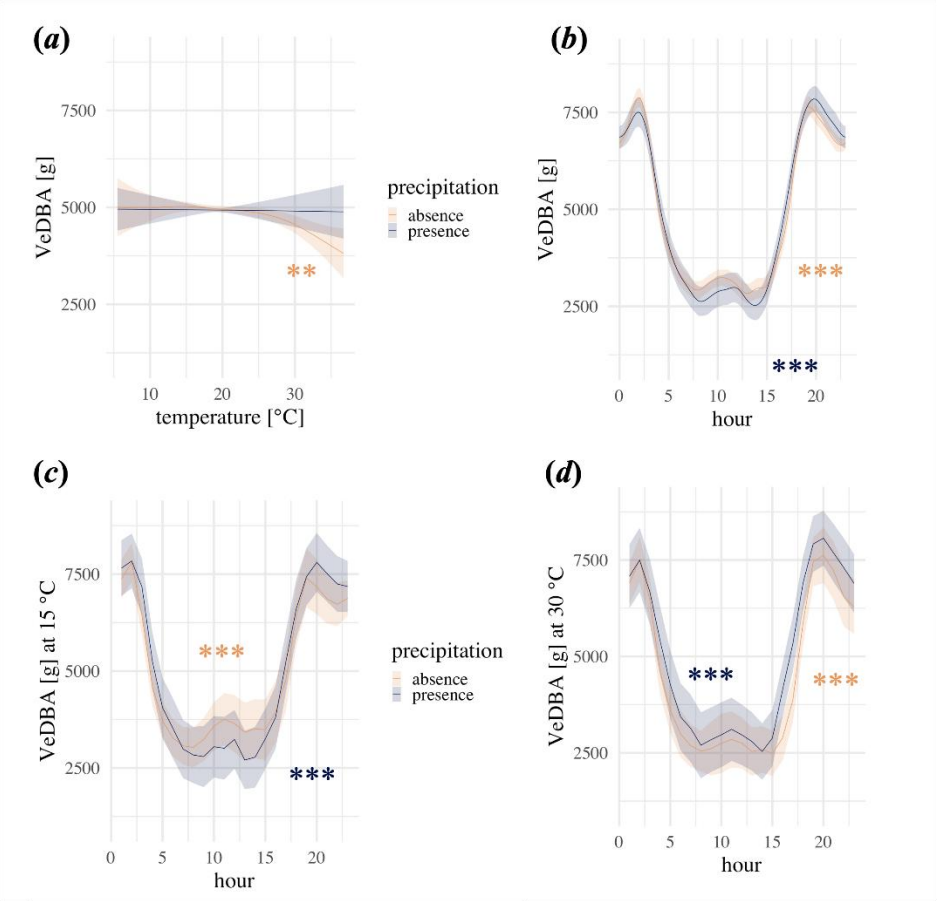

Figure 8: Effect of temperature and hour of the day on the hourly sum of VeDBA. (a) & (b) show the main effects of temperature and time grouped by precipitation presence (blue) or absence (orange). (c) & (d) show the effect of time on the hourly sum of VeDBA at 15 °C and 30 °C. The lines visualise the model estimates, the shaded areas represent the model 95 % confidence intervals. Asterisks represent significance levels: *** < 0.001 < ** < 0.01 < * < 0.05.

Changes of VeDBA in direct response to different weather conditions were tested using hourly data in the first set of models (Table 3). When precipitation was absent, there was a significant negative relationship between temperature and VeDBA, revealing an exponential decrease of VeDBA with increasing temperatures (Figure 8a). This effect was not there when precipitation was present. Regardless of the precipitation, the hour of the day significantly influenced VeDBA in $GAM1_{VeDBA}$. VeDBA was ~ 60 % higher during the night (10 pm – 4 am) than compared to during the day (5 am – 9 pm). The interaction between temperature and hour of day was also significant, indicating that the effect of temperature varies across the day (Figure 8b). This was most visible in the difference between the late afternoon (4 pm – 6 pm) and sunset (8 pm – 10 pm) when temperatures were high versus low. For example, when precipitation was

absent and temperatures were high (~ 30 °C), VeDBA increased from late afternoon to sunset by 70 %, whereas when temperatures were lower (~ 15 °C), VeDBA only increased by 37 % (Figure 8c&d). This was less apparent when precipitation was present. Here, VeDBA increased by 41 % and 44 % from late afternoon to sunset when temperatures were high or low.

Table 3: Detailed summary table of the generalised additive models used to detect the effects of temperature and time. Response variables are VeDBA ($GAM1_{VeDBA}$) and SL ($GAM1_{SL}$). Predictors are precip = precipitation presence or absence, temp = temperature (measured hourly), hour = hour of the day, and animalID = ID for each individual, added as a random effect. Smoothed terms are represented within s(), tensor interaction smooths within ti(). ":" indicates the factor interaction with precipitation (level of precipitation).

		$GAM1_{VeDBA}$					**$GAM1_{SL}$**				
Component	**Term**	**Estimate**	**Std Error**	**t-value**	**p-value**		**Estimate**	**Std Error**	**t-value**	**p-value**	
parametric coefficients	(Intercept)	4930.346	259.245	19.018	**0.0000**	***	180.481	11.052	16.330	**0.0000**	***
	precip_presence	128.780	78.848	1.633	0.1024		8.862	6.088	1.456	0.1455	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**		**edf**	**Ref. df**	**F-value**	**p-value**	
smooth terms	s(temp): precip_absence	3.228	3.915	3.985	**0.0060**	**	1.025	1.044	2.962	0.0794	
	s(temp): precip_presence	1.023	1.045	0.008	0.9673		1.016	1.030	0.923	0.3377	
	s(hour): precip_absence	17.655	22.000	162.594	**0.0000**	***	20.381	22.000	211.738	**0.0000**	***
	s(hour): precip_presence	12.261	22.000	67.765	**0.0000**	***	16.004	22.000	86.077	**0.0000**	***
	ti(hour,temp): precip_absence	44.592	415.000	0.253	**0.0000**	***	71.077	416.000	0.380	**0.0000**	***
	ti(hour,temp): precip_presence	26.436	305.000	0.249	**0.0000**	***	36.489	293.000	0.390	**0.0000**	***
	s(animalID)	21.955	23.000	94.232	**0.0000**	***	20.231	21.000	45.605	**0.0000**	***

Significance codes: 0 <= '*' < 0.001 < '**' < 0.01 < '*' < 0.05**

Adjusted R-squared: 0.294, Deviance explained 0.297

N: 26400

Adjusted R-squared: 0.351, Deviance explained 0.356

N: 23265

Std Error = Standard Error; edf = effective degree of freedom; Ref.edf = reference edf; N = number of observations

The SL in $GAM1_{SL}$ showed no significant relationship with temperatures by precipitation. Hour of day revealed a significant effect on SL, which increased by ~ 52 % during the night (10 pm – 4 am) as compared to the day (5 am – 9 pm). Additionally, SL changed with temperature across different hours of the day as indicated by the significant effect of the interaction between temperature and hour of the day. For example, at high temperatures (~ 30 °C) and precipitation absence, SL increased by 275 % from late afternoon (4 pm – 6 pm) to sunset (8 pm – 10 pm) and by 159 % at lower temperatures (15 °C). When precipitation was present, the increase of SL from late afternoon to sunset was 259 % at high temperatures and 126 % at lower temperatures.

4.2.2. Seasonal activity and step length patterns

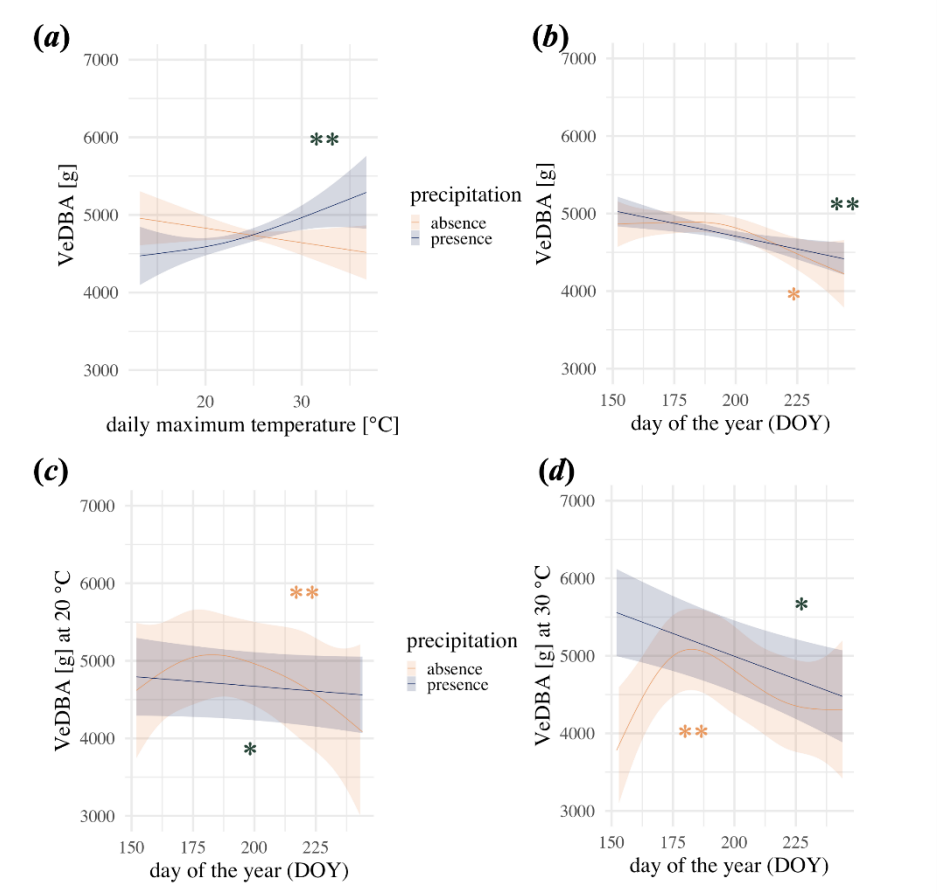

Figure 9: Effect of daily maximum temperature and day of the year on the daily average VeDBA. (a) & (b) show the main effects of temperature and time grouped by precipitation presence (blue) or absence (orange). (c) & (d) show the effect of time on the hourly sum of VeDBA at 20 °C and 30 °C. The lines visualise the model estimates, the shaded areas represent the model 95 % confidence intervals. Asterisks represent significance levels: *** < 0.001 < ** < 0.01 < * < 0.05.

In the next set of models of seasonal activity, I tested the effect of weather throughout the whole summer season using daily data (Table 4). In $GAM2_{VeDBA}$, VeDBA and daily maximum temperature showed a significant positive relationship when precipitation was present and a negative, yet insignificant relationship when precipitation was absent (Figure 9a). VeDBA significantly decreased throughout the summer season (June to August) regardless of precipitation (Figure 9b). The interaction between daily maximum temperature and DOY showed a significant effect with varying patterns based on precipitation presence or absence. When precipitation was absent and maximum temperatures were ~ 20 °C, VeDBA increased by 2 % from June to July but decreased by 10 % from July to August (Figure 9c). At daily maximum temperatures ~ 30 °C, the increase of VeDBA was 6 % from June to July, followed by a 10 % decrease from July to August (Figure 9d). When precipitation was present, VeDBA decreased linearly by 2 % from June to July and from July to August at daily maximum

temperatures ~ 20 °C (Figure 9c). At maximum temperatures ~ 30 °C, VeDBA also decreased linearly by 7 % from June to July and from July to August (Figure 9d).

Table 4: Detailed summary table of the generalised additive models used to detect the effects of maximum temperature and time. Response variables are VeDBA ($GAM2_{VeDBA}$) and SL ($GAM2_{SL}$). Predictors are precip = precipitation presence or absence, Tmax = daily maximum temperature, DOY = day of the year, and animalID = ID for each individual, added as a random effect. Smoothed terms are represented within s(), tensor interaction smooths within ti(). ":" indicates the factor interaction with precipitation (level of precipitation).

		$GAM2_{VeDBA}$					**$GAM2_{SL}$**				
Component	**Term**	**Estimate**	**Std Error**	**t-value**	**p-value**		**Estimate**	**Std Error**	**t-value**	**p-value**	
parametric coefficients	(Intercept)	4745.987	280.492	16.920	**0.0000**	***	176.934	11.053	16.008	**0.0000**	***
	precip_presence	97.540	70.324	1.387	0. 0.1657		-2.060	5.098	-0.404	0.6863	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**		**edf**	**Ref. df**	**F-value**	**p-value**	
smooth terms	s(Tmax): precip_absence	1.003	1.006	1.600	0.2064		1.001	1.001	0.001	0.9846	
	s(Tmax): precip_presence	1.563	1.945	6.065	**0.0058**	**	1.001	1.001	0.047	0.8300	
	s(DOY): precip_absence	2.190	2.691	3.192	**0.0252**	*	5.193	6.224	4.319	**0.0002**	***
	s(DOY): precip_presence	1.000	1.001	9.998	**0.0016**	**	2.141	2.622	3.520	**0.0178**	*
	ti(DOY,Tmax): precip_absence	7.391	9.152	2.419	**0.0098**	**	4.015	82.000	0.099	**0.0271**	*
	ti(DOY,Tmax): precip_presence	1.009	1.018	4.884	**0.0268**	*	18.387	126.000	0.282	**0.0063**	**
	s(animalID)	22.120	23.000	38.158	**0.0000**	***	17.614	19.000	20.017	**0.0000**	***

Signif. codes: 0 <= '*' < 0.001 < '**' < 0.01 < '*' < 0.05**

Adjusted R-squared: 0.482, Deviance explained 0.499

N: 1118

Adjusted R-squared: 0.417, Deviance explained 0.458

N: 715

Std Error = Standard Error; edf = effective degree of freedom; Ref.edf = reference edf; N = number of observations

$GAM2_{SL}$ showed slightly different significant effects. There was no significant relationship between SL and maximum temperature. SL was significantly influenced by DOY and the interaction of daily maximum temperature and DOY, independently of precipitation. SL increased throughout the summer season (June to August). At the same time, the effect of DOY on SL was influenced by the daily maximum temperature. From June to July, SL first increased by 2 % but then increased by 19 % from July to August when precipitation was absent and maximum temperatures were ~ 20 °C. At maximum temperatures ~ 30 °C, SL first decreased by 3 % from June to July and then increased by 20 % from July to August. This effect was different when precipitation was present, with SL decreasing by 2 % from June to July and increasing by 4 % from July to August at maximum temperatures ~ 20 °C. At daily maximum temperatures ~ 30 °C, SL increased linearly by 9 % from June to July and from July to August.

4.2.3. Heatwave activity and step length patterns

Table 5: Detailed results of the generalised linear mixed models used to examine the effect of heatwaves on wild boar activity. The response variables are VeDBA (GLM_{VeDBA}) and SL (GLM_{SL}) and predictor variables are indicated as precip = precipitation presence or absence, Heatwave length = number of days > 27.6 °C, and Tmax mean = mean daily maximum temperature within one heatwave. ":" = interaction term

	GLM_{VeDBA}			**GLM_{SL}**		
Predictors	**Estimates**	**CI**	**p-value**	**Estimates**	**CI**	**p-value**
(Intercept)	87.26	-14168.16 – 14342.69	0.990	4123.49	-2521.79 – 10768.77	0.224
Precip_presence	-24.82	-16146.76 – 16097.11	0.998	-3619.41	-10285.97 – 3047.15	0.287
Heatwave length	-358.96	-1626.67 – 908.76	0.579	390.12	-381.18 – 1161.42	0.322
Tmax mean	158.68	-323.25 – 640.61	0.519	-142.60	-385.51 – 100.30	0.250
Heatwave length: precip_presence	472.09	-821.05 – 1765.23	0.474	-400.05	-1171.66 – 371.56	0.310
Tmax mean:precip_presence	-9.84	-545.63 – 525.95	0.971	132.99	-110.47 – 376.45	0.284

CI = confidence intervals **Significance codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05**

Marginal R^2 / Conditional R^2 0.051 / 0.601 | Marginal R^2 / Conditional R^2 0.220 / 0.220

In the last part of the analysis, I investigated the effect of heatwave duration in interaction with precipitation on average daily wild boar body motion and travel movement (Table 5). There was no significant effect of heatwave length on VeDBA or SL, as well as no significant interaction of heatwave length with maximum daily temperature during the heatwaves.

4.3. Selection of sleep sites based on environmental conditions

Table 6: Summary table of the generalised linearised model predicting the effect of human disturbance in form of distance to different structures on wild boar sleeping sites. The predictors are added as main factors.

	$GLM1_{dist}$			
Predictors	**Log-Odds**	**CI**	**p-value**	
(Intercept)	-1.97	-2.32 – -1.62	**<0.001**	***
Distance to forest edge	0.12	-0.03 – 0.27	0.114	
Distance to paths	-0.08	-0.19 – 0.02	0.128	
Distance to roads	0.51	0.41 – 0.60	**<0.001**	***
Distance to buildings	-0.22	-0.38 – -0.06	**0.006**	**

CI = confidence intervals **Significance codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05**

Marginal R^2 / Conditional R^2 0.060/ 0.205

The first model ($GLM1_{dist}$) testing if sleep sites of wild boars are affected by human disturbance revealed a significant effect of the distance to roads and the distance to buildings (Table 6). According to the model, wild boars were most likely to select sleep sites farther away from roads (Figure 10a). For example, at a distance of 100 m to roads, the probability of the selection for a sleep site was ~ 7 %, whereas at a distance of 1000 m, the probability was at ~ 27 %. At the same time, wild boars were more likely to select sleep sites closer to buildings (Figure 10b), with a probability of ~ 24 % at a distance of 100 m and ~ 16 % at a distance of 1000 m. Although non-significant, wild boars showed a trend of selecting sleep sites farther away from the forest edge and closer to paths.

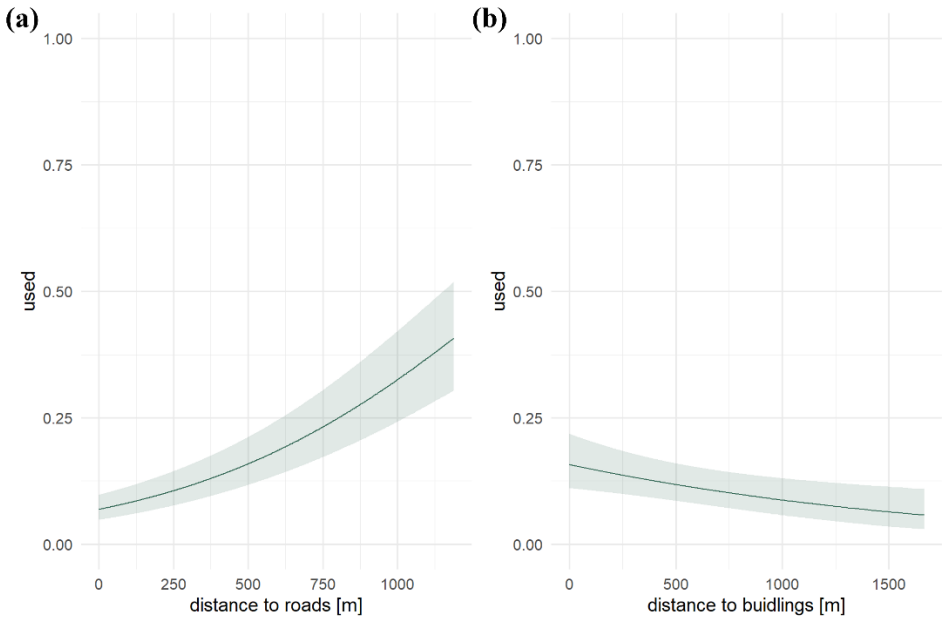

Figure 10: Effect of human disturbance (in form of distance to different structures) on wild boar sleeping site locations. (a) shows the effect of distance to roads and (b) shows the distance buildings. The lines visualise the model estimates, the shaded areas represent the model 95 % confidence intervals.

Table 7: Summary table of the generalised linearised model predicting the effect of habitat on wild boar sleeping sites. In the table, TCD stands for tree cover density, HLI stands for heat load index, TWI stands for topographic wetness index, and SRAI stands for solar radiation index. The predictors are added as main effects and as interaction terms marked with ":". Heatwave was added as a binomial factor, where "1" stands for within heatwave and "0" stands for outside of heatwaves.

	$GLM1_{hab}$			
Predictors	**Log-Odds**	**CI**	**p-value**	
(Intercept)	-1.13	-1.71 – -0.56	**<0.001**	***
heatwave	-1.05	-1.62 – -0.48	**<0.001**	***
TCD	-0.94	-1.30 – -0.57	**<0.001**	***
HLI	-0.09	-0.21 – 0.03	0.150	
TWI	-0.46	-0.64 – -0.29	**<0.001**	***
SRAI	0.06	-0.06 – 0.18	0.336	
Distance to rivers	-0.22	-0.37 – -0.06	**0.006**	**
Tree stand age	-0.66	-0.80 – -0.52	**<0.001**	***
slope	-0.23	-0.36 – -0.11	**<0.001**	***
Forest type	-0.09	-0.37 – 0.19	0.520	
HLI:heatwave	0.09	-0.15 – 0.34	0.468	
TWI:heatwave	-0.17	-0.58 – 0.24	0.424	
SRAI:heatwave	-0.11	-0.38 – 0.16	0.425	
Distance to rivers:heatwave	-0.09	-0.42 – 0.24	0.601	
Tree stand age:heatwave	-0.17	-0.48 – 0.14	0.287	
Slope:heatwave	0.30	0.04 – 0.55	**0.022**	*
Forest type:heatwave	1.10	0.49 – 1.72	**<0.001**	***

CI = confidence intervals

Significance codes: 0 <= '*' < 0.001 < '**' < 0.01 < '*' < 0.05**

Marginal R^2 / Conditional R^2
0.173 / 0.381

In the second model including habitat traits as the predictors ($GLM1_{hab}$), I found a significant effect of the tree cover density (TCD), heatwave, topographic wetness index (TWI), distance to rivers, tree stand age, and slope (Table 7, Figure 11). Additionally, the model revealed a significant effect of the interaction between slope and heatwave, as well as dominant tree type and heatwave. Here, the probability of wild boars' selection a sleep site was around 49 % at a tree cover density of 20 % and was 25 % at a TCD of 80 %. There was also a negative effect of the topographic wetness index. At a TWI of 5 (dryer), the probability for sleep site selection was 56 %, whereas at an index of 15 (wetter), the probability was 12 %. The probability of selecting a sleep site ~ 100 m away from a river was 36 %, whereas it was 25 % ~ 300 m away. Tree stand age also negatively affected the probability of selecting a sleep site, where sleep sites were selected with 54 % when within trees around 0-10 years of age. In older tree stands with an age between 90-100 years of age, the probability was 15 %. A slope of 1 % resulted into a

probability of sleep site selection of 36 %, whereas a slope of 10 % changed the probability to 28 %. This pattern was the same outside of heatwaves, where the probability was ~ 44 % at a slope of 1 %, and ~ 24 % at a slope of 10 %. During heatwaves, the probability of selecting a sleep site was nearly equal and even increased slightly on a higher slope (28 % at a slope of 1 % and 32 % at a slope of 10 %). Lastly, during heatwaves wild boars seemed to select more sleep sites within coniferous forest parts (36 % probability) as compared to deciduous forest (23 %), whereas it is almost equal outside of heatwaves (39 % in leafy forest and 37 % in coniferous forest).

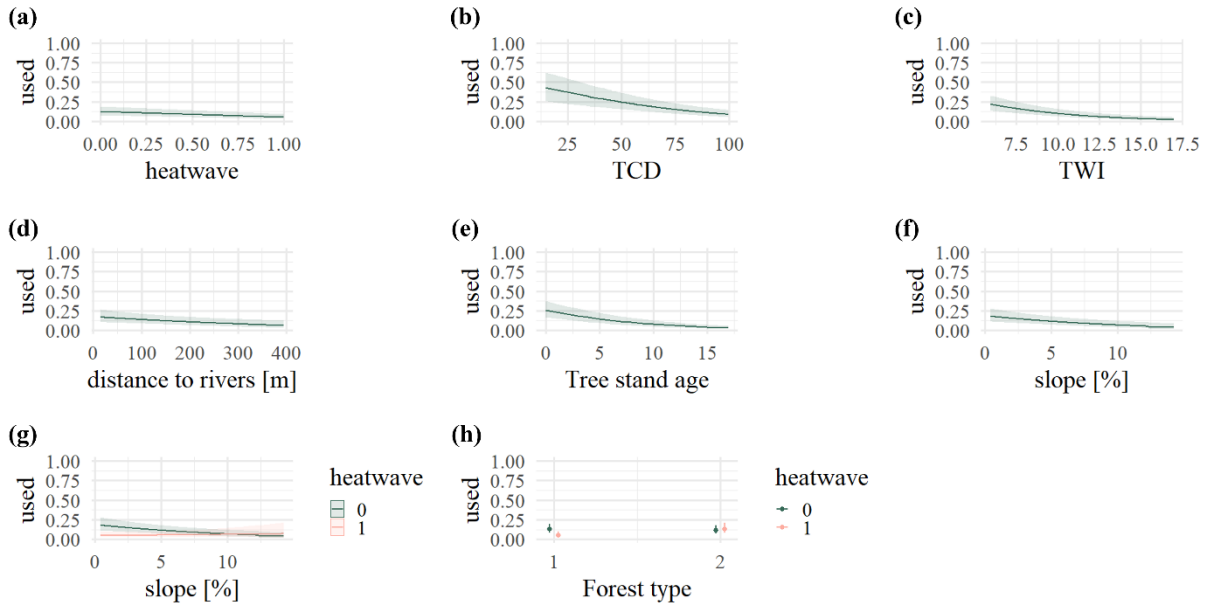

Figure 11: Effect of habitat characteristics on wild boar sleeping site locations. (a) shows the effect of heatwaves, (b) shows the effect of tree cover density, (c) shows the effect of topographic wetness index, (d) shows the distance to rivers, (e) shows the effect of tree stand age (summarised in classes from 0-15 representing the age in 10-year steps), (f) shows the effect of slope, (g) shows the interaction between slope and heatwave, and (h) shows the interaction between forest type and heatwave. "1" stands for within heatwave, while "0" stands for outside of heatwaves. Forest type of "1" corresponds to leafy trees and "2" corresponds to coniferous trees. The lines visualise the model estimates, the shaded areas represent the model 95 % confidence intervals.

Table 8: Summary table of the generalised linearised model predicting the effect of human disturbance in form of distance to different structures on revisitation of wild boar sleeping sites. The predictors are added as main effects.

	$GLM2_{dist}$		
Predictors	**Log-Mean**	**CI**	**p-value**
(Intercept)	-0.12	-0.65 – 0.41	0.659
Distance to forest edge	-0.04	-0.59 – 0.51	0.888
Distance to paths	0.08	-0.27 – 0.43	0.657
Distance to roads	0.07	-0.37 – 0.50	0.756
Distance to buildings	0.07	-0.49 – 0.63	0.812

CI = confidence intervals

Significance codes: 0 <= '*' < 0.001 < '**' < 0.01 < '*' < 0.05**

Marginal R^2 / Conditional R^2
0.006 / 0.321

Model 3 and Model 4 investigated how the revisitation of sleep sites is affected by human disturbance ($GLM2_{dist}$) and other habitat traits ($GLM2_{hab}$). In $GLM2_{dist}$, I found no significant effect of any human disturbance parameter (Table 8). However, in $GLM2_{hab}$ I found significant effects of the TWI, tree stand age, and slope (Table 9). Dryer areas with a TWI of 5 were visited more than wetter areas with a TWI of 15 (3.9 revisits compared to 0.3 revisits; Figure 12a). The revisitation was higher in younger tree stands, e.g., within trees between 11-20 years of age, sites were visited 3.6 times, whereas sites within trees between 101-110 years of age were visited 0.7 times (Figure 12b). Slope had a negative effect of the revisitation (Figure 12c). Sites at a slope of 1 % were revisited more than two times (e.g., 2.2 times), while sites at a slope of 10 % were not revisited (e.g., 0.5 times; Figure 12c).

Table 9: Summary table of the generalised linearised model predicting the effect of human disturbance in form of distance to different structures on revisitation of wild boar sleeping sites. In the table, TCD stands for tree cover density, HLI stands for heat load index, TWI stands for topographic wetness index, and SRAI stands for solar radiation index. The predictors are added as main effects.

	$GLM2_{hab}$			
Predictors	**Log-Odds**	**CI**	**p-value**	
(Intercept)	0.30	-0.64 – 1.25	0.527	
TCD	-1.00	-2.17 – 0.17	0.093	
HLI	0.07	-0.26 – 0.40	0.663	
TWI	-0.49	-0.92 – -0.05	**0.027**	*
SRAI	0.18	-0.17 – 0.53	0.304	
Distance to roads	-0.05	-0.43 – 0.34	0.813	
Tree stand age	-0.85	-1.25 – -0.44	**<0.001**	***
slope	-0.33	-0.63 – -0.03	**0.030**	*

CI = confidence intervals

Significance codes: 0 <= '*' < 0.001 < '**' < 0.01 < '*' < 0.05**

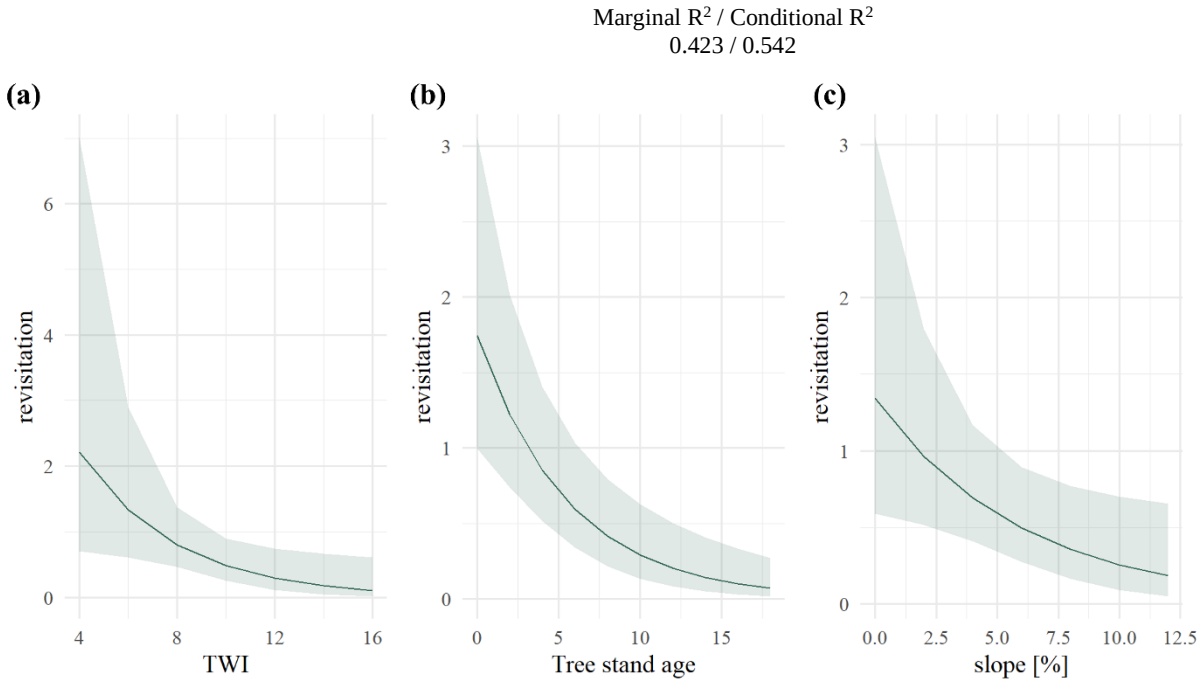

Figure 12: Effect of habitat characteristics on sleep site revisitations. (a) shows the effect of topographic wetness index, (b) shows the effect of tree stand age (summarised in classes from 0-15 representing the age in 10-year steps), and (c) shows the effect of slope. The lines visualise the model estimates, the shaded areas represent the model 95 % confidence intervals.

6. Discussion

6.1. Hormones

Stress hormones (GCs) are used as a marker for stress in various animals and experimental designs. GCs are responsible for energy release and suppression of processes not needed for immediate survival (e.g., digestion, growth, immune system) during a stressful event (Tryphonopoulos, Letourneau and Azar, 2014). However, it is important to first understand natural differences in cortisol concentrations across individuals, as well as between assays and type of hormone measured. I sampled blood and faeces of wild boars shot after driven hunts in Germany and the Czech Republic and investigated how age and sex influenced hormone concentrations. Blood cortisol was analysed using radioimmunoassay (RIA; Germany) and enzyme-immunoassay (EIA; Czech Republic). For the FCMs, I chose an EIA targeting 5α-pregnane-3ß,11ß,21-triol-20-one (Touma et al. 2003).

6.1.1. Correlation of blood cortisol and FCM concentrations

As expected, serum cortisol levels and FCMs in the Czech Republic did not correlate. FCMs are metabolised through the liver, excreted in the bile, and re-metabolised in the intestine (Taylor, 1971). The metabolism of hormones is influenced by various factors, including sex, diet, and intestinal microbiota, essentially changing the time until hormone metabolites can be found in faeces (Goymann, 2012). Since I took blood and faecal samples at the same time, FCMs are most likely to reflect cortisol concentrations from the day before. Additionally, I detected great individual variation in the cortisol and FCM concentrations in all samples, highlighting the effect of individual stage of life (e.g., metabolism, reproductive state, diseases).

6.1.2. Effects of hunting and natural factors

I assumed that acute GC concentrations naturally increase due to the hunts, which are likely to increase the magnitude of the stress reaction (Bradshaw and Bateson, 2000; Gentsch, Kjellander and Röken, 2018) and the connected increased vigilance and movement. GCs were previously found to be higher after hunts in wild boars (Gentsch, Kjellander and Röken, 2018) and during the hunting season in other ungulates (e.g., impala and greater kudu, (Hariohay *et al.*, 2023)). When compared to a study defining “trauma” and “normal” levels of wild boars (Gentsch, Kjellander and Röken, 2018), cortisol concentrations from Germany indeed showed a high percentage of trauma cortisol levels (54 %; (Güldenpfennig *et al.*, 2021)). However, I expected a larger percentage of trauma levels. Unfortunately, since I used a different assay with the Czech samples, I cannot directly compare the cortisol concentrations with the German samples.

Nonetheless, the general trends and differences between males and females in combination with age class are the same in both countries.

As expected, I found differences between sex and age classes, with females generally having higher serum cortisol levels (in both Germany and Czech Republic) and males having higher FCMs. Differences of cortisol levels between sexes were also found in several other species. In general, females were found to have a more pronounced stress response (Reeder and Kramer, 2005; Goel *et al.*, 2014). Literature suggests sex differences in reproduction as the main reason for differences in the HPA axis activation. Oestrogen was found to increase HPA function, whereas testosterone reduces it (Handa *et al.*, 1994). At the same time, females were found to be more affected by psychological and social stress (Goel *et al.*, 2014). Female wild boars live in social groups, consisting mostly of mothers with their offspring, while male wild boars leave the groups when reaching puberty (Kaminski *et al.*, 2005). Besides the benefits of association in female wild boar, costs like resource competition (Krause and Ruxton, 2002) could lead to specific social pressure, which resumes in higher cortisol concentrations in females, as well as in group living male piglets (juvenile males). The higher cortisol concentrations in females might be connected to the Energy Mobilization Hypothesis, which states that GC concentrations will be highest during energetically costly times of the year (Michael Romero, 2002). Driven hunts performed during winter overlap with the main gestation period in our study area. There is a high chance that most of the female wild boars sampled were pregnant, which is most likely connected to a high energetic cost. The possibility, that a female wild boar is pregnant, increases with age and weight (Rosell, Navas and Romero, 2012; Orłowska, Rembacz and Florek, 2013; Bergqvist, Paulson and Elmhagen, 2018). Therefore, the chance of pregnancy, combined with increased social stress, would explain the high cortisol concentrations in older females found in our study. However, I did not check for pregnancies during our sampling process. Additionally, only some studies showed that GCs are increasing during late pregnancy (e.g., in degus, (Bauer *et al.*, 2014); baboons, (Beehner *et al.*, 2006); rabbits, (Mulay, Giannopoulos and Solomon, 1973)), whereas other studies did not find the same effects (e.g., in sheep, (Brunet and Sebastian, 1991); cows, (Patel *et al.*, 1996)).

This leaves us with the question about why FCMs were higher in males, while blood cortisol was higher in females. Without directly comparing cortisol with FCM concentrations, I explained above why females might have a stronger cortisol release in response to a stressor. Increased cortisol metabolites in hair and faeces in males were also found, among others, in Egyptian mongoose (Azevedo *et al.*, 2019) and pine marten (Barja *et al.*, 2011). However, there

are also studies reporting no effect (e.g., Koalas, (Santamaria *et al.*, 2021)) or higher cortisol metabolites in female individuals (e.g., western quoll, (Robley *et al.*, 2010)). Since FCMs reflect the cortisol levels of the period before sampling, I assume that the FCM concentrations in our study actually reflect undisturbed basal GC levels. Following the Energy Mobilization Hypothesis, male wild boars might use more energy during fall and winter due to the breeding season/rut, consequently increasing basal GC levels. Male reproductive costs might include energy and nutrient demands associated with reproductive behaviour, like courtship behaviour and territorial defence. GCs in males were also found to increase during mating season in other species, e.g., numbats (Hogan *et al.*, 2012) and sea lions (Myers, Litz and Atkinson, 2010). At the same time, hormones are metabolised differently between sexes, including type of metabolites. (Goymann, 2012) explained that measuring a particular metabolite might only reflect the cross-reactivity of the assay antibody, but not the actual hormone level differences between the sexes.

Therefore, I suggest that females might have a stronger immediate reaction to a stressor (in this case the hunt) which can be measured with blood cortisol, while the actual level of FCMs will depend on season, type of metabolite, and type of assay used. Season was also deemed the most important factor influencing GC levels in various other studies (e.g., mountain gazelles, (Karaer *et al.*, 2024); muskoxen, (Di Francesco *et al.*, 2021)), but more species-specific research is needed.

6.2. Effects of heat on wild boar activity

Increased heat as a result of climate change might add as another stressor. Wild boar, same as domestic pigs, have reduced sweat glands and a thick layer of adipose tissue, likely making them susceptible to heat (Ruf *et al.*, 2023). I used multisensory collars to investigate if wild boars change their travel movement (measured using step length (SL)) and body motion (measured using VeDBA) in response to summer temperatures and precipitation. I found that step length and VeDBA showed a weak correlation, driven by the fact that dynamic body acceleration (DBA) captures even small-scale body motions (e.g., shaking of the head or body) that cannot be measured using GPS. Consequently, while VeDBA measurements revealed reduced activity during higher temperatures, SL measurements were not able to show the same. Temporal patterns in both SL and VeDBA within the season were distinct yet contrasting between both measurements. Neither of the metrics revealed a decrease in activity with the duration of heatwaves. The negative effect of high temperatures was always mitigated by rainfall.

6.2.1. Reduced activity at high temperatures without rain

When it did not rain, I observed that wild boars decreased their activity at high temperatures intra-daily and during higher daily maximum temperatures, but only when measured using VeDBA. At the same time, rain increased wild boar activity. This may highlight the importance of humidity for wild boar thermoregulatory behaviour. Wild boars lack sweat glands and have to rely on other mechanisms to use evaporative cooling, e.g., through wallowing (Bracke, 2011; Olczak, Nowicki and Klocek, 2015). Rain may wet the skin and provide wetter ground as well as water holes which would increase wallowing activity. Besides the increased activity caused by easier cooling of the body, the increased rolling and shaking caused by wallowing would also increase body motion. However, when it did not rain and it was dry, it seemed like wild boars reduced their physical activity to minimise the increase of body temperature and reduce resulting energy needed for thermoregulation (Terrien, Perret and Aujard, 2011). These short-term behaviours will not be picked up by travel data (hourly SL), explaining why I did not observe the same significant relationships in our models. Similar results about reduced activity in response to hotter days were also found in other species, for example greater kudu (Owen-Smith, 1998), mouflon (Bourgoin *et al.*, 2011), and African antelope (Berry, Dammhahn and Blaum, 2023).

The length of the heatwave and the average daily maximum temperature had no effect on the activity of wild boars. According to our definition, it appears plausible that during the heatwaves, there was sufficient temperature fluctuation, leading to cooler nights that counteracted the impact of warmer daytime temperatures. It appeared that wild boars could find enough water supplies and thermal shelter to lessen the effects of hotter times. Examining the outcomes of our initial model at the same time makes this clear. However, the limited number of defined heatwaves (n = 14) may prevent us from observing an effect. A lack of statistical power and precision may result from small sample sizes.

6.2.2. Temporal effects on activity interaction with the weather

Wild boars in our area showed a primarily nocturnal temporal pattern in both metrics. These results agree with those found in previous studies (e.g., Russo, Massei and Genov, 1997; Lemel, Truvé and Söderberg, 2003; Keuling, Stier and Roth, 2008b; Johann, Handschuh, Linderoth, Dormann, *et al.*, 2020; Gaudiano *et al.*, 2022). Although wild boar physiology makes us assume that they are not used to a nocturnal lifestyle, different explanations for this can be found in the

literature. One of the most supported hypotheses underscores the importance of human disturbance. Wild boars were found to demonstrate high behavioural plasticity in response to human pressure, for example changing their activity in response to hunting pressure (Podgórski *et al.*, 2013; Johann, Handschuh, Linderoth, Dormann, *et al.*, 2020). In our study area, hunting is performed as driven hunts in winter and single shooting during the remaining year. At the same time, there are a lot of people using the forest for recreational activities. I assume the nocturnal activity of our wild boars is an adaption to decades-long hunting pressure (Brivio *et al.*, 2017) and other human activity. While the overall activity was higher during the night than compared to the daylight, our data showed two activity peaks at dusk and dawn. This was more visible in VeDBA measurements than in SL. Since wild boars move from their resting sites to other areas of activity, it is most likely that the activity peak resulted from actual locomotion activity. The following short decrease of activity around midnight might be caused by feeding behaviour, since feeding behaviour is slower (Spitz and Janeau, 1990). DBA was found to increase with speed (Olsen, Dybkjær and Simonsen, 2001; Bidder *et al.*, 2012) suggesting higher VeDBA during travel movement than during feeding/rooting movement. Our results also showed a higher VeDBA activity peak at sunset when temperatures were high than compared to lower temperatures. This might be caused by a combination of decreasing temperatures after sunset, the search for water sources, feeding activity, and the time available for activity due to short nights. Wild boars are likely to maximise the efforts of their active phase while minimising the duration of movement, essentially increasing their activity for a shorter period than on milder nights. An increase of nocturnal activity in response to higher temperatures were previously described in wild boars (Brivio *et al.*, 2017), as well as ibex (Brivio *et al.*, 2024), free-ranging sheep (Leu *et al.*, 2021), and reindeer (Trondrud *et al.*, 2023).

I also observed a contrasting seasonal temporal pattern in body motion (VeDBA) and travel movement (SL). Whereas wild boars decreased their body motion from June to August, SL increased throughout the summer. It seems possible that this be related to the nature of the metrics used. Besides the increase in DBA with speed, higher energy expenditure was also linked to rapid turning in an animal's track (Wilson *et al.*, 2013). This leads us to believe that continuous, straight, and slow travel movement will result in lower VeDBA and longer SL, whereas fast travel with rapid turnings will result in higher VeDBA, but shorter SL. It is difficult to explain why wild boars changed from short bursts of activity at the beginning of summer to long and slow movement at the end of the summer. One possible explanation draws a connection to the harvest of crop fields, which started mid-July. When enough shelter is

provided, it was observed that wild boars preferred crop fields as all-day habitat in summer (Keuling, Stier and Roth, 2009). Hence, it may be possible that the harvest in July caused a loss of shelter (especially at higher temperatures) and confinement to the forest habitat, explaining the shift in overall wild boar activity. At the same time, the change of habitat also results in a change of substrate animals move on. It was shown that more mechanical work is needed to walk on softer substrate like sand (Lejeune, Willems and Heglund, 1998), which consequently reflects in higher DBA (Gleiss, Wilson and Shepard, 2011; Bidder, Qasem and Wilson, 2012). Another factor might be a change of foraging behaviour between the two habitats. While foraging in forest habitat might result in longer travel distances between food patches and resting sites, food is available everywhere within the crop fields without the need of travel. All these factors (change of habitat, substrate, and increased travel movement while foraging) might explain the observed increase of SL and decrease of VeDBA. On top of this, I observed distinct seasonal patterns of VeDBA and SL in interaction with daily maximum temperature. For example, at higher daily maximum temperatures (around 30 °C) and no rain, wild boars first increased their body motion (VeDBA) from June to July but then decreased the motion from July to August, whereas travel movement (SL) first decreased from June to July and then increased in August. This pattern differed when it rained. Again, it seems to highlight the importance of rain on thermoregulation in wild boars as well as their behavioural plasticity in response to different environmental stressors. However, at the moment I lack further information about the exact behaviour explaining the differences between VeDBA and SL. This should be a priority during future research.

6.3. Selection of sleep sites based on environmental conditions

Sleep is fundamental for animal health and well-being, with the selection of optimal sleeping locations being crucial for minimizing disturbance and ensuring physiological recovery (Mortlock *et al.*, 2024). Wild boars are regarded as a very successful and resilient species, based on traits like opportunistic feeding (Massei and Genov, 2004) and high reproductive rate (Mauget, 1982; Gethöffer, Sodeikat and Pohlmeyer, 2007; Lutz Briedermann, 2009). They are tolerant to human disturbance (Podgórski *et al.*, 2013) and able to adapt to a wide range of habitats. At the same time, wild boars have to rely on behavioural thermoregulation to mitigate the heat during summer (Bracke, 2011; Olczak, Nowicki and Klocek, 2015).

In this study, I investigated wild boar sleep site selection in a suburban forest during summer, assessing the influence of human disturbance and microclimatic habitat traits. I hypothesised

that wild boars would select sleep sites with less human disturbance and more favourable climatic conditions, especially during heatwaves.

6.3.1. Human disturbance and sleep site selection

Our first set of models revealed that wild boars selected sleep sites farther away from roads but, interestingly, closer to buildings. These results are in contradiction to results found in a similar study, where no effect of proximity to villages or roads during the non-hunting season was found (Fradin and Chamaillé-Jammes, 2023). The revisitation of sleep sites in our study was not affected by human disturbance. The suburban nature of our study area – a forest surrounded by settlements and in close proximity to Prague – implies consistently high levels of human activity (Olejarz *et al.*, 2023). Given this context, wild boars in our study area may be well habituated to human presence, displaying behavioural tolerance rather than avoidance. Nonetheless, sleep sites were selected in quieter areas away from roads or paths. In ecosystems lacking natural predators, such as the wolf, humans may represent the primary perceived threat (Cristescu, Stenhouse and Boyce, 2013; Keuling *et al.*, 2013). The preference for locations away from roads may therefore reflect anti-predation behaviour directed towards humans. However, the proximity to buildings seems counterintuitive to this interpretation. Possible factors influencing this choice could be reduced human disturbance around the specific buildings during the day, potential thermal buffering, or perhaps easier access to food resources nearby.

6.3.2. Microclimatic and habitat effects

In the second part of our analysis, I investigated the influence of various microclimatic variables on sleep site selection in interaction with heatwaves. I found that wild boars preferred sleep sites with less tree cover density, lower wetness index (dryer areas), closer to rivers, and within younger tree stands. Similarly, revisitation was higher in dryer areas and within younger tree stands.

Wild boars in our study area were primarily nocturnal and slept during the day (Mortlock *et al.*, 2024). Previous studies in wild boars found that they are more likely to select areas with dense vegetation cover that reduce visibility to protect against disturbance (Dardaillon, 1986; Saïd *et al.*, 2012; Fradin and Chamaillé-Jammes, 2023). This has also been found in other wildlife species, e.g., roe deer (Mysterud, 1996), red deer (Adrados *et al.*, 2008), lynx (Podgórski *et al.*, 2008), and wolves (Bojarska *et al.*, 2021). Our results suggest that wild boars preferred areas with lower tree cover density. I interpret this as an indirect indicator of denser understorey

vegetation. Tree cover density measures the percentage of canopy cover over an area. Lower overstorey cover is connected to higher understorey cover (De Lombaerde *et al.*, 2019) and could be connected to more open forest habitat in areas with more dense tree canopies. It is possible, therefore, that wild boars preferred areas with lower TCD because there was more understorey and shrubs available. This interpretation is further supported by our finding that wild boars preferred younger tree stands – typically characterised by dense vegetation and limited visibility. Personal field observations also confirm that sleep sites were located within coniferous tree schools, highlighting the importance of cover for concealment.

Beyond visibility, vegetation cover also plays a critical role in thermoregulation (Germaine, Germaine and Boe, 2004; Aubry *et al.*, 2013). Both forest density and tree composition play an important role in understorey temperatures, although the buffering effect of forest density might be larger than the number of broadleaf trees (Díaz-Calafat *et al.*, 2023). Our findings indicated that wild boars selected more sleep sites within coniferous trees during heatwaves, which could indicate that they prioritise favourable cooling properties in extreme conditions. At the same time, denser understorey could provide wild boars with higher visibility cover.

In addition to seeking thermal refuge in dense vegetation, access to water sources is another critical component of wild boar thermoregulation. The closer proximity to rivers might stem from the need for evaporative cooling as well as fresh-water supply for drinking in the summer. Female wild boars were found to build their nests in locations with abundant plant cover and nearby water (Fernández-Llario, 2004). This preference for closer proximity to rivers might stem from the need for evaporative cooling and fresh-water supply during summer. This contrasts with observations by Stillfried et al., 2017, who found rural wild boars selected areas farther from water bodies but aligns with their findings for urban wild boars. Given our study area's suburban nature, characterized by surrounding human settlements and constant recreational activity, it is plausible that our wild boar population exhibits behavioural adaptations similar to urban populations, including increased tolerance to human presence near water sources.

6.3.3. Terrain characteristics and revisitation

Lastly, I found that wild boars selected and revisited sleep sites located on more even terrain. Such areas may offer a certain level of comfort and security, often corresponding to denser understorey or tree schools that provide visibility cover. In contrast, steep areas typically have less vegetation that can count as cover. However, other studies have found a selection of steeper

slopes for resting (e.g., black-tailed deer (Bose *et al.*, 2018); female red deer (Adrados *et al.*, 2008)) as a form of protection against predators. Since I do not have natural predators of wild boars in our study area, I believe that our wild boar population is not in need of such an anti-predator strategy.

In summary, our study reveals that while wild boars in this suburban environment demonstrate specific responses to human disturbance (e.g., avoiding roads but accepting proximity to buildings), the selection and revisitation of sleep sites were predominantly driven by microhabitat traits such as tree stand age, wetness index, and slope. These patterns highlight the critical importance of vegetation cover for wild boars during diurnal rest periods, serving dual roles in providing both visibility protection and essential thermal buffering, particularly during heatwaves. Since wild boars count as invasive in some areas, knowledge about their habitat selection, especially their sleep site selection, might help with implementing efficient management strategies. While maintaining shrubs and understorey for daytime resting habitat helps with keeping animals in an area (Bojarska *et al.*, 2021), removing those could help reducing wild boar presence in other areas.

8. Conclusions

In this thesis, I investigated the stress reactivity of free-roaming wild boars in response to different anthropogenic and environmental pressures. By integrating traditional hormonal analyses with novel behavioural indicators, my research aimed to provide a comprehensive understanding of their adaptive mechanisms and the challenges they face in human-dominated landscapes. This understanding is crucial for effective wildlife management, animal welfare considerations, and biodiversity conservation in a rapidly changing world. All objectives of this thesis were met.

My research highlights the remarkable adaptive capacity of wild boars yet also showcases the physiological and behavioural costs associated with persistent stressors. The thesis described several key insights:

- **Hormonal responses to stress:** The analysis of "stress hormones" revealed significant individual variability in cortisol and faecal cortisol metabolite (FCM) concentrations. Serum cortisol levels were generally higher in females in response to hunting across both study areas, while basal FCMs were higher in males. This divergence suggests a stronger acute stress response in females, potentially linked to reproductive costs and social pressures within their social groups. This aligns with the Energy Mobilization Hypothesis (Michael Romero, 2002). Conversely, the higher FCMs in males might reflect increased energetic demands during the breeding season. The lack of correlation between serum cortisol and FCMs, coupled with the influence of factors such as sex, age, diet, and microbiota on hormone metabolism emphasises the complexity of interpreting stress biomarkers in wild populations. My work supports the critical need for species-specific validation and careful consideration of confounding factors when using glucocorticoids as stress markers.
- **Behavioural and activity adjustments to environmental heat:** I utilised advanced accelerometery data (VeDBA) and GPS-derived step length to demonstrate that wild boars significantly alter their activity patterns in response to ambient temperatures and precipitation. During periods of high temperatures and absent precipitation, wild boars reduced their body motion both intra-daily and seasonally, suggesting a strategy to conserve energy and minimize thermoregulatory stress. The mitigating effect of precipitation, likely facilitating wallowing and evaporative cooling, allowed for increased activity even in warm conditions. While VeDBA and step length showed a weak correlation, highlighting the ability of VeDBA to capture fine-scale movements,

both metrics showed opposing changes throughout the summer season. The specific behavioural mechanisms underlying the opposing patterns between VeDBA and step length remain to be clarified and offer exciting opportunity for future research. The behavioural plasticity, including a predominantly nocturnal pattern, further illustrates their adaption to both climate stressors, such as temperature, and human disturbance, such as hunting pressure and recreational activities. It remains to be seen, for how long wild boars will be able to cope with heat stress.

- **Selection and revisitation of sleep sites:** Using GPS locations of free-ranging wild boars in a suburban forest, I described how wild boars strategically select and revisit sleep siters based on environmental conditions and human disturbance. Sites further from roads but closer to buildings were preferred. This indicates an adaptive response to minimize human threat, despite the wild boar's general tolerance to human presence in suburban environments. Furthermore, sleep site selection was influenced by habitat traits such as lower tree cover density (suggesting a preference for undergrowth/shrubs for concealment), lower topographic wetness index, proximity to rivers, and younger tree stands. During heatwaves, a notable shift towards coniferous forests was observed, indicating a trade-off between visibility cover and thermal buffering capacity. Revisitation patterns echoed these preferences, with dryer areas and younger tree stands being frequented more often.

This research attempts to highlight the need of employing a multi-indicator approach in wildlife stress research, that covers physiological and behavioural metrics for an integrated understanding of an animal's state. The observed behavioural plasticity of wild boars in the face of changing anthropogenic and environmental stressors provides valuable insights into how resilient species adapt to rapidly changing environments. Methodologically, the detailed insights gathered from accelerometery data highlight the need of its broader adoption in ecological studies to capture subtle yet significant behavioural adjustments.

While my thesis might improve our understanding, certain limitations must be considered. The inability to directly compare cortisol values across different assays and the susceptibility of being influenced by factors outside of our control highlights challenges in hormonal interpretation. Future research should prioritise clarifying the precise physiological, behavioural and environmental components contributing to hormonal variation while continuously developing more advanced methodologies and comprehensive concepts of stress measurement in free-ranging animals.

At the same time, the observed adaptions to heat stress raise questions about the long-term sustainability of these strategies under accelerating climate change. Continuous monitoring and predictive modelling are essential to project the impacts of rising temperatures (and possibly more extreme weather changes) on animal populations. With regard to the wild boar, such studies could reveal a shift in the limiting season for population growth and geographical spread, with significant implications for management and conservation.

In practice, the findings of this thesis highlight the importance of integrating behavioural and physiological indicators into wildlife management to better assess and mitigate stress in free-ranging species. This means adopting multi-indicator monitoring approaches that combine non-invasive hormone sampling with fine-scale movement data to obtain a comprehensive view of animal welfare. Management strategies should prioritise the maintenance of key habitat features that buffer stress, such as dense undergrowth, access to water, and thermal refuges, while limiting anthropogenic disturbances during critical periods such as reproduction or prolonged heat events. The demonstrated heat sensitivity of wild boars further highlights the need to incorporate climate adaption measures – ensuring availability of cooling opportunities and monitoring behavioural shifts as early warning signals of thermal stress. Finally, fostering long-term, standardised monitoring programs that link physiological and behavioural responses to environmental change will be crucial for evidence-based management and the conversation of resilient wildlife populations in increasingly human-dominated landscapes.

9. Literature

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Appendix

List of Articles

Primary

Güldenpfennig Justine, Schmicke Marion, Hoedemaker Martina, Siebert Urusla, Keuling Oliver (2021) ‘An approach to assess stress in response to drive hunts using cortisol levels of wild boar (*Sus scrofa*)’, *Sci Rep* 11, 1638. https://doi.org/10.1038/s41598-021-95927-2

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Secondary

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Appendix

Appendix

Literature search strategy

Database	Search Query
Web of Science	TS=("free ranging animal*" OR wildlife OR “wild life”)) AND (TS=(stress* OR cortisol OR glucocorticoid* OR FCM OR FGM)) AND (TS=("animal welfare" OR "movement pattern*" OR "reproduct*" OR "disease transmission" OR "host parasite dynamic*" OR "physiological disorder*" OR behavio*r OR fitness OR adaptation OR resilience OR age OR sex)) AND (ALL=(mammal* OR "wild boar" OR "Sus scrofa" OR ungulate* OR herbivore* OR carnivore* OR primate* OR rodent* OR bat* OR cetacean* OR "large carnivore*" OR "large herbivore*")) NOT (ALL=(bird* OR avian OR reptile* OR amphibian* OR fish OR insect* OR invertebrate*))
PubMed	("free ranging animal*"[tiab] OR wildlife[tiab] OR "wild life"[tiab]) AND ("stress *"[tiab] OR cortisol[tiab] OR glucocorticoid*[tiab] OR FCM[tiab] OR FGM[tiab] OR "Stress, Physiological"[Mesh] OR "Cortisol"[Mesh] OR "Glucocorticoids"[Mesh]) AND ("animal welfare"[tiab] OR "movement pattern*"[tiab] OR reproduct*[tiab] OR "disease transmission"[tiab] OR "host parasite dynamic*"[tiab] OR "physiological disorder*"[tiab] OR behavio*r[tiab] OR fitness[tiab] OR adaptation[tiab] OR resilience[tiab] OR age[tiab] OR sex[tiab] OR "Animal Welfare"[Mesh] OR "Reproduction"[Mesh] OR "Disease Transmission"[Mesh] OR "Biodiversity"[Mesh] OR "Population Dynamics"[Mesh]) AND (mammal*[tiab] OR mammalian[tiab] OR "wild boar"[tiab] OR "Sus scrofa"[tiab] OR ungulate*[tiab] OR herbivore*[tiab] OR carnivore*[tiab] OR

	primate*[tiab] OR rodent*[tiab] OR bat*[tiab] OR cetacean*[tiab] OR "large carnivore*"[tiab] OR "large herbivore*"[tiab] OR "Mammals"[Mesh]) NOT (bird*[tiab] OR avian[tiab] OR reptile*[tiab] OR amphibian*[tiab] OR fish[tiab] OR insect*[tiab] OR invertebrate*[tiab] OR "Birds"[Mesh] OR "Reptiles"[Mesh] OR "Amphibians"[Mesh] OR "Fishes"[Mesh] OR "Insects"[Mesh] OR "Invertebrates"[Mesh])
Scopus	(TITLE-ABS-KEY("free ranging animal*") OR TITLE-ABS-KEY(wildlife) OR TITLE-ABS-KEY("wild life")) AND (TITLE-ABS-KEY(stress*) OR TITLE-ABS-KEY(cortisol) OR TITLE-ABS-KEY(glucocorticoid*) OR TITLE-ABS-KEY(FCM) OR TITLE-ABS-KEY(FGM)) AND (TITLE-ABS-KEY("animal welfare") OR TITLE-ABS-KEY("movement pattern*") OR TITLE-ABS-KEY(reproduct*) OR TITLE-ABS-KEY("disease transmission") OR TITLE-ABS-KEY("host parasite dynamic*") OR TITLE-ABS-KEY("physiological disorder*") OR TITLE-ABS-KEY(behavio*r) OR TITLE-ABS-KEY(fitness) OR TITLE-ABS-KEY(adaptation) OR TITLE-ABS-KEY(resilience) OR TITLE-ABS-KEY(age) OR TITLE-ABS-KEY(sex)) AND (TITLE-ABS-KEY(mammal*) OR TITLE-ABS-KEY(mammalian) OR TITLE-ABS-KEY("wild boar") OR TITLE-ABS-KEY("Sus scrofa") OR TITLE-ABS-KEY(ungulate*) OR TITLE-ABS-KEY(herbivore*) OR TITLE-ABS-KEY(carnivore*) OR TITLE-ABS-KEY(primate*) OR TITLE-ABS-KEY(rodent*) OR TITLE-ABS-KEY(bat*) OR TITLE-ABS-KEY(cetacean*) OR TITLE-ABS-KEY("large carnivore*") OR TITLE-ABS-KEY("large herbivore*")) AND NOT (TITLE-ABS-KEY(bird*) OR TITLE-ABS-KEY(avian) OR TITLE-ABS-KEY(reptile*) OR TITLE-ABS-KEY(amphibian*) OR TITLE-ABS-

	KEY(fish) OR TITLE-ABS-KEY(insect*) OR TITLE-ABS-KEY(invertebrate*))