# The effects of hunting and landscape structure on wild boar behavior, social structure and physiology in urban, agricultural and natural areas in Israel

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A THESIS SUBMITTED FOR THE DEGREE

“DOCTOR OF PHILOSOPHY”

Dissertation by Publications

University of Haifa

Faculty of Natural Sciences

Department of Evolutionary and Environment Biology

August 2021

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The contributions of the collaborators in each of the chapters are:

### Chapter 1: General introduction

This chapter was written by Achiad Davidson under the academic supervision of Uri Shanas and Dan Malkinson.

### Chapter 2: Wild boars' foraging and risk perception — variation among urban, natural and agricultural areas

Conceived, designed and performed the research: Achiad Davidson (supervised by Uri Shanas and Dan Malkinson). Analyzed the data: Achiad Davidson (supervised by Uri Shanas and Dan Malkinson). Wrote the paper: Achiad Davidson (supervised by Uri Shanas and Dan Malkinson). All authors read and approved the paper.

### Chapter 3: Age and sex-dependent vigilance behavior modifies social structure of hunted wild boar populations

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### Chapter 4: Do boars compensate hunting with higher reproductive hormones?

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### Chapter 5: General discussion

This chapter was written by Achiad Davidson under the academic supervision of Uri Shanas and Dan Malkinson.

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Achiad Davidson

## Abstract

In recent decades human populations have increased substantially and expanded in urban and rural areas, resulting in increased human-wildlife conflicts. Concomitantly, wild boar (*Sus scrofa*) populations have increased in the last 40 years worldwide, particularly in the vicinity of agricultural and urban areas. The consequences of these population increases include elevated economic costs resulting from boars transferring epidemics to livestock and humans and damage to gardens in urban areas and agricultural crops. For instance, the estimated annual costs of damage to agriculture by wild boars in Europe is €80,000,000. The most common and wide spread management tool that is used in attempts to control wild boar population increases is culling. It has been recently estimated in Europe that more than 3 million wild boars are hunted yearly. However, despite the high hunting pressure, the number of wild boars continues to grow. Recent studies demonstrated that high hunting pressure causes juvenile females to reproduce earlier, resulting in shorter generation times, leading to higher reproduction rates. This cause and effect may be one of the main reasons for the rapid population growth of wild boar populations.

This study attempts to compare and evaluate the effects of hunting on wild boars behavior, social structure and physiology in four different land uses in the Carmel region in northern Israel: urban areas with and without hunting, agriculture areas with high hunting pressure and nature reserves with no hunting.

To study the risk perception of wild boars while foraging I evaluated the combined effects of hunting and different land-use types on their behavior. I installed corn-supplemented feeding devices in four land-use types – hunting combinations: urban areas with and without hunting, and rural areas, namely agricultural areas with hunting, and nature reserves without hunting. The results show that boars in agricultural areas, which are exposed to high hunting pressure, showed significantly higher risk perception and reduced foraging compared to boars in nature reserves. However, surprisingly, the results further suggested that wild boars in urban areas perceive substantially lower risk of predation regardless of hunting activities while foraging, compared to wild boars in rural areas (nature reserves and agriculture).

To further understand the risk perception of wild boars in rural areas and to account also for their social structure, I installed motion-triggered cameras along movement trails. I identified the age and sex of individual wild boars and the size and structure of their social groups, and quantified hunting intensity in agricultural areas (hunting permitted) and nature reserves (hunting prohibited). Results indicated significant differences in the vigilant behaviour of wild boars between agricultural areas and nature reserves. In agricultural areas, adult females were significantly more vigilant compared to adult males. Additionally, in these areas we found significantly more adult males and less family groups with females. Furthermore, male yearlings were significantly more vigilant in agricultural areas compared to female yearlings. Male yearlings tended to roam significantly more with family groups in agricultural areas compared to nature reserves, where they tended to roam alone or in groups.

To explore the physiological effects of hunting, I compared steroid hormone levels in the hair of female wild boars from populations exposed to high hunting pressure with those exposed to substantially lower hunting pressure. Furthermore, I tested steroid hormone levels from hair of female wild boars roaming alone or as part of a group. I found no hormonal signs for stress in the hunted boars. Cortisol levels were low in both high and low hunting groups. Yet, progesterone levels were higher in females that were exposed to high hunting pressure. Additionally, females roaming in a group also had higher progesterone levels compared to females roaming alone.

In conclusion, this study presents evidence that increased predation risk, caused by human hunting, leads to: higher risk perception (e.g. increased vigilance behavior and reduced foraging), variations in social structure and higher reproductive hormones in rural wild boar populations. The results further suggested that urban boars show significantly lower risk perception compared to rural boars possibly due to habituation of urban boars to humane presence. Moreover, these results provide evidence that high hunting pressure causes significant changes to the behavior and social structure of wild boars, however it does not cause chronic stress, but positively impacts a reproductive hormone in female wild boars. This response may be one of the reasons leading to the worldwide rapid population growth of wild boars, despite the high hunting pressure they are exposed to, and provides a better understanding of the biology of wild boars.

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# Chapter 1

## General Introduction

Human–wildlife conflicts are defined as actions, by wildlife or humans that have negative effects on the other; these include actual threats posed by wildlife to human life or economic resources, and the perception that wildlife threatens human safety, property, or food (Nyhus, 2016). Examples for such interactions include among others, vehicle collisions (Gunson et al., 2011), agricultural crops damages (Conover et al., 2018), and wildlife loss (Mateo-Tomás et al., 2012). The conflict between wildlife and humans has been manifested in human – wild boar (*Sus scrofa*) interactions, and has been in the center of both public and scientific research lately. During the past 40 years, wild boars expanded their populations world-wide and increased their over-all geographic distribution range as well as their population densities in many areas within their range (Marsan et al., 1995; Ueda and Kanzaki, 2005; Apollonio et al., 2010). This population increases and invasions of new areas have resulted in high economic costs, including high risk of epidemics transfer to livestock and people, vehicle collisions, reduction in plant and animal abundance and richness, but mostly increased damages to urban gardens/infrastructure and agricultural crops (Schley and Roper, 2003; Genov and Massei, 2004; Massei et al., 2011; Barrios-Garcia and Ballari, 2012; Thurfjell et al., 2015). For instance, the estimated annual costs of damage to agriculture by wild boars in Europe is €80,000,000 (Apollonio et al., 2010) .

Culling is the most common and widespread management tool applied throughout the world in attempts to minimize the conflict with wild boars in urban and agricultural areas (Toigo et al., 2008; Gamelon et al., 2011; Keuling et al., 2013). The number of wild boars harvested has consistently increased over the past few decades worldwide (Massei et al., 2015). For instance, Linnell et al. (2020) estimate that more than 3 million wild boars are hunted every year in European countries. Massei et al. (2015) estimate that approximately 20% of the European wild boars are hunted annually. Thus, despite the high hunting pressure they are exposed to, the number of wild boars is on a constant rise. The high mean annual hunting index of wild boar populations together with the high hunting pressure that they are subjected to makes them an excellent species to explore how hunting may affect the behavior, social structure and physiology of a wild mammal.

### Wild boars biology

Wild boars are a long-lived species. They may live up to ten years in nature and twenty years in captivity, and they are characterized by the highest reproductive rate among ungulates, with annual increases in population that may exceed 100% (Bieber and Ruf, 2005). Wild boars are commonly found in a wide variety of habitats and climatic conditions, ranging from semiarid lands to tropical forests, mountains, and marshes. This species is one of the most widely distributed large mammals in the world and the most widely distributed ungulate in the world. The natural range of the species extends from Eastern Russia, Japan and Southeast Asia to Western Europe and the Mediterranean basin (Massei and Genov, 2004). In some European countries where they have been locally extirpated, their populations have been re-established (UK, Denmark, Sweden, Estonia and Finland; Apollonio et al., 2010; Linnell et al., 2020).

Wild boars are opportunistic omnivores, feeding on all types of organic matter (Ballari and Barrios-García, 2014). Their diet is comprised mainly of plant material (~ 90%) such as roots, acorns, nuts, green plant material and agricultural crops. The rest of their diet consists of fungi and animals, such as worms, snails, arthropods, fish, birds, bird eggs and also small mammals and carcasses (Giménez-Anaya et al., 2008). However, as monogastrics, wild boars have a limited capacity for digesting cellulose, and their survival and reproductive output depend on the availability of high-energy food, such as acorns in natural areas and cereals, corn, olives and nuts in agricultural areas (Massei et al., 1996). Due to their habit of rooting for food, wild boars cannot survive in areas where droughts harden the soil or snow cover persists for several consecutive weeks (Massei et al., 2011).

The body structure of the wild boars is well adapted for running. It is covered with hard hair and a thick skin, which protect them when penetrating into the dense bush. Its body length reaches up to 180 cm, its height is 102-30 cm at shoulder height and adults usually weigh 50-200 kg. Males are larger than females, their bodies are longer and they weigh more. The fur is of brown-gray-black colors. Pregnancy lasts 115 days and piglets are usually calved during spring (March-June). Piglets are born striped with alternating brown and yellow longitudinal stripes, which gradually fade and disappear completely at the age of four months. The number of piglets in a litter usually ranges from three to eight. Piglets nurse usually for about 3-4 month. However, beginning at the age of two weeks, the piglets are able to eat solid food and join their mother in her search for food (Mendelson and Yom-tov, 1987). Reproductive success is mainly determined by basic environmental factors such as food availability. Wild boar females have to reach a threshold body mass of 27–33 kg before breeding for the first time.

This threshold body mass is relatively low (33–41% of adult body mass) compared to that reported in most other ungulates, which is about 80% (Servanty et al., 2009).

The home range of wild boar adult females ranges from 2 to 6 km$^2$, while the home range of males is larger and stands at 10-20- km$^2$ (Boitani et al., 1994). After parturition, females restrict their movement to smaller areas near the parturition site, and isolate themselves from the rest of the females herd for one to two weeks (Morelle et al., 2015). During this period, the females move less and reach only a small number of resting sites. These resting sites are surrounded by patches that maximize the safety of the mother and the piglets and the availability of resources, thus helping to increase the probability of success in raising the piglets (Morelle et al., 2015). However, lactation increases the energetic requirements of the females, thus they devote much time for foraging activities (Russo et al., 1997). The females gradually increase their movement range along with the age of the piglets (Morelle et al., 2015). Except for differences between males and females, home ranges may differ also due to differences in the age, group size and habitat characteristics like vegetation density and hunting. The home range is usually smaller when food availability is high. When environmental conditions change or when the food sources decline, wild boars increase the number of visits to sites that have high-energy food sources, and increase their movement rates within their home range, in order to acquire more food to meet their basic energetic needs (Boitani et al., 1994; Morelle et al., 2015).

In natural and undisturbed habitats, the social structure of the wild boar includes several closely related philopatric females (Kaminski et al., 2005; Truve and Lemel, 2003) with piglets and yearlings, ranging from 6 to 30 individuals (Boitani et al., 1994; Kaminski et al., 2005). The female groups mostly depend on the leading sows to facilitate group cohesion (Sodeikat and Pohlmeyer, 2003). Males congregate with females in autumn, during the rut period, establishing large mixed groups (Cousse et al., 1994; Fernandez-Llario et al., 1996; Kaminski et al., 2005). As piglets grow, the mother-piglet bonds loosen and piglets become increasingly independent (Cousse et al., 1994; Kaminski et al., 2005). Most female yearlings stay within their natal home range and often with their mother's group (Kaminski et al., 2005; Nakatani and Ono, 1995). In contrast, male yearlings usually disperse, roughly between the age of 8 to 14 months, starting in autumn, during the mating season, when adult males join the family groups (Truve and Lemel, 2003; Podgorski et al., 2018).

## Customary explanations of wild boars population increase and expansion

The wild boar demographic expansion and increase in numbers has been explained mainly by increased food availability (Gethoeffer et al., 2007), especially in urban and agricultural areas (food left by people to feed boars and pets, domestic rubbish and agricultural crops). In addition, their population expansion has been explained by their unique prolificacy (Ruiz-Fons et al., 2006) , together with the wild boar being a niche generalist (Schley and Roper, 2003; Acevedo et al., 2006), its opportunistic feeding on a wide variety of plants and animals (Baubet et al., 2004; Maselli et al., 2014), lack of predators, the urbanization of natural habitats and increase in refuge sites at the edge of agricultural lands (Schley and Roper, 2003; Keuling et al., 2008; Barrios-Garcia and Ballari, 2012).

## Human - wild boar conflicts in agriculture and urban areas

In the vicinity of agricultural areas, the wild boars will often take advantage of crops, mainly during the dry season when resources are scarce in natural areas (Massei et al., 1996; Giménez-Anaya et al., 2008; Rosell et al., 2012). The increased invasion of boars to agricultural areas in search of food and water, has intensified human-boar conflicts (Thurfjell et al., 2009; Barrios-Garcia and Ballari, 2012; Schlageter and Haag-Wackernagel, 2012). Therefore, identifying the factors influencing wild boars foraging habits has been suggested to provide important information for organizing culling efforts in specific areas and improving their efficacy (Honda and Kawauchi, 2011), or for identifying alternative methods of controlling the population and decreasing crop damages (e.g., odours, fences) (Massei et al., 2011) .

Because wild boars also thrive in human-modified areas, they often invade human residential areas (Herrero et al., 2006). In urban areas wild boars feed on human waste and consume vegetation, arthropods and earthworms found in private and public gardens. These food items are considerably important for their diet, mainly during the dry season where they are scarce in natural areas (Massei et al., 1997; Baubet et al., 2004). In Europe, increasing numbers of wild boar sightings were reported in urban and suburban areas such as Berlin, Cracow and Barcelona and many other European cities, where culling may not be an option (Cahill et al., 2003; Podgórski et al., 2013; Massei et al., 2015). Nevertheless, studies on the behavior and demography of wild boars in urban areas are limited (Geisser and Reyer, 2005; Podgórski et al., 2013). Thus, new information on the factors affecting wild boar urban invasion could be useful for developing new management protocols.

## The effects of hunting on wild boars spatial behavior and reproduction

As mentioned above, hunting is the most common and widespread management tool applied throughout the world to try minimizing the conflict with wild boars (Toigo et al., 2008; Gamelon et al., 2011; Keuling et al., 2013). Many studies have shown that hunting affects wild boars spatial behavior. For instance; it changes their activity (Keuling et al., 2008) and dispersal patterns (Keuling et al. 2010) and causes increased spatial exploitation, resulting in larger resting ranges and more interspersed resting sites (Scillitani et al., 2010, Said et al., 2012). Moreover, Keuling et al. (2010) found that under high hunting pressure male yearlings demonstrate lower dispersal rates, maybe because they are likely to be shot during dispersal, and thus have a strong pressure to remain in their natal group.

In addition to its foraging and social structure effects, hunting had been shown to affect different reproductive traits in various ways. For example, high hunting pressure selects for earlier sexual maturity and causes juvenile females to reproduce earlier with increasing adult mortality (Toigo et al., 2008; Gamelon et al., 2011; Servanty et al., 2011). From an evolutionary point of view, the selection for earlier sexual maturity allows the population to adapt to high hunting pressure caused by humans, and to the generation times to shorten, eventually leading to higher reproduction in wild boar populations (Toigo et al., 2008; Servanty et al., 2009, 2011). This cause and effect may be one of the main reasons leading to the worldwide rapid population growth of wild boars.

I focus on three topics to explain the effects of hunting on wild boars behavior, social structure and physiology:

### 1. Evaluating the risk perception of wild boars through their foraging behavior

As mentioned above, numerous studies have shown that hunting affects the spatial behavior of wild boars (Keuling et al., 2010; Said et al., 2012; Thurfjell et al., 2013), but to date, no study has directly tested the effect of hunting on their risk perception. A well-documented method to study the effects of predation risk on the behavior of wildlife is through assessing their risk perception while foraging by measuring their giving up densities (GUD - the amount of food left in a patch) (Brown, 1988). GUDs can provide quantitative measures of foraging efficiencies and quantitative proxy for wild boars' risk perception in different land-use types (Kotler et al., 1991; Brown et al., 1994; Kotler et al., 2016). Most of the human - wild boar conflicts result from the foraging habits of wild boars in urban and agricultural areas (Apollonio et al., 2010;

Barrios-Garcia and Ballari, 2012; Massei et al., 2015). However, studies on the foraging behavior of wild boars in these areas are scarce (Geisser and Reyer, 2005; Podgórski et al., 2013), and a clear understanding of their foraging behavior in human-dominated environments is lacking. Furthermore, to the best of my knowledge, no study has yet tested the effects of hunting and different land-use properties on the risk perception of wild boars comparing foraging (GUDs) in urban, agriculture and natural areas.

### 2. Exploring the effects of hunting on wild boars vigilance behavior and social structure

Another complementary method to study the effects of hunting on wild boars risk perception is through assessing their vigilance behavior. Vigilance behavior is an important indicator which can reflect individuals' perceptions of and responses to the stress caused by hunting (Lima and Dill, 1990; Roberts, 1996; Lima and Bednekoff, 1999). Despite this, only few studies have directly studied the vigilance behavior of wild boars. Quenette and Gerard (1992), and later Podgorski et al. (2016) explored and demonstrated how group size may affect collective and individual vigilance and the degree of synchronisation of vigilance among group members; however, they did not test effect of human disturbance and hunting on the vigilance behavior of individuals taking into account their age and sex .

Anecdotal evidence suggests that hunting may destroy the family-group and therefore lead to a chaotic social structure among the remaining smaller and younger animals, eventually affecting the reproduction strategies of wild boars (Bieber et al., 2019). Furthermore, selective hunting of adult males is very common (Milner et al., 2007; Toigo et al., 2008; Poteaux et al., 2009). This may cause a decline in the numbers of territorial adult males that dominate reproduction with the females during the mating season. This decline, may lead to the contribution of numerous reproducing young males to the next generation, even within the same social group (Poteaux et al., 2009). However, a clear understanding of the effect of hunting on the seasonal social organization of wild boars is still lacking (Bieber et al., 2019). Moreover, to the best of my knowledge, no study has yet tested if differences in individual vigilance behavior may predict possible changes in the structure of social organization among wild boar populations.

### 3. Investigating the effects of hunting on wild boars stress and reproduction hormones

The predation-stress hypothesis has been proposed as a general mechanism for explaining the negative effect of predation risk on reproduction, through a chronic activation of the stress response mechanism. In recent years it has been receiving more empirical support (Clinchy et al., 2013; Dulude-de Broin et al., 2020; Rey, 2020). However, there are some evidences that in certain systems, the predation-stress hypothesis does not apply (Creel et al., 2009), and the ecological conditions supporting it in different species, are not fully understood (Creel et al., 2009; Creel, 2018; Dulude-de Broin et al., 2020). Animals cope with, and respond to, predators partly by activating their hypothalamic–pituitary-adrenal (HPA) axis (stress response), resulting in the release of glucocorticoids (GCs) hormones (Boonstra, 2013; Clinchy et al., 2013). Hunting bouts may cause chronic or short-term stress that may result in higher levels of GCs (Bateson & Bradshaw, 1997; Creel et al., 2002; Bryan et al., 2015). Chronic elevation of GCs can interrupt with the hypothalamic-pituitary-gonadal (HPG) function, however, short pulses of GC secretion normally do not (Moberg, 1991; Romero, 2004; Sapolsky, 2005). Thus, reproductive hormones can provide an additional insight into the effects of hunting on the social structure, behavior and reproduction of animals. For, example, progesterone is elevated in females of many vertebrate species during pregnancy and the estrus period and therefore can serve as an indicator of long-term population-level reproductive activity (Anderson 2009; Bryan et al., 2015; Cattet et al., 2017). Furthermore, progesterone in females might be elevated when social conditions are unstable and thus reflect the stressful social environment (Brandt et al., 2009; Bryan et al., 2013, 2015). To date, no studies have examined the stress and reproductive hormones in wild boar populations under different hunting pressures.

## 1.1 Main research objectives

The main objective of my work was to extend our understanding on the effects of hunting on wild boars population dynamics in different landscapes. Specifically, I explored how hunting affects wild boar behavior, social structure and physiology in urban, agricultural and natural landscapes in Israel. Understanding these processes may assist in developing improved management protocols of wild boars' populations in Israel and worldwide to reduce conflicts with humans. The conceptual relationships affecting boar behavior, social structure and physiology, and the interactions among them, are represented in a conceptual model (Fig. 1).

The specific objectives were to:

1. Evaluate the impact of hunting in different land-uses on the foraging behavior and risk perception of wild boars.
2. Study the effects of hunting on the vigilance behavior and social structure of wild boars.
3. Assess the influence of hunting and social structure on the stress and reproduction hormonal levels of wild boars.

## 1.2 Hypotheses

H1. Wild boars exposed to high hunting pressure consume less food (higher GUDs).

H2. Wild boars exposed to high hunting pressure from all ages and sexes exhibit higher vigilance levels.

H3. High hunting pressure cause variations in the social structure of wild boar populations.

H4. Female wild boars exposed to high hunting pressure show higher levels of stress hormones and accordingly lower reproductive hormones.

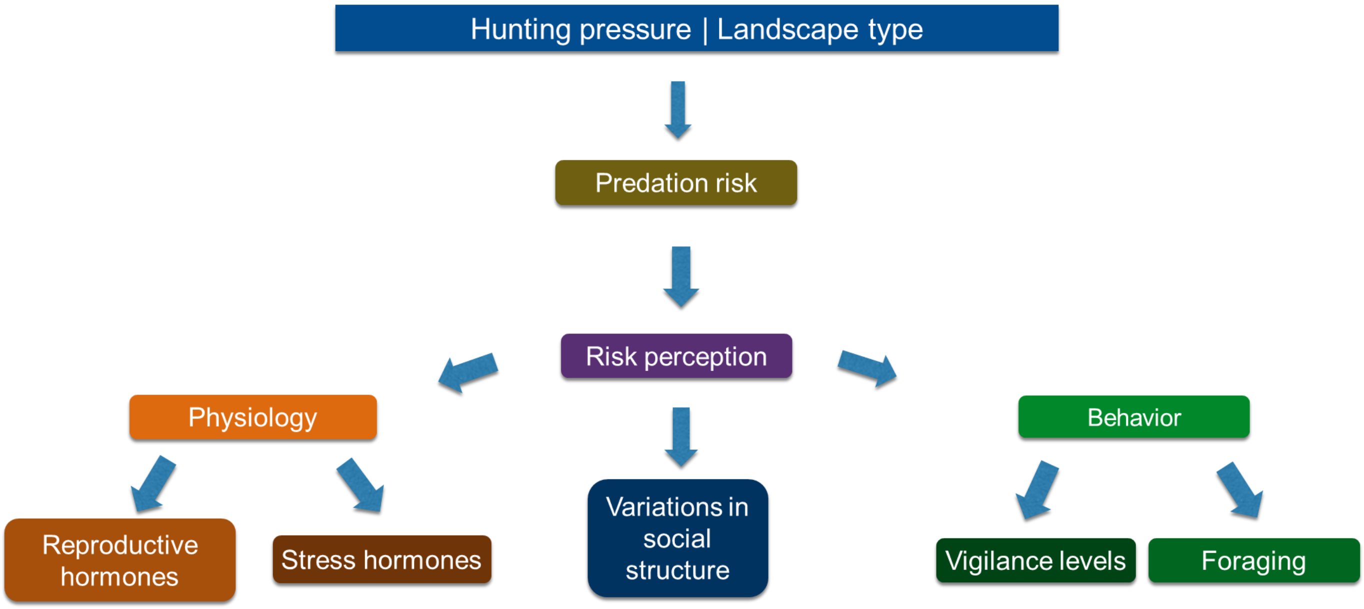

**Figure 1:** A conceptual model representing my hypotheses.

## 1.3 Detailing of the dissertation chapters

This dissertation is composed of three data chapters:

In chapter 1 (submitted to *the Journal of Mammalogy,* 2020), I investigated the combined effects of hunting and land-use types on the foraging patterns of wild boars. In particular, I tested the willingness of boars to consume food from artificial feeding devices in four different land uses – rural areas: nature reserves (no hunting) and agricultural areas (hunting), and urban areas: urban-hunting and urban-no hunting. This willingness of boars to consume food enabled me to evaluate the risk perception, as expressed by wild boars' foraging behavior. To do so, I used feeding devices with corn in order to assess three behavioral proxies: 1) whether wild boars ate or not, 2) the time from the moment the boars arrived at the feeding device until they began eating and 3) The amount of corn they ate. These behavioral indicators provided quantitative measures of foraging efficiencies and were used as a quantitative proxy for wild boars' risk perception in the different land uses.

In chapter 2 (submitted to *Journal of Wildlife Research,* 2020), I investigated the effects of human disturbance and hunting on individual's vigilance and social structure of wild boars. Specifically, I tested the vigilance of wild boars of different age and sex groups in nature reserves (hunting prohibited) and adjacent agricultural areas (hunting permitted) within the same geographic landscape.

Last, in chapter 3 (submitted to *Conservation Physiology*, 2021), I investigated the effects of hunting and social structure on stress and reproductive hormones (cortisol and progesterone respectively) of female wild boars in northern Israel. Specifically, I tested the hormones levels in hair of female wild boars roaming alone or as part of a group in high and low hunting pressure areas.

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# Chapter 2

## Wild boars' foraging and risk perception — variation among urban, natural and agricultural areas

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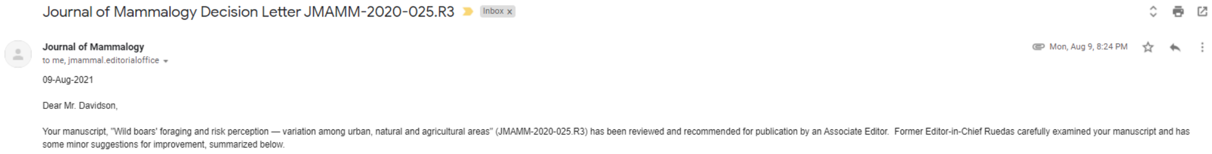

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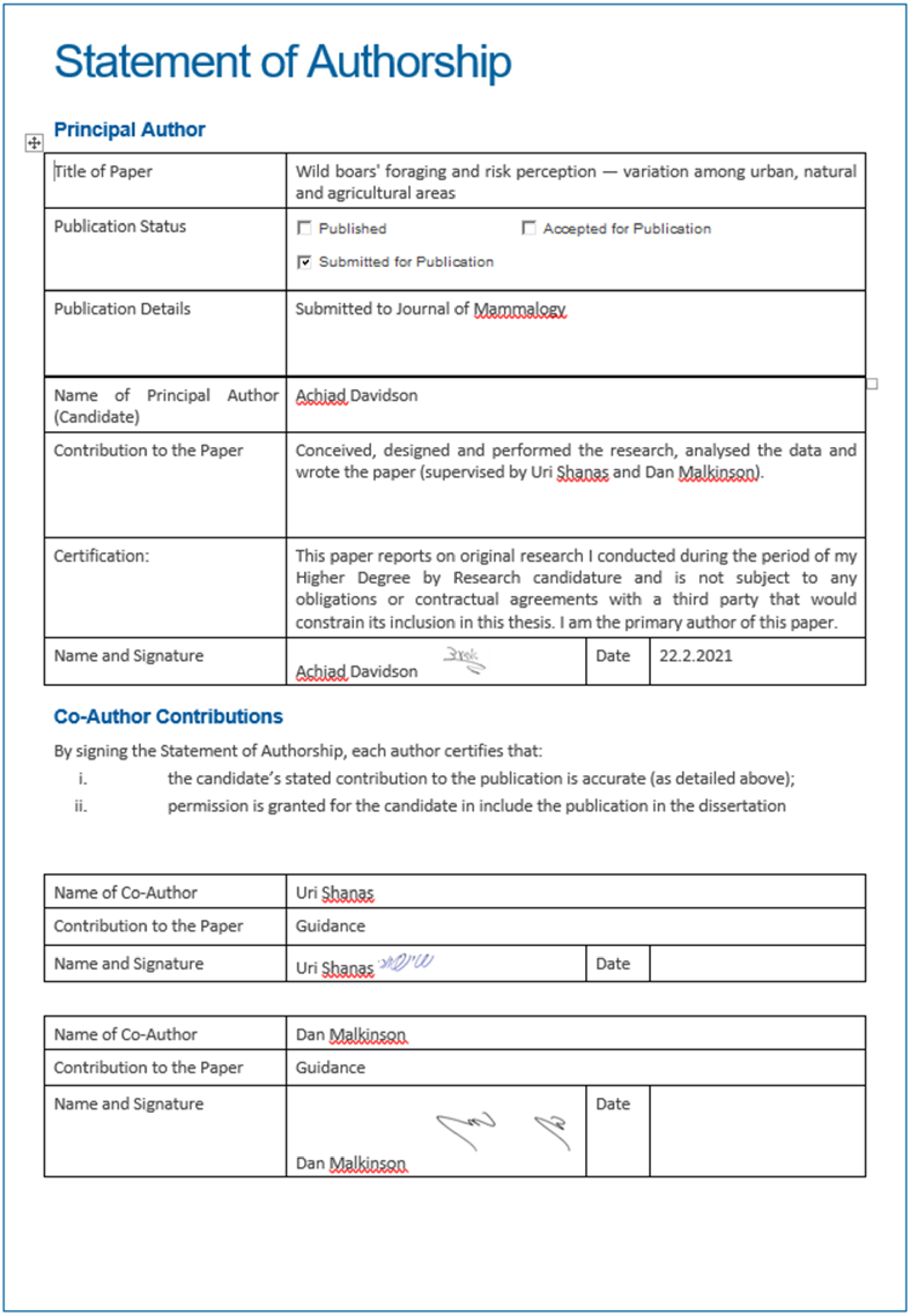
Your manuscript, "Wild boars' foraging and risk perception — variation among urban, natural and agricultural areas" (JMAMM-2020-025.R3) has been reviewed and recommended for publication by an Associate Editor.  Former Editor-in-Chief Ruedas carefully examined your manuscript and has some minor suggestions for improvement, summarized below.



# Statement of Authorship

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| | | | |
|---|---|---|---|
| Title of Paper | Wild boars' foraging and risk perception — variation among urban, natural and agricultural areas | | |
| Publication Status | ☐ Published ☐ Accepted for Publication<br>☑ Submitted for Publication | | |
| Publication Details | Submitted to Journal of Mammalogy | | |
| Name of Principal Author (Candidate) | Achiad Davidson | | |
| Contribution to the Paper | Conceived, designed and performed the research, analysed the data and wrote the paper (supervised by Uri Shanas and Dan Malkinson). | | |
| Certification: | This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper. | | |
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By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the dissertation

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# Wild boars' foraging and risk perception — variation among urban, natural and agricultural areas

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Key words: behavior, hunting, land uses, predation risk

## Abstract

When making foraging decisions, animals evaluate the risk of being preyed upon or hunted. This applies particularly to large-bodied, long-lived species with a long evolutionary history of human persecution such as wild boars (*Sus scrofa*). Wild boar populations are rapidly expanding throughout natural, agricultural and urban areas worldwide, thus, escalating human-wild boar conflicts. Most of these conflicts are associated with crop and garden damages by foraging wild boars. To study the foraging behavior of wild boars across a gradient of human risk, we evaluated the combined effects of hunting, land use type, and wild boar group size and structure on boar use of feeding devices. We installed corn-supplemented feeding devices in four land-use types – hunting combinations: urban areas with and without hunting, and rural areas, namely agricultural areas with hunting, and nature reserves without hunting. Our results show that rural areas and urban areas were the most important predictors of the wild boars' decision to eat or not and the time it took them to start eating (TBE).

Additionally, our study suggests that TBEs of urban boars were significantly lower compared to boars from nature reserves. Additionally, we found that TBEs of urban boars were significantly lower than TBEs of boars in nature reserves. In conclusion, our results suggest that the foraging behavior of wild boars vary spatially, in correspondence to the different land-use types. We propose that the readiness of boars to forage in urban areas results from their habituation to human presence, and lower perception of risk.

## INTRODUCTION

When making foraging decisions, animals evaluate the quality and quantity of different food patches in the landscape, as well as the risk of being preyed upon or hunted. As the perceived risk of predation increases, foraging animals resort to anti-predator behaviors that increase their safety at the expense of foraging efficiency and intake (Sih 1980; Fortin et al. 2005; Hernandez & Laundre 2005). Such anti-predator responses may involve changing foraging activity in space and time, shifting activity from risky to safe patches, or increasing vigilance levels (Lima & Dill 1990; Kotler et al. 1994; Brown 1999). Therefore, if the risk of predation varies among patches across the landscape, the patches with higher food resources left unapproached by the foragers should be the ones that are perceived as patches with a higher risk (Brown 1988; Kotler et al. 1994; Fortin & Fortin 2009). Thus, by evaluating the unconsumed resources, the risk perception of foraging wild boars (*Sus scrofa*) at different land uses can be quantified (Laundre et al. 2001). Such information can be useful to understand the distribution and behavior of species in the face of predators, hunters and other anthropogenic activities and disturbances (Hayward et al. 2011). It has been suggested that human presence has a similar or even greater effect on wildlife behavior than do predators (Montgomery et al. 2020). For instance, several studies have demonstrated that ungulate habitat selection is strongly associated with different land use factors that might influence the perceived risk of predation, caused by humans, while foraging (Tadesse & Kotler 2012; Le Saout et al. 2014; Hayward et al. 2015). Behavioral responses to the risk of predation caused by humans, can be quite complex, thus they may generate chronic risk in a landscape that influences proactive risk-foraging trade-offs (Keuling et al. 2008; Sunde et al. 2009; Marchand et al. 2014). These complex behavioral responses may apply to particularly large-bodied, long-lived species such as wild boars, which have a long history with humans as a source of risk (Keuling et al. 2010; Scillitani et al. 2010; Thurfjell et al. 2013).

Despite the risk that humans pose to wild boars, wild boars are attracted to food subsidies in areas of high human activity. Thus, in agriculture areas, wild boars show high reproductive success, due to higher anthropogenic food and resource abundance (Kaminski et al. 2005; Barrios-Garcia & Ballari 2012; Massei et al. 2015). The high reproductive success result in substantial increases of population densities in agricultural areas (Massei et al. 2015). Similarly, wild boars thrive in urban and suburban areas (Herrero et al. 2006; Cahil et al., 2012; Stillfried et al. 2017). In urban areas, wild boars feed on human waste and consume plants, arthropods, and earthworms found in private and public gardens (Massei et al. 1997; Baubuet et al. 2004; Cahil et al., 2012). Over the past few decades, their substantial population increases in agriculture, urban and suburban areas have intensified human-boar conflicts (Apollonio et al. 2010; Barrios-Garcia & Ballari 2012; Massei et al. 2015). These conflicts include elevated economic costs, disease spillover to livestock and humans, and damages to gardens and infrastructure in urban areas and to agricultural crops (Thurfjell et al. 2009; Barrios-Garcia & Ballari 2012; Massei et al. 2015). Massei et al. 2011 reported several methods commonly used worldwide in order to control wild boars populations. Nevertheless, there is still a need for innovative management protocols in order to mitigate human-boar conflicts (Massei et al. 2015). For instance, most of the conflicts are a result of the foraging habits of wild boars (Apollonio et al. 2010; Barrios-Garcia & Ballari 2012; Massei et al. 2015). However, studies on the foraging behavior and risk perception of wild boars populations that are exposed to hunting in urban and agriculture areas are scarce (Geisser & Reyer 2004; Podgorski et al. 2013), and a clearer understanding of their behavior in human-dominated environments is lacking. Thus, there is a need to study wild boar foraging behavior under hunting pressure in human-modified landscapes, given the differential behavioral ecology of this species in different environments.

Hunting is the most common and widespread management tool applied throughout the world to minimize conflict with wild boars in urban and agricultural areas (Toigo et al. 2008; Gamelon et al. 2011; Keuling et al. 2013). However, despite the high hunting pressure, the number of wild boars world-wide continues to grow (Massei et al. 2015). Massei et al. (2015) analyzed wild boar population hunting trends in Europe and calculated as a mean annual hunting index of harvested wild boar populations (the ratio of the number of wild boars hunted in consecutive years) of approximately 20%. The high mean annual growth rate of wild boar populations together with the high hunting pressure that they are subjected to makes them an excellent species to explore the effects of hunting and different land uses on animal's risk perception and foraging behavior.

Human activities and hunting have a significant impact on wild boars' behavior. For example, it affects their dispersal patterns (Keuling et al. 2010) and increases spatial occupancy (Keuling et al. 2008), leading to larger resting ranges and more interspersed resting sites (Scillitani et al. 2010). Hunting may also cause wild boars to select safer habitats, even at the expense of resource abundance (Said et al. 2012). Although it has been shown that hunting affects the spatial behavior of wild boars (Thurfjell et al. 2013), very few studies tested directly the effect of human activities and hunting on their foraging behavior. Focardi et al. (2015) found that different wild boar group structures and sizes affect the effective foraging time of wild boars. However, they did not explore the effect of human disturbance and hunting in different land uses on their foraging behavior.

In this study, we investigated the combined effects across land-use types and social structures on the foraging patterns of wild boars in Israel. In particular, we tested the willingness of boars to consume food from artificial feeding devices in four different land uses – rural areas: nature reserves (no hunting) and agricultural areas (hunting), and urban areas: urban (hunting) urban (no hunting). Furthermore, we explored the spatial variation in the risk perception, as expressed by wild boars' foraging behavior in different landscapes. Thus, we studied the combined effects of two anthropogenic factors that may potentially influence wild boars' foraging behavior: hunting and different land use types. To do so, we used feeding devices with corn in order to assess three behavioral proxies: 1) whether wild boars ate or not (EDE – Eat Did-not Eat), 2) the time from the moment the boars arrived at the feeding device until they began eating (TBE – Time Before Eating) and 3) The amount of corn they ate (ACE -Amount of Corn Eaten). These behavioral indicators provided quantitative measures of foraging efficiencies and were used as a quantitative proxy for wild boars' risk perception in the different land uses (Kotler et al. 1991; Brown et al. 1994; Kotler et al. 2016). Accordingly, we hypothesized that in areas with hunting and in urban areas, where interactions with humans are frequent and intense 1) wild boars will leave more unforaged feeding devices, 2) will take longer time to start eating and 3) they will eat less food. Finally, it has been suggested in the literature that larger group sizes are associated with lower vigilance behavior (Roberts 1996; Pays et al. 2012; Podgórski et al. 2016). Accordingly, we hypothesized that wild boars foraging in smaller groups and females with piglets will tend to forage less from the feeding devices, will take longer time to initiate eating and will eat less food.

## METHODS

### *The study area*

The study took place in the Carmel coastal mountain range in northern Israel (Fig. 1), an area approximately 600 km$^2$, with an elevation ranging from 0 to 546 m above sea level. The climate is Mediterranean, and the annual rainfall varies between 700 mm in the higher regions of the Carmel to 500 mm in the lower areas, falling mainly (80%) between December and February. The vegetation is a typical Mediterranean maquis (Neeman et al. 1995; Hadar et al. 1999), with patches of cultivated areas. Within the region, there are several towns, including the city of Haifa.

Within this study area, the main predator of wild boar in Israel, wolves (*Canis lupus*), are absent. However, there are other factors causing the mortality to wild boars, in the past decade the Israel Nature and Parks Authority (INPA) has recorded selective hunting activities in this study area. This region exhibits the highest wild boar hunting pressure in Israel, as well as the highest reported number of human-wild boar conflicts in urban and agricultural landscapes (Lider 2012; Malkinson 2015). Hunting is permitted in agricultural areas and within the city of Haifa (Urban - hunting). Hunting is forbidden in the nature reserves and other cities and towns, including the city of Nesher (Urban - no hunting), which borders the city of Haifa. The nature reserves and agriculture areas were the rural landscapes to be studied. They do not provide an ideal setting for comparison due to differences in landscape structure. However, due to hunting taking place in agricultural areas, as opposed to nature reserves, we chose the most optimal design possible.

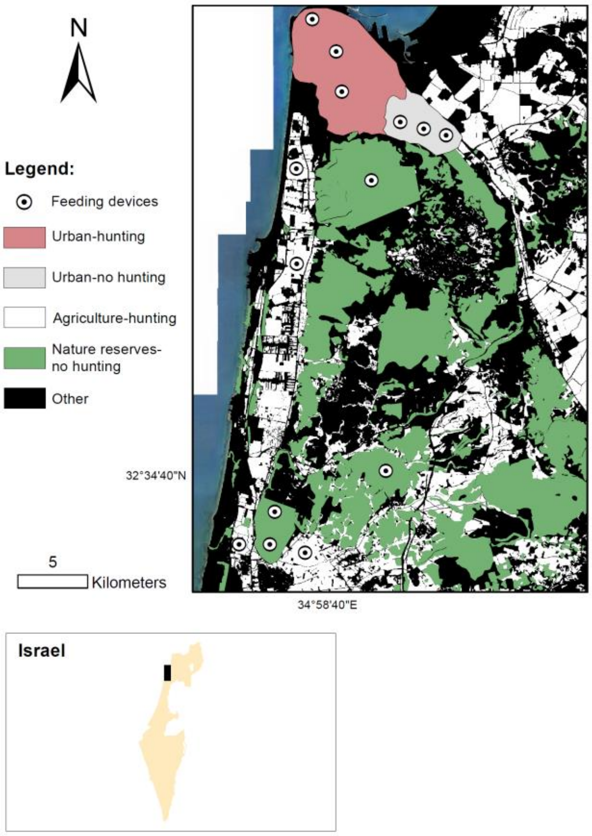

**Figure 1:** The study area in the Carmel coastal mountain range, Israel, including the four different land-use types.

### *Assessing foraging behavior*

To assess wild boars' risk perception while foraging in different land uses, we installed 14 feeding devices: 4 in nature reserves, 4 in agricultural farms, 3 in urban-hunting and 3 in urban-no hunting. We conducted the field experiment during a three week period, at the end of the dry season (September 2016), when natural food and water availabilities are in their lowest (Woodall 1983; Caley 1993; Massei et al. 1997). Additionally, we installed feeding devices during this period of the year in post-harvested orchards, and thus within this land use no significant alternative food sources were available for foraging wild boars. To determine the optimal locations of the feeding devices, we searched for wild boars' digging signs, scats, footprints, tree-rubbing marks and mud wallows in all the studied land-use types. Next, each device was systematically placed in areas with signs of wild boars' activity, and inside relatively dense vegetation cover, in order to most closely resemble the environmental conditions in the vicinity of all the devices. Furthermore, we choose a minimal distance between each feeding device of 1,500 m, in order to minimize the probability that a single group would feed at more than a single device.

The wooden feeding devices measured 40 x 60 cm and were 20 cm deep (walls were 2 cm thick). The top part of the devices was covered by a 15 x 15 cm metal mesh. The devices were elevated off the ground by 15 cm wooden legs, and the uppermost part of the device was 35 cm above the ground. All four corners of the devices were tied with a metal wire to iron fence posts, in order to prevent the boars from overturning the devices. Each feeding device contained an aluminum feeding tray measuring 35 x 56 x 5 cm. We placed the trays on a 5 cm polystyrene block, which created a space of 15 cm between the feeding tray and the mesh cover. We supplied each feeding tray with 300 g of maize thoroughly mixed with 600 g of nonedible, 4 cm long pieces of plastic irrigation pipe to increase the handling time of the food (Iribarren & Kotler 2012). Covering the feeding devices with the mesh prevented wild boars from pushing the nonedible substrate out of the wooden feeding devices. Moreover, the device mimicked wild boars' natural foraging behavior by forcing them to push their muzzles between the links of the mesh as they do when burrowing into the soil in search of food (Baubuet et al. 2004). We stocked the feeding devices with maize for 48 hours, and then collected, sieved, and weighed the remaining grains in the field using an electronic balance (+/- 0.1 g). Then we restocked the devices (every 48 hours for 9-11 times for each feed device) with additional 300 g of corn grains mixed with 600 g of plastic pipes.

### *Exploring foraging behavior and group size and structure*

We monitored each feeding device with a video-camera trap (intervals of 20 sec, refractory period of 1 sec, resolution 12 MP, 640 × 480 pixels per frame). We recorded whether they ate or not (EDE – Eat Did-not Eat) as an indicator that provided a quantitative measure of foraging efficiencies for whether the feeding devices were acceptable or not for the wild boars (Kotler et al. 1991; Brown et al. 1994; Kotler et al. 2016). If any individual pushed its head into the feeding device, then we considered as if the entire group have eaten. Furthermore, we recorded the time from the moment the boars arrived at the feeding device until they began eating (TBE – Time Before Eating) as a behavioral indictor for assessing wild boars' risk perception of hunters (Focardi 2015, Kotler et al. 2016). Additionally, in order to determine the giving-up densities (GUDs) in the different land uses we weighed the remaining grains every 48 hours as described above. GUDs are defined as the amount of unconsumed food after foraging exploitation, and have been used to assess the risk perception in natural setups (Brown 1988; Brown 1994; Kotler et al. 1994). Our results indicated that whenever the boars ate they consumed all of the 300 g corn we provided in the feeding devices. Thus, in this study, the GUDs assumptions could not be met because a decelerating gain of energy with diminishing returns was not observed. Consequently, we differed to measure boars’ willingness to eat as a proxy for risk perception. Therefore, we measured the ACE (Amount of Corn Eaten – the weight of the corn consumed) as a behavioral indicator that provided a quantitative proxy for wild boars' risk perception in the different land-use types (Kotler et al. 2016). Furthermore, examining the ACEs in the different land-use types allowed us to assess their propensity to consume food from the devices (Kotler et al. 1991; Brown et al. 1994), thus helping us explore the underlying factors dictating the spatial variation in the risk perception of wild boars. In addition, we individually identified the different groups of wild boars that visited the different feeding devices according to group structure, temporal behavior (when they are usually active during the day), and the morphological characteristics (scares, size, wounds etc.) of its individuals. We also recorded the group size and structure of the different groups: family group, sub-adult group, solitary male, solitary female, solitary sub-adult. The study followed protocols in accordance with the American Society of Mammalogists guidelines (Sikes 2016).

### *Land-use cover*

We studied the relationship between land-use cover and wild boars' foraging behavior around the feeding devices in a 750 m radius buffer zone. The daily home-range sizes of wild boars in rural areas are relatively small (1-1.6 km$^2$) compared to other ungulates, considering the potential mobility of the species (Boitani et al. 1994; Russo et al. 1997; Morelle et al. 2015). Furthermore, it had been shown that boars in urban areas have smaller daily home ranges (0.9 km$^2$) compared to those in rural areas (Podgorski et al. 2013). Thus, the 750 m radius buffer (an area of 1.76 km$^2$) generally covers the common home-range of wild boars in urban areas and the daily movement range of wild boars in rural areas. To control for pseudo-replication in the spatial locations of the feeding devices, the minimal distance between each feeding device was 1,500 m in order to make sure that different analysis buffers will not overlap.

Within each buffer, we characterized the relevant land-use factors; specifically, agriculture, built areas, nature reserves, weighted hunting pressure, roads and vegetation cover. We assessed autocorrelation, which was found to exist between nature-reserve cover and vegetation cover, and roads was auto correlated with built areas. Accordingly, we removed vegetation cover and roads from the analysis. Next, based on a 25m resolution land use layer (HAMAARAG 2016) we summed the number of pixels agriculture, built areas and nature reserves comprise within each of the buffers using ArcMap (ESRI 2018). Then, we estimated the weighted hunting pressure as follows: the agricultural areas within the study region were divided into nine polygons, and each was assigned a hunting pressure from 1-3 (1 representing low hunting pressure and 3, high hunting pressure). Because INPA does not formally record the precise location of hunting events, expert opinions of three different INPA ecologists and rangers as well as local hunters were consulted to estimate hunting pressure within each polygon. For each buffer, the weighted hunting pressure was calculated according to the proportions of the different hunting polygons within it. Similarly, we classified the hunting pressure within the city of Haifa on the scale of 1-3, based on hunting data provided by the local municipality. As hunting does not occur in nature reserves, we assigned the nature reserves polygons with a value of zero.

### *Evaluating the ACE and TBE in four different land-use types*

We compared the ACE (amount of corn eaten) and TBE (time before eating) of the four hunting/no hunting–urban/rural combinations. Since the ACE and TBE were not normally distributed, we used a Kruskal-Wallis test (Breslow 1970) to compare between the different land-use combinations. We pairwise compared all land uses with a Mann-Whitney test (Rice 1989). However, because we performed six pairwise comparisons for the ACE (i.e., between all possible pair-combinations of the land uses) and three for the TBE (i.e., agricultural areas were not included in the TBE analysis because wild boars did not eat from the devices there), we used the False Discovery Rate (FDR), which is commonly used in studies with large numbers of pairwise tests, in order to control the type I error (Narum 2006).

### *Model development and evaluation*

We assembled sets of 13 alternative models as a basis for exploring the effects of different land-use factors and boar's social factors on wild boars' foraging behavior (see complete list of models in Appendix 1). In some of the models, we treated the land-use factors as categorical variables, including: urban areas or rural areas, and land use (agriculture, nature reserves, urban hunting, urban no-hunting). In other models, we treated the coverage of agriculture, built areas, and nature reserves as well as hunting pressure as continuous variables (Appendix 1). For social factors, we included group size and categories that depicted group structure: family group, sub-adult group, solitary male, solitary female, solitary sub-adult (Appendix 1). We conducted exploratory linear-regression analyses individually to identify the general relationships between the explanatory variables (land use and social) and the response variables (EDE and TBE). For EDE, we summed for each feeding device the number of times different groups were assigned "eat" or "didn't eat." The mean TBE was calculated for each group and for each feeding device. Furthermore, we did not find any autocorrelation between the percentage of built area, agriculture, and nature reserve.

We used GLMs (General Linear Models) to investigate the relationships between the dependent variables, EDE, and TBE, and explanatory variables land-use and social factors. Due to the relatively small numbers of random-effects levels (3-4 feeding devices per land-use) the assumptions of Generalized Linear Mixed Models (GLMMs) could not be met, and thus we resorted to GLMs. To do so, we formulated 12 alternative models. All GLMs were ranked according to their fit to the empirical data using a model-selection approach, whereby the maximum log-likelihoods of the models were compared (Burnham & Anderson 2002). EDE was binomially distributed – zero indicated eat and one indicated did not eat (link function = "logit"), and TBE was best characterized by the Gamma distribution (link function = "inverse") that best fit the empirical data, following Mangiafico (2016). The relative support for each model was evaluated using the Akaike Information Criterion (AIC). The corrected AIC (AICc) score enabled us to rank and compare the models. In addition, the "Akaike weight" of each model was used to estimate the probability that a given model is the best model within the given set of alternatives (Burnham & Anderson 2002).

The model-selection approach does not evaluate the goodness of fit of the models, yet this information is critical, especially for evaluating the prediction potential of the high-ranking models. In GLMs, where $R^2$ values cannot be formally calculated, Dobson (2002) offered to use the proportional increase in explained deviance, pseudo $R^2$, as an alternative. This value is a relative measure comparing models that are using the same data. Accordingly, we used the proportional increase in the deviance in the empirical data explained by the model, the Nagelkerke/Cragg and Uhler pseudo $R^2$, as recommended by Mangiafico (2016). The procedures — GLMs, $R^2$, model averaging, and model selection — were conducted in R, using mainly the AICcmodavg, lme4, MASS packages (R Core Team, 2014).

## RESULTS

### *The effect of social and land-use factors on whether wild boars ate or not (EDE)*

A total of 9,037 videos were filmed, of which 3,805 captured wild boars. Wild boars appeared at all 14 feeding devices. We quantified the wild boars' risk perception by examining the EDE in different land-use types. Wild boars in agricultural areas did not consume corn from any of the feeding devices (zero out of the 34 times they were filmed in proximity to the feeding devices), however in nature reserves they ate 38% of the times, 5 out of 13 (Fig. 2, Appendix 2). In urban areas with hunting wild boars ate 80% of the times (37 out of 46) and in urban areas without hunting wild boars ate 83% of the times (45 out of 54) they were filmed by the feeding devices (Fig. 2, Appendix 2). Moreover, the urban/rural model was the best model to explain the relationship between any of the social and land-use factors on EDE (Akaike weight of 0.999, $R^2$ =0.99, Table 1). The hunting pressure model was second best but had a negligible Akaike weight (6.1E-12, Table 1). Furthermore, the univariate model of built cover and multivariate model of built cover + nature cover model were ranked third and fourth respectively, but with negligible Akaike weights of 1.6E-13 and 2.1E-13. The null model (i.e., a model with no social or land-use factors, only an intercept) had the lowest $R^2$ (0.00) and an Akaike weight of 6.6E-16 (Table 1). None of the social structure factors (group size and structure) had a significant effect on EDE. Urban areas and rural areas were found to be the most important predictors affecting EDE (urban areas for eating and rural areas for not eating).

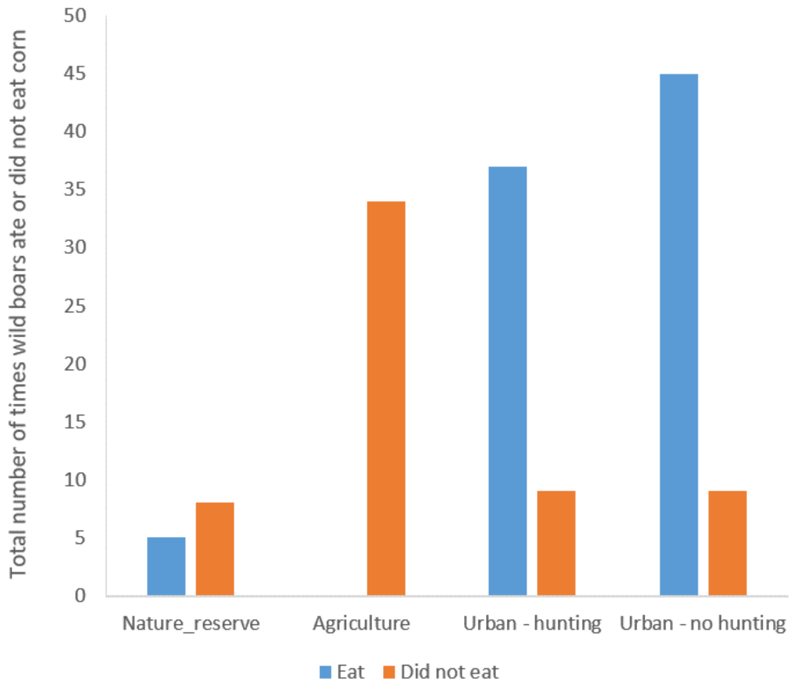

**Figure 2:** The effect of different land-use types on the number of times wild boars ate or did not eat (EDE) corn from the feeding devices.

**Table 1: EDE** — Model-selection statistics of the effects of social and land use-factors on whether the wild boars ate. Alternative GLMs were sorted by AICc and model weight. Only models, which yielded significant coefficients, and the null model (intercept only) are presented. Hunting pr. indicates: Weighted hunting pressure and Nature-cover indicates: Nature-reserves cover.

| Model | Coefficient | Estimate | Std. error | *z* value | *P*-value | ΔAICc | Weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Urban/Rural | | | | | | 0.00 | 0.999 | 0.99 |
| | Intercept(Rural) | 0.107 | 0.038 | -4.499 | <0.001* | | | |
| | Urban | 0.974 | 0.009 | 6.750 | <0.001* | | | |
| Hunting pr. | | | | | | 51.66 | 6.1E-12 | 0.78 |
| | Intercept | 0.781 | 0.068 | 4.473 | <0.001* | | | |
| | Hunting Pr. | 0.351 | 0.091 | -4.363 | <0.001* | | | |
| Built areas | | | | | | 58.35 | 2.1E-13 | 0.64 |
| | Intercept | 0.328 | 0.088 | -2.109 | 0.034 | | | |
| | Built areas | 0.500 | 0.099 | 3.632 | <0.001* | | | |
| Built areas + Nature cover | | | | | | 58.96 | 1.6E-13 | 0.70 |
| | Intercept | 0.225 | 0.069 | -2.620 | 0.008 | | | |
| | Built areas | 0.500 | 0.099 | 3.859 | <0.001* | | | |
| | Nature cover | 0.500 | 0.100 | 1.627 | 0.103 | | | |
| Intercept | | | | | | 69.91 | 6.6E-16 | 0.00 |
| | Intercept | 0.591 | 0.096 | 2.214 | 0.026* | | | |

### *Time from arrival to the beginning of eating (TBE)*

The TBEs from the feeding devices were significantly different among the land-use types (Kruskal-Wallis test $H_{(2)} = 18.14$, $P < 0.001$ with FDR correction, Fig. 3). The mean TBEs in the different land uses were: nature reserves $\bar{x}$ =700.2 sec, $SD$ = 784.9 ($n$ = 5), urban-no hunting $\bar{x}$ =33.5 sec, $SD$ = 81.8 ($n$ = 81) and urban-hunting $\bar{x}$ =19.7 sec, $SD$ = 49.6 ($n$ = 53). The Mann-Whitney pairwise comparisons between all land uses revealed two significant comparisons: nature reserves vs. urban-no hunting ($P < 0.001$), nature reserves vs. urban-hunting ($P < 0.001$). The TBEs of boars in agricultural areas are absent from this test because boars in agricultural areas did not consume any corn from the feeding devices (Fig. 2 and 3, Appendix 2). The only GLM that yielded a significant relationship with TBE was the urban/rural model (Akaike weight of 0.975, $R^2 = 0.80$, Table 2). None of the other models yielded significant relationships between the dependent and independent variables. The null model had a very low Akaike weight (0.025) and $R^2 = 0.00$ (Table 2). Urban areas and rural areas were found to be the most important predictors affecting wild boars' TBE (urban areas for low TBE and rural areas for high TBE).

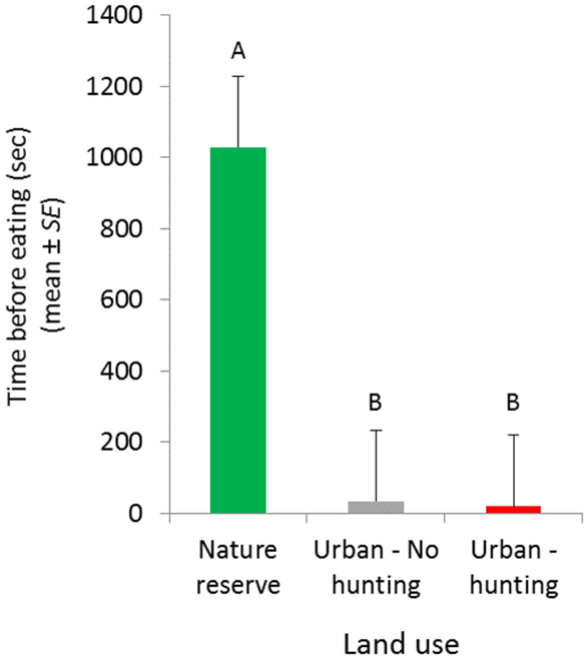

**Figure 3:** The time from the moment boars arrived at the feeding device until they started eating (TBE). Letters represent differences between land-use types.

**Table 2: TBE** — Model-selection statistics of the effects of social and land-use factors on wild boars' time before eating (TBE) from a feeding device. Alternative GLMs were sorted by AICc and model weight. Only models, which yielded significant coefficients, and the null model (intercept only) are presented.

| Model | Coefficient | Estimate | Std. error | *z* value | *P*-value | ΔAICc | Weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Urban/Rural | | | | | | 0.00 | 0.975 | 0.80 |
| | Intercept | 0.001 | <0.001 | 1.920 | 0.103 | | | |
| | Urban | 0.021 | 0.007 | 3.071 | 0.021* | | | |
| Null model | | | | | | 7.35 | 0.025 | 0.00 |
| | Intercept | 0.005 | 0.002 | 1.871 | 0.104 | | | |

### *Evaluating the amount of corn eaten in four different land-use types (ACE)*

ACEs were significantly different across the land-use types (Kruskal-Wallis test $H_{(3)}$ = 103.89, $P < 0.001$ with FDR correction, Fig. 4). The mean ACEs in the different land uses were: agriculture areas $\bar{x} = 0$ g, $SD = 0$ ($n = 40$), nature reserves $\bar{x} = 41.6$ g, $SD = 103.7$ ($n = 36$), urban-hunting $\bar{x} = 288.8$ g, $SD = 56.6$ ($n = 27$) and urban-no hunting $\bar{x} = 288.8$ g, $SD = 56.6$ ($n = 27$). The Mann-Whitney pairwise comparisons between all land-use types revealed five significant comparisons: Agriculture vs. Urban-hunting ($P < 0.001$), Agriculture vs. Urban-no hunting ($P < 0.001$), Nature reserves vs. Urban-no hunting ($P < 0.001$), Nature reserves vs. Urban-hunting ($P < 0.001$), agriculture vs. nature reserves ($P = 0.015$). The only Mann-Whitney pairwise comparison that was not significant was urban-no hunting vs. urban-hunting ($P = 1$) - both land uses resulted in the exact same values; only in one occasion (out of 27) in each of them the boars did not eat at all and at the rest of the bouts they ate all the corn in both land uses (Appendix 2).

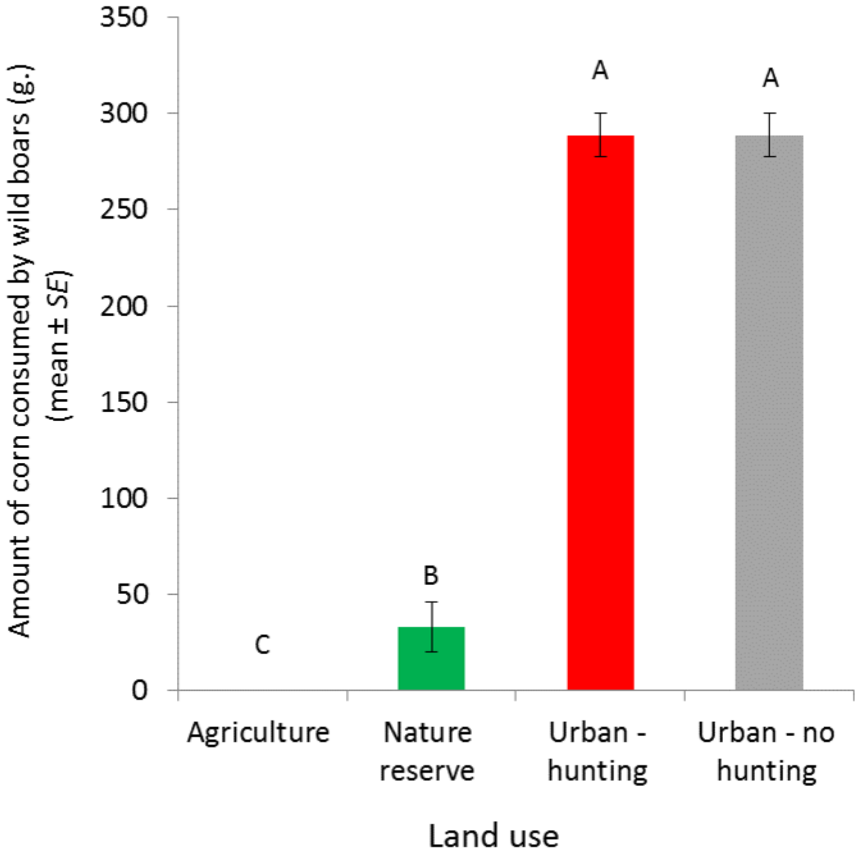

**Figure 4:** The effect of land-use types on the amount of corn eaten (ACE) by wild boars. Letters represent differences between land-use types.

## DISCUSSION

Landscape-level variation in risk from predators and humans can shape patterns of risk perception and foraging behavior (Brown 1988; Kotler et al. 1994; Fortin & Fortin 2009). Our approach of evaluating wild boars' foraging patterns in relation to different land use types indicated that the willingness of boars to consume food from artificial feeding devices varies spatially, depending on land use type. Our results (Figures 2, 3, and Tables 1, 2) suggest that wild boars in rural areas perceive a greater risk of predation compared to wild boars in urban areas. Moreover, this perception of risk was independent of the presence of hunting in urban areas that took place during the study and is permitted year around. However, we also found that agricultural boars, that are subjected to high hunting pressure, showed significantly higher risk perception while foraging compared to nature reserves boars. Our work provides an analysis of the important land-use factors shaping wild boars' behavioral responses to the risk of hunting, as revealed by three different behavioral proxies: EDE, TBE, and ACE, thereby indicating a spatial variation in the perception of risk that shapes prey animals’ behavioral preferences while foraging.

Our GLM analyses suggested that the urban/rural-area factor was the most important predictor of whether wild boars ate from our feeding devices (EDE). Additionally, we found that boars in agricultural areas did not eat any food from any of the feeding devices during the experiment. In rural areas, this finding suggests that in agricultural areas, hunting and other intensive human activities are associated with higher foraging risks than those in nature reserves. However, urban boars were found to be more likely to eat from our feeding devices compared to rural areas boars, indicating a lower perceived risk of urban boars. Additionally, we recorded much higher visiting frequencies of wild boars to our feeding devices in urban areas (100) compared to rural areas (47). This result may also reflect lower perceived risk of wild boars in urban areas compared to rural areas. Moreover, the results indicate significant differences between the TBEs in urban areas compared to nature reserves, with shorter TBEs in urban areas. These results were further supported by the GLMs that showed that the urban/rural-area factor was the only important predictor affecting the time it took wild boars to start eating, as urban areas showed low TBEs and rural areas high TBEs. Consequently, this may suggest that wild boars in rural areas showed higher levels of neophobia to the feeding devices compared to urban boars. Many animals show an aversion to novelty; a behavior known as neophobia. In the wild, avoiding novel predators, foods, objects and locations, shape life history and influence how animals react to new environments. For example, neophobia levels have been reported to be positively correlated with increased physiological stress (Greggor et al. 2015). Thus, higher levels of neophobia of rural boars to our feeding devices, compared to urban boars, suggest higher risk perception of rural boars.

Our ACE analysis in the four different land-use types further supported the EDE and TBE results. The ACE results suggest that compared to wild boars in agricultural areas, wild boars in nature reserves ate significantly more corn. As described above, it has already been shown that high hunting pressure has a significant impact on wild boar movement and space-use patterns (Keuling et al. 2010; Scillitani et al. 2010; Said et al. 2012). However, to the best of our knowledge, no study has yet demonstrated the differential effect of hunting on the risk perception of wild boars while foraging in different landscapes. Moreover, higher ACEs in urban areas compared to rural areas further suggest that urban wild boars show lower perceived risk compared to wild boars in rural areas.

Surprisingly, for both EDE and TBE all other social (group size and structure) and land-use factors (agriculture/built/nature cover and hunting pressure) contributed little to explaining foraging behavior compared to the urban/rural-area factor. These results are in contrast to the findings of Focardi et al. (2015) that showed that different wild boar group structures and sizes affect the foraging time of wild boars. Thus, our study system suggests that the foraging behavior of wild boars is more strongly driven by land use type than group size and structure. These results further indicate that the risk perception of wild boars in urban areas during foraging is significantly lower compared to boars outside urban areas, probably due to their habituation to human presence. We propose that such a strong habituation may explain the lack of effect of hunting on the foraging behavior of boars in urban areas; in other words, lower neophobia of urban boars and habituation to humans overrides the effects of hunting.

Among wildlife, habituation is defined as the loss of fear response to the presence of humans after repeated, non–consequential encounters (Cahil et al., 2012). Habituation of wild boar has largely been motivated by direct feeding by people and is also facilitated by the proximity of densely vegetated areas close to the city limits (Stillfried et al. 2017). In the cities of Haifa and Nesher this phenomenon is exacerbated by abundant food sources available in trash bins, and the city parks which provide ample water and food sources during the harsh feeding seasons. Habituation processes in Mediterranean areas like Israel, may occur even faster due to limitations of food sources in natural maquis habitats during the months of summer drought (Cahil et al., 2012). The differences in human presence and activities between urban areas and rural areas are immense and have been previously shown to affect wild boars' space-use patterns and movement behavior. Podgórski et al. (2013) demonstrated that boars inhabiting urban areas had smaller home ranges and were almost exclusively nocturnal in contrast to wild boars in rural areas. Stillfried et al. (2017) showed that wild boars in urban areas preferred natural areas located closely to roads and houses and had a shorter flight distance compared to wild boars in rural areas. This higher tolerance of anthropogenic activities indicates considerable behavioral plasticity suitable to adjust to human-dominated environments, which may explain the recent rapid demographic expansion of wild boars world-wide (Stillfried et al. 2017).

To the best of our knowledge, previous studies did not quantify wild boars' preferences while foraging on the same food resource in different land-use types. Yet, our research design was incomplete; the study lacked agricultural areas without hunting and nature reserves with hunting. Furthermore, we conducted our research only during the dry season. Thus, we encourage further research that will incorporate agricultural areas without hunting and nature reserves with hunting, during winter/spring seasons and develop protocols that may allow the use of GLMMs. Nevertheless, we found that wild boars in urban areas, with or without hunting, were more willing to risk accessing the corn in spite of the ample food available in these areas. This finding indicates that even when abundant food is in close vicinity to the feeding devices in urban areas, it is not an important factor in determining whether boars are less likely to take risks to access corn. Furthermore, in our study, the reduction in the foraging intake, as expressed by ACE and EDE, and changes in the time of foraging activity (i.e., TBE) provided a standard measure for wild boars' willingness to consume food from artificial feeding devices (Brown et al. 1994, Focardi 2015, Kotler et al.  2016). This willingness is related to the animals’ propensity to exploit anthropogenic resources, and perception of risk, which is a function of an animal’s habituation, neophobia (Greggor et al. 2015), and actual risk of being hunted (Kotler et al. 1994, Iribarren & Kotler 2012, Hayward et al. 2015). Measurements of the willingness to consume food enabled us to quantify wild boars' foraging patterns and better understand how the animals’ risk perception varies spatially according to different land use types, which reflect different types of human activities (Laundre et al. 2001). Human-boar conflicts include among others, elevated economic costs due to damages to gardens and infrastructure in urban areas and to agricultural crops (Thurfjell et al. 2009; Barrios-Garcia & Ballari 2012; Massei et al. 2015). Thus, our analyses provide important insights, which can be applied for management. For example, due to the habituation and lower levels of neophobia, urban boars could probably be trapped relatively easily for fertility control or other management purposes (Massei et al. 2011). We provide a detailed assessment of the important land-use features working together to shape wild boars' behavioral responses to humans while foraging. Furthermore, the methods applied herein provide direct insights into the most important factors affecting the foraging behavior and risk perception of wild boars.

## ACKNOWLEDGMENTS

We would like to thank Burt Kotler for his invaluable advices, Mika Volov for her valuable contributions to the fieldwork, Yossi Volov for building the feeding devices, and Ben Rosenberg, Yonatan Harael, Liron Tal, Barak Barchiel and Lishay Ben Yanai from the INPA for their priceless advice. We are grateful to Liat Hadar and Amir Arnon for their support and encouragement. The study was financed by a research grant provided by the Ramat Hanadiv Project of the Rothschild Foundation.

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# APPENDICES

**Appendix 1:** The complete set of alternative GLMs, testing the effect of different land-use and social factors on wild boars' foraging behavior and risk perception.

| **Alternative models** |
|---|
| H1: Urban areas or rural areas — categorical |
| H2: Land use: agriculture, nature reserves, urban-hunting, urban-no hunting — categorical |
| H3: agriculture cover — continuous |
| H4: built-area cover — continuous |
| H5: nature-reserve cover — continuous |
| H6: hunting pressure — continuous |
| H7: Null model – intercept only |
| H8: nature-reserve cover + agriculture cover |
| H9: agriculture cover + built-area cover |
| H10: built-area cover + nature-reserve cover |
| H11: built-area cover + nature-reserve cover + agriculture cover |
| H12: Group size — continuous |
| H13: Group structure: family group, sub-adult group, solitary male, solitary female, solitary sub-adult — categorical |

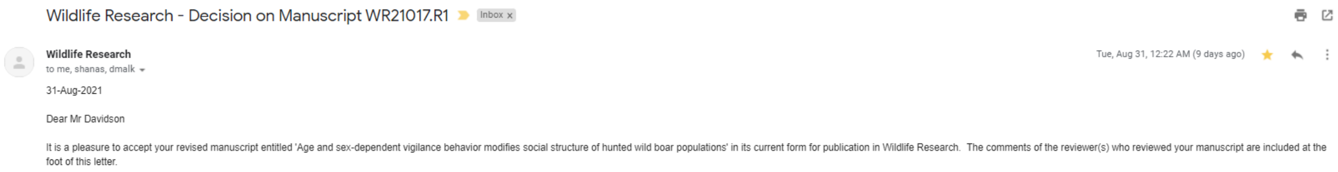
**Appendix 2:** A summary statistics table per feeding device for EDE, TBE and ACE.

| Location | Land use type | Eat | No eat | Mean TBE | Mean ACE |
|---|---|---|---|---|---|
| Beit Oren | Nature reserve | 4 | 1 | 765.8 | 150.0 |
| Haifa 1 | Urban hunting | 16 | 5 | 4.7 | 300.0 |
| Haifa 2 | Urban hunting | 6 | 1 | 100.2 | 266.6 |
| Haifa 3 | Urban hunting | 15 | 3 | 36.4 | 300.0 |
| Magan Michael | Agriculture | 0 | 14 | NA | 0.0 |
| Nesher 1 | Urban No hunting | 12 | 2 | 34.0 | 300.0 |
| Nesher 2 | Urban No hunting | 15 | 1 | 54.8 | 300.0 |
| Nesher 3 | Urban No hunting | 18 | 6 | 21.4 | 266.6 |
| Ramat Hanadiv 1 | Nature reserve | 0 | 1 | NA | 0.0 |
| Mount Chorshan | Nature reserve | 1 | 3 | 438.0 | 37.5 |
| Kfar Galim | Agriculture | 0 | 11 | NA | 0.0 |
| Hanadiv valley | Agriculture | 0 | 2 | NA | 0.0 |
| Megadim | Agriculture | 0 | 7 | NA | 0.0 |
| Ramat Hanadiv 2 | Nature reserve | 0 | 3 | NA | 0.0 |

# Chapter 3

## Age and sex-dependent vigilance behaviour modifies social structure of hunted wild boar populations

The manuscript was accepted for publication in Wildlife Research.



Wildlife Research - Decision on Manuscript WR21017.R1

**Wildlife Research**
to me, shanas, dmalk

Tue, Aug 31, 12:22 AM (9 days ago)

31-Aug-2021

Dear Mr Davidson

It is a pleasure to accept your revised manuscript entitled 'Age and sex-dependent vigilance behavior modifies social structure of hunted wild boar populations' in its current form for publication in Wildlife Research.  The comments of the reviewer(s) who reviewed your manuscript are included at the foot of this letter.

# Statement of Authorship

## Principal Author

| | | | |
|---|---|---|---|
| Title of Paper | Age and sex-dependent vigilance behavior modifies social structure of hunted wild boar populations | | |
| Publication Status | ☐ Published ☐ Accepted for Publication<br>☑ Submitted for Publication | | |
| Publication Details | Submitted to Journal of Wildlife Research | | |
| Name of Principal Author (Candidate) | Achiad Davidson | | |
| Contribution to the Paper | Conceived, designed and performed the research, analysed the data and wrote the paper (supervised by Uri Shanas and Dan Malkinson). | | |
| Certification: | This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper. | | |
| Name and Signature | Achiad Davidson | Date | 22.2.2021 |

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By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the dissertation

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# Age and sex-dependent vigilance behaviour modifies social structure of hunted wild boar populations

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**Short summary**

We studied the behaviour of wild boars in hunting permitted (agriculture) and prohibited (nature reserves) landscapes. Under hunting pressure, yearling males are more vigilant than yearling females and yearling males tend to remain in their family group and not disperse. Furthermore, adult females are more vigilant than adult males and show preference for hunting prohibited lands. We propose that hunting pressure alters wild boar’s behaviour and social structure.

## Abstract

**Context:** Human activities, in general, and hunting, in particular, often have significant impacts on the behaviour of wildlife through the anti-predator behaviours they evoke. Wild boar populations are rapidly expanding worldwide and their population densities are increasing.

**Aims:** We examined hunting effects in a combination with different land-use factors on the behaviour and social structure of wild boars (*Sus scrofa*) in Israel. Specifically, we examined differences in vigilant behaviour and social structure in agricultural areas (hunting permitted) and nature reserves (hunting prohibited).

**Methods:** We installed motion-triggered cameras to record wild boars' social structure and vigilance behaviour along movement trails. We identified the age and sex of individual wild boars and the size and structure of their social groups, and quantified hunting in each of the studied areas.

**Key results:** Results indicated significant differences in the vigilance behaviour of wild boars between agricultural areas and nature reserves. In agricultural areas, adult females were significantly more vigilant compared to adult males. Additionally, in these areas we found significantly more adult males and less females leading family groups. Furthermore, male yearlings were significantly more vigilant in agricultural areas compared to female yearlings. Male yearlings tended to roam significantly more with family groups in agricultural areas compared to nature reserves, where they tended to roam alone or in groups.

**Conclusions:** These results indicate social and behavioural differences between wild boars in agricultural areas and nature reserves, suggesting that hunting may have a significant impact on their social structure and behaviour.

**Implications:** Overall, our findings support the behavioral and social consequences of human hunting. Long-term implications of altered behavioral and social responses should be considered in management and conservations strategies. For instance, the high proportion of male yearlings in family groups in agricultural areas in autumn (mating season) may offer young males early access to reproductive females, even within the same social group. This may eventually lead to an increase in the reproductive potential of female wild boars.

## Introduction

Prey species commonly react to increased levels of predation risk by showing anti-predator behaviour (Lima and Bednekoff 1999). Such responses usually involve changing the foraging activity in time or space, such as shifting activity to safe patches and exhibiting higher levels of vigilance (Lima and Dill 1990; Kotler et al. 1994; Brown 1999). Human activities, in general, and hunting actions, in particular, often have significant impacts on the behaviour and spatial distribution of wildlife through the anti-predator behaviours they evoke (Frid and Dill 2002). The detrimental effects of hunting on animals’ behaviour have been well documented (Tolon et al. 2009;  Saïd et al. 2012). When risk is perceived as high, the immediate responses can be a decrease in activity rates (Kaczensky et al. 2006; Podgorski et al. 2013), a rapid flight behaviour to escape the risk (Sunde et al. 2009; Thurfjell et al. 2013) and/or the use of safer areas (Tolon et al. 2009;  Saïd et al. 2012). However, responses can also be more complex and perpetuate after the risk has disappeared, especially when they include spatial disruptions (Keuling et al. 2008; Sunde et al. 2009; Marchand et al. 2014). This applies particularly to large-bodied, long-living species with a lengthy evolutionary history of human persecution, such as wild boars (*Sus scrofa*) (Keuling et al. 2010; Scillitani et al. 2010; Thurfjell et al. 2013)

Over the past few decades, wild boar populations have increased worldwide and expanded their overall geographic distribution particularly in the vicinity of agricultural areas (Marsan et al. 1995; Apollonio et al. 2010; Massei et al. 2015). These population increases have intensified human-boar conflicts (Barrios-Garcia and Ballari 2012; Schlageter and Haag-Wackernagel 2012; Thurfjell et al. 2013), leading to elevated economic costs, resulting from epidemics to livestock and humans, and damages to agricultural crops and to gardens and infrastructure in urban areas (Apollonio et al. 2010; Barrios-Garcia and Ballari 2012; Massei et al. 2015). Furthermore, in natural areas, boars' feeding habits, particularly rooting disturbance, can reduce plant cover and diversity, and affect different animal communities through predation and habitat destruction (Barrios-Garcia and Ballari 2012).

Hunting is the most common and widespread management tool applied throughout the world to minimise conflicts with wild boars in agricultural areas (Toigo et al. 2008; Gamelon et al. 2011; Keuling et al. 2013). Furthermore, the number of wild boars harvested has consistently increased over the last three decades worldwide (Massei et al. 2015). For instance, a recent study by Linnell et al. (2020) estimates that more than seven million wild boars are hunted every year in European countries. However, despite the high hunting pressure, the number of wild boars in European countries continues to increase with a mean annual growth rate of approximately 20%, ensuing in ineffective culling efforts (Massei et al 2015).

The mortality of individuals, especially of adults, due to hunting has been considered a potential driver of variations in the social organisation of wild boar populations (Poteaux et al. 2009). These variations may facilitate the breakup of the boars' polygynous mating system and thus accelerate the turnover of adults within the matrilineal groups (Poteaux et al. 2009). However, a clear understanding of the effect of hunting on the social structure of wild boars is still lacking.

The social structure of the wild boar includes several closely related philopatric females (Truve and Lemel 2003; Kaminski et al. 2005) with piglets and yearlings, ranging from 6 to 30 individuals (Boitani et al. 1994; Kaminski et al. 2005). The matrilineal social organisation is centred on adult females and their offspring (Kaminski et al. 2005). The female groups mostly depend on the leading sows to facilitate group cohesion (Sodeikat and Pohlmeyer 2003). Males congregate with females in autumn, during the rut period, establishing large mixed groups (Cousse et al. 1994; Fernandez-Llario et al. 1996; Kaminski et al. 2005). Piglets are commonly born in spring; as they grow, the mother-piglet bonds loosen and piglets become increasingly independent (Cousse et al. 1994; Kaminski et al. 2005). While most female yearlings stay within their natal home range and often within their mother's group (Nakatani and Ono 1995; Kaminski et al. 2005), male yearlings usually disperse, roughly between the age of 8 to 14 months, starting in autumn when adult males join the family groups (Andrzejewski and Jezierski 1978; Truve and Lemel 2003; Podgorski et al. 2018). However, local contingencies can lead to deviations from these traditional social patterns (Maselli et al. 2014), leading us to question whether high hunting pressure could account for seasonal variations in the social organisation of wild boar.

The elevated hunting pressure that wild boars are subjected to significantly affects their behaviour. For example, it affects their dispersal patterns (Keuling et al. 2010), and leads to larger resting ranges and more interspersed resting sites (Keuling et al. 2008; Scillitani et al. 2010). Hunting may also cause wild boars to select safer habitats, even at the expense of decreased resource abundance (Saïd et al. 2012). Although several studies have shown that hunting affects the spatial behaviour of wild boars (Keuling et al. 2010; Saïd et al. 2012; Thurfjell et al. 2013), very few studies have directly tested the effect of hunting on their vigilance behaviour. Quenette and Gerard (1992) and, later, Podgorski et al. (2016) explored and demonstrated how group size may affect collective and individual vigilance and the degree of synchronisation of vigilance among group members; however, they did not find a significant effect of human disturbance and hunting on the vigilance of individuals according to their age and sex. Furthermore, to the best of our knowledge, no study has yet tested if differences in individual vigilance behaviour may predict possible changes in the structure of social organisation among wild boar populations.

In this study, we investigated the effects of human disturbance and hunting on individual's vigilance and social structure of wild boars in northern Israel. Specifically, we tested the vigilance of different age and sex groups of wild boars in nature reserves (hunting prohibited) and adjacent agricultural areas (hunting permitted) within the same geographic landscape. Moreover, we explored whether variations in vigilance behaviour by age and sex can explain changes in the social structure of wild boars. Applying non-invasive approaches, we quantified differences in the vigilance and social structure of wild boars in response to different land-use factors. We hypothesised that in agricultural areas, where wild boars are exposed to high hunting pressure and frequent interactions with humans, individuals of all ages and sexes will exhibit higher vigilance and, consequently, different social organisations compared to those in nature reserves will emerge.

## Methods

### *Study area*

The study took place in the Carmel Mountain and its coastal range in northern Israel (Figure 1), an area of approximately 600 km$^2$, with an elevation ranging from 0 to 546 m above sea level. The climate is Mediterranean, and the annual rainfall varies between 700 mm in the higher elevations of the Carmel and 500 mm in the lower areas of the coastal planes, falling mainly (80%) between December and March. The natural vegetation is a typical Mediterranean maquis (Neeman et al. 1995; Hadar et al. 1999), intermixed with cultivated areas, which are dominated by orchards of citrus, almonds and olives and fields of corn and wheat. Within the region several small villages are present. Of this region, approximately 124 km$^2$ are protected within a proclaimed national park and nature reserves.

Within this study area, the main predator of wild boars in Israel, the wolf, is absent. However, there are other factors causing mortality to wild boars that have been recorded in the past decade by Israel Nature and Parks Authority (INPA), especially selective hunting. This region exhibits the highest hunting pressure in Israel, as well as the highest reported number of human-wild boar conflicts in agricultural landscapes (Lider 2012) and urban areas (Malkinson 2015). Hunting is permitted in agricultural areas throughout the year and prohibited in nature reserves year-round. Nature reserves and agricultural areas do not provide an ideal setting for comparison due to differences in landscape structure. However, as hunting in the region takes place in all agricultural areas, and none occurs in nature reserves, this design was the most optimal we could devise.

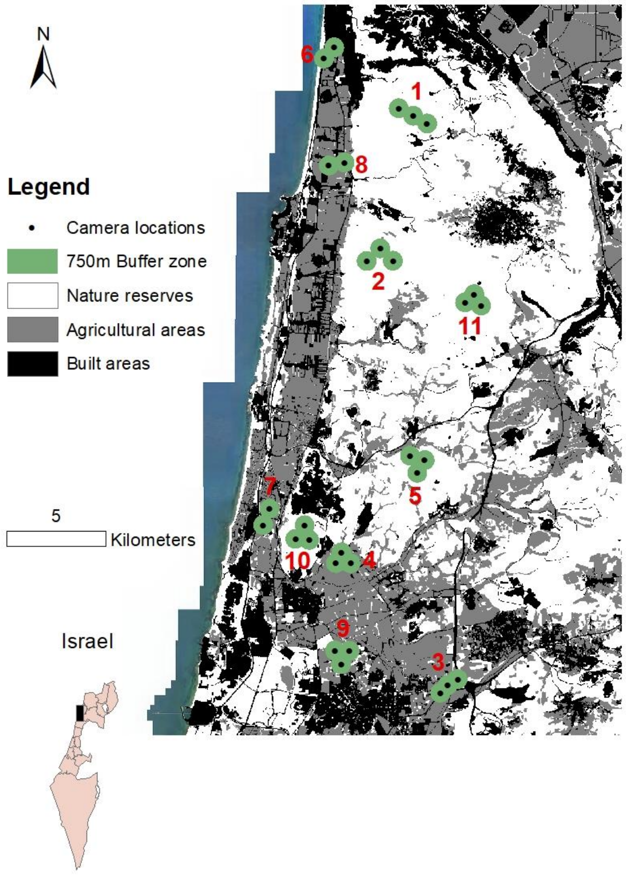

**Figure 1:** The study area in the Carmel coastal mountain range, Israel, including the agricultural areas (hunting permitted) and nature reserves (hunting prohibited), and sampling sites (numbered).

*Assessing social structure and vigilance*

To assess wild boars' vigilance behaviour and social structure, we installed 30 motion-triggered cameras in agricultural areas and nature reserves (Figure 1). We used Bushnell Trophy camera traps (model 119445). Camera traps were set to capture videos in 20-sec intervals, with a refractory period of 1 sec, a resolution of 12 MP, and 640 × 480 pixels per frame. Census efforts did not differ among the sampling seasons and were performed for 21 days, twice a year, for two years (spring and autumn of 2016 and 2017). To determine the optimal locations for the cameras, we searched for wild boars' digging signs, scats, footprints, tree-rubbing marks and mud wallows (Maselli et al. 2014). Cameras were installed on tree trunks or iron poles, approximately 1 m above the ground at locations with signs of wild boar presence, to maximise the chances of capturing wild boars and their behaviour by the cameras (Huckschlag 2008; Ebert et al. 2010). Our goal was not to define the populations densities but to document as many social groups as possible (Maselli et al. 2014). Cameras were installed in spots with dense vegetation cover that resemble the natural vegetation structure of the location. For further details concerning the camera trap system and its installation, see Huckschlag (2008).

Camera traps were placed in 11 different sites: five in nature reserves and six in agricultural fields (Figure 1). In each site, we installed 2–3 camera traps approximately 750 to 1,000 m away from each other to reduce the probability of capturing the same individuals in more than one camera (Huckschlag 2008; Maselli et al. 2014). The selected sites in nature reserves were selected as far as possible from the reserve's boundary and from agricultural areas, and vice versa for sites located in agricultural areas. We individually identified the video-trapped wild boar groups and categorised them according to group structure and size (Nakatani and Ono 1995; Maselli et al. 2014), and temporal behaviour (the hours of activity during a 24-hour period). The morphological characteristics of the individuals were also recorded (size, wounds, etc.). Each individual was assigned to an age and sex cohort: adult male or female (more than 2 years old), yearling/subadult male or female (1 to 2 years old), and piglet (less than 1 year old - piglets sex was not recorded, because it cannot be recognized by videos). Usually family groups include one or more adult females with piglets and female yearlings. However, during a preliminary study, we also observed family groups with male yearlings. Thus, in order to distinguish between family groups with or without male yearlings, we recorded the sex of yearlings, in general, and within family groups, in particular. Stratford et al. (2020) found highly dynamic sub-group formation in spotted hyenas (*Crocuta crocuta*), thus making it difficult to establish social group size. Wild boar herds are not commonly characterized by highly dynamic sub-group formations (Kaminski et al. 2005). To estimate group structure, we meticulously analysed the videos and recorded different sub-group formations. Furthermore, during a preliminary study, we noticed that because the cameras were installed for 21 consecutive days, usually the same groups and individuals were recorded a few times during this period (in a single night or on a course of a few days or weeks), thus enabling us to more easily identify sub-groups that were eventually merged into a bigger group or as a separate group by itself. Finally, in cases where the same social group was recorded more than once by a camera or in a site, we counted that group only once (i.e., noted their group structure and size only once).

All of the recorded videos were stored in folders according to camera locations, and were watched using windows media player. To assess vigilance, we determined whether an individual stood still and scanned the surroundings with his head lifted, interrupting its ongoing behaviour (Altmann 1974; Podgorski et al. 2016; Erdtmann and Keuling 2020). The recognition of the vigilant act was unambiguous. For each individual within each group, we determined the animal's vigilance activity as a binary response variable (vigilant: 1; non-vigilant: 0) at each second of the 20-sec video sequence (Altmann 1974; Podgorski et al. 2016; Erdtmann and Keuling 2020).

### *Land-use cover*

Around each camera, we quantified the land-use cover in a 750 m radius buffer zone (an area of 1.77 $km^2$). The home-range sizes of wild boars are relatively small compared to other similarly sized ungulates, considering the potential mobility of the species (Russo et al. 1997; Podgorski et al. 2013; Morelle et al. 2015). For instance, in rural areas in Italy, which has a Mediterranean climate and vegetation similar to Israel, Boitani et al. (1994) found that the core of the home ranges of wild boars were <1.0$km^2$. Furthermore, Russo et al. (1997) also found in Italy, that the average daily home range size of wild boars was 0.33$km^2$. Thus, the 750 m radius buffer zone generally covers the average daily home range of wild boars in rural areas.

Within each buffer zone, we characterised the relevant land-use factors; specifically, agriculture, built areas, and nature reserves, as well as the weighted hunting pressure. Based on a 25 m resolution land use layer (HAMAARAG 2016) we summed the number of pixels of agriculture, built areas and nature reserves within each of the different buffer zones using ArcMap (ESRI 2018). Then we estimated the weighted hunting pressure as follows: the agricultural areas were divided into nine polygons and each was assigned a hunting pressure from 1 to 3 (1 representing low hunting pressure and 3, high hunting pressure). Because INPA does not formally record the exact location of hunting events, we used expert opinions of three different INPA ecologists and rangers and cross-validated them with local hunters' to estimate the hunting pressure within each polygon. For each camera's buffer zone, the weighted hunting pressure was calculated according to the proportions of the different polygons within it. As hunting does not occur in nature reserves, the hunting polygons for the nature reserves were assigned a value of zero. Hof HaCarmel Regional Council, is the only area within the study region that the INPA thoroughly records hunting events. Thus, we used Hof HaCarmel hunting records as a benchmark reference for the rest of the polygons in the study site. The hunting pressure in Hof HaCarmel was assigned by the INPA ecologists and rangers with a value of 3, Based on an average of 40 hunting campaigns/week that are carried out continuously throughout the year. On average 870 boars/year were hunted in Hof HaCarmel during the years 2016-2017 which has a Jurisdiction of 190km$^2$. Other regions that were assigned with the value of 3 have similar hunting intensities. In low hunting pressure areas INPA rangers estimate that the average number of hunting campaigns is approximately 3 per week throughout the year. Finally, for each camera location, we investigated vigilance and social structure as dependent on land use and hunting pressure.

### *Model development and evaluation*

A set of models were assembled as a basis for exploring the effects of different land-use factors on wild boars' social structure and vigilance (Table 1). The land-use model was treated as a categorical model, and included agriculture and nature reserves. In other models, the spatial extent of agriculture, built areas, nature reserves, as well as hunting pressure, were treated as continuous variables (Table 1). Ideally, we would have chosen to use Generalised Linear Mixed Models (GLMM), which are very useful in dealing with pseudo-replication (Bolker et al. 2009; Zuur and Ieno 2016). However, due to the relatively small numbers of random-effects levels, the assumptions of GLMMs could not be met. Thus, in order to control for the possible pseudo-replication imposed by the spatial location of cameras within the same site, we merged overlapping camera buffer zones within the same site; i.e., in cases where two or more buffer zones overlapped in the same site, the overlapped sections were evaluated only once for the land-use cover analysis. Consequently, in these cases, we pooled the behavioural and social-structure data of cameras within the same site. Because we individually identified the video-recorded wild boars’ groups in each camera, we were able to ensure that the same social group did not appear in two different sites in the same site. Accordingly, General Linear Models (GLM) were used to investigate the relationships between the dependent variables: social structure categories (Table 2) and vigilance, with the land-use factors.

**Table 1:** The complete set of alternative GLMs, testing the effect of different land-use factors on wild boars' vigilance and social structure.

| **Alternative models** |
|---|
| H1: Land use: agriculture and nature reserves — categorical |
| H2: agriculture cover — continuous |
| H3: built-area cover — continuous |
| H4: nature-reserve cover — continuous |
| H5: hunting pressure — continuous |

**Table 2:** Categorisation of social groups.

| Social groups | Description |
|---|---|
| Family group | One or more adult females with piglets and yearlings |
| Mixed group | Adult males, adult females and young |
| Group of adult males | Two or more adult males, without adult females, subadults or piglets in close proximity |
| Group of adult females | Two or more adult females, without adult males, subadults or piglets in close proximity |
| Group of subadults | Group of subadults (of either sex), without adults or piglets in close proximity |
| Group of piglets | Group of piglets (of either sex), without adults or subadults in close proximity |
| Solitary adult male | An adult male, without other adult males or females, subadults or piglets in close proximity |
| Solitary adult female | An adult female, without other adult females or males, subadults or piglets in close proximity |
| Solitary subadult | A subadult (of either sex), without other subadults, adults or piglets in close proximity |
| Solitary piglet | A piglet (of either sex), without other piglets, adults or subadults in close proximity |

To do so, five alternative GLMs were formulated. All GLMs were ranked according to their fit to the empirical data using a model-selection approach, whereby the maximum log-likelihoods of the models were compared (Burnham and Anderson 2002). Social structure categories (Table 2) were analysed as the absolute number of occurrences of a given category in relation to a different one. This enabled us to treat the occurrences as a binomial variable, where in each analysis one group structure was addressed as 'binomial success' and the other as a 'binomial failure'. Vigilance was analysed as a proportion of individuals that did or did not exhibit vigilant behaviour. Thus, the social structure categories and vigilance behaviour were all modelled as binomial variables, following Dobson (2002) and Mangiafico (2016). The relative support for each model was evaluated using Akaike Information Criterion (AIC). The corrected AIC (AICc) score was used to rank and compare the models. In addition, the 'Akaike Weight' of each model was used to estimate the probability that a given model is the best model within the given set of alternatives (Burnham and Anderson 2002).

The model-selection approach does not evaluate the goodness-of-fit of the models, yet this information is critical, especially for evaluating the prediction potential of the high-ranking models. In GLMs, where $R^2$ values cannot be formally calculated. Dobson (2002) offered to use the proportional increase in explained deviance, pseudo $R^2$, as an alternative. This value is a relative measure comparing models that are using the same data. Accordingly, we used the Nagelkerke/Cragg and Uhler pseudo $R^2$, as recommended by Mangiafico (2016). The procedures — GLMs, $R^2$, and model selection — were conducted in R (R Development Core Team, 2014).

## Results

### *Evaluating vigilance in nature reserves and agricultural areas*

A total of 42,167 videos were filmed, of which 5,554 captured wild boars at 11 different sites in nature reserves and agricultural areas during the two-year camera census in the spring and autumn of 2016–2017. Wild boars appeared at all camera locations at the study sites. None of the individuals or groups of wild boars that were recorded were filmed in different sites. From a total of 2169 individuals that were recorded we identified 1947 different individuals by age and sex (89%) (Appendix 1). Furthermore, we managed to individually identify the sex of 94% of the adults and 74% of the yearlings recorded (Appendix 1). For our analysis we used only data of individuals that were recognized by both age and sex. For our analysis we used only the data we had of individuals that were recognized by both their age and sex. Season did not have a significant effect on vigilance, thus we pooled the vigilance data from spring and autumn and analysed them together as a single data set. Group size did not have a significant effect on the vigilance behaviour of wild boar. The nature-reserve land-use cover model best explained the relationship among land-use factors and the vigilance of all individuals (all sexes and ages together). Significant differences in the vigilance behaviour of wild boars were observed between nature reserves and agricultural areas: the ratio of non-vigilant to vigilant wild boars increased as the proportion of nature-reserve cover increased, indicating decreasing vigilance with increasing nature-reserve cover (Akaike weight of 0.961, $R^2 = 0.96$, Table 3) (Figure 2).

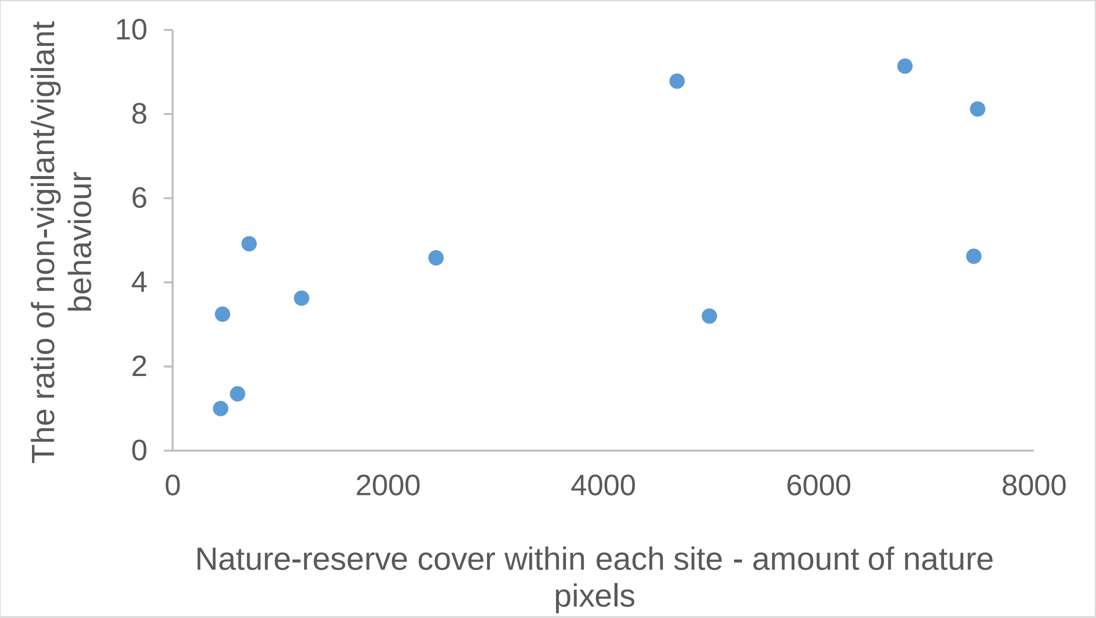

**Figure 2:** The proportion of non-vigilant to vigilant wild boars (of all sexes and ages together) as a function of the amount of nature-reserve cover within each site (amount of nature pixels).

All other models also revealed that wild boars were significantly more vigilant in agricultural areas (hunting permitted) compared to nature reserves (hunting prohibited). A negative effect on vigilance was found for all the factors representing agricultural areas (agriculture cover, built-area cover and hunting pressure), and there was a significant difference between agriculture and nature reserves for the land-use categorical model (Table 3).

**Table 3:** Model-selection statistics of the effects of the land-use factors on the vigilance of all individuals (all sexes and ages together). Models were ranked by AICc and model weight. Only the top 3 ranked models and the null model (Intercept only) are presented (the full table is presented as appendix 2 in the Supplementary Material). Agriculture (Agri), Nature reserves (Nature) and Hunting pressure (Hunting pr.).

| Model | Coefficient | Estimate | Std. error | *z* value | *P*-value | ΔAICc | Weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Nature cover | | | | | | 0.00 | 0.954 | 0.96 |
| | Intercept | 0.708 | 0.113 | 6.238 | <0.001* | | | |
| | Nature cover | 0.001 | 0.002 | 5.803 | <0.001* | | | |
| Land use | | | | | | 7.20 | 0.032 | 0.93 |
| | Intercept | 0.890 | 0.096 | -2.656 | <0.001* | | | |
| | Nature/Agriculture | 0.795 | 0.151 | 5.265 | <0.001* | | | |
| Agri cover | | | | | | 7.72 | 0.021 | 0.92 |
| | Intercept | 1.777 | 0.127 | 13.989 | <0.001* | | | |
| | Agriculture cover | -0.003 | 0.006 | -5.358 | <0.001* | | | |
| Intercept only | | | | | | 32.77 | 7.3E-08 | 0.00 |
| | Intercept | 1.260 | 0.073 | 17.200 | <0.001* | | | |

*Sex- and age-dependent vigilance*

Adult females (Appendix 3), male and female yearlings together (Appendix 4) and male yearlings (Appendix 5) were all significantly more vigilant in agricultural areas (hunting permitted) compared to nature reserves (hunting prohibited). The nature-reserve-cover model best explained the effect of land-use factors on females' vigilance: vigilance decreased with increasing nature-reserve cover (Akaike weight of 0.79, $R^2 = 0.90$, Appendix 3). The agriculture-cover model best explains the effect of land-use factors on the vigilance of all yearlings together: vigilance increased with increasing agriculture cover (Akaike weight of 0.99, $R^2 = 0.92$, Appendix 4). The agriculture-cover model also best explained the effect of land-use factors on male yearlings' vigilance: vigilance increased with increasing agriculture cover (Akaike weight of 0.96, $R^2 = 0.83$, Appendix 5). For adult males and female yearlings, none of the tested models yielded significant relationships.

*Social structure differences between nature reserves and agriculture areas*

We quantified wild boars' social structure by examining their social occurrences in nature reserves and agricultural areas at 11 different sites during the two-year camera census in the spring and autumn of 2016–2017 (Appendix 6). Based on our identification of the social groups and individuals, none of them were observed and recorded in more than one site. Furthermore, we did not have any sub-group that was not identified as part of a bigger group or as a separate group by itself. In nature reserves (hunting prohibited), family groups were most predominant and constituted 29% of all social groups recorded by camera traps (Figure 3). However, in agricultural areas (hunting permitted), the most predominant social group recorded were of adult males (26%) and family groups constituted only 17% of all social groups recorded (Figure 4).

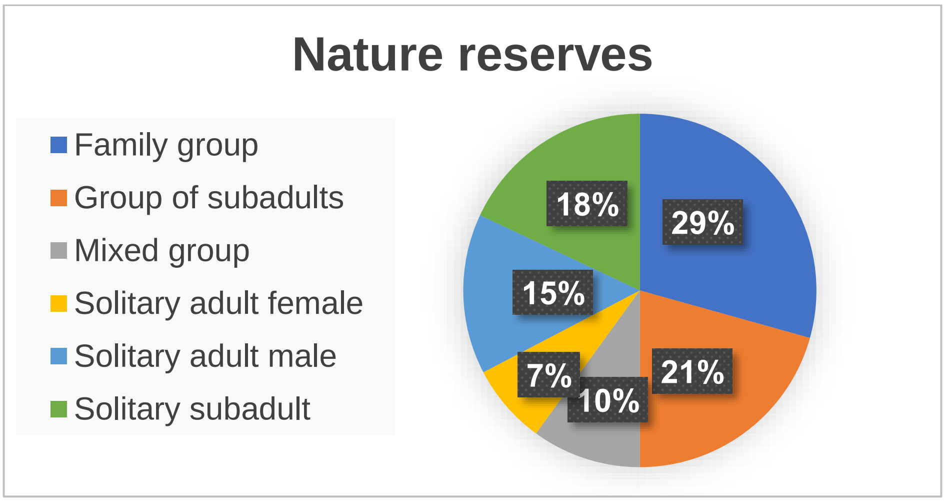

**Figure 3:** The proportion of different social groups recorded in nature reserves during the two-year camera census efforts in the spring and autumn of 2016–2017.

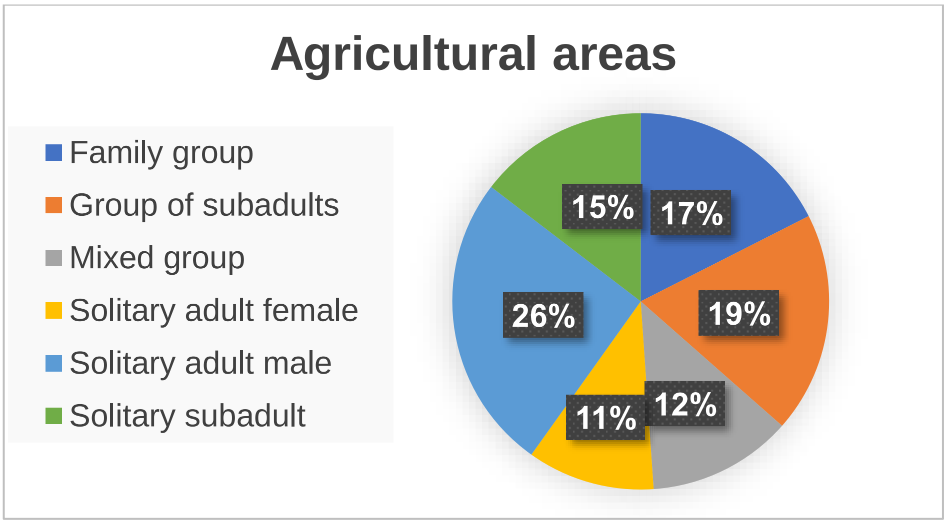

**Figure 4:** The proportion of different social groups recorded in agricultural areas during the two-year camera census efforts in the spring and autumn of 2016–2017.

Moreover, in autumn we found that in agricultural areas, the ratio of adult males to family groups increased significantly with increasing built-area cover, thus the best explanatory model was built-area cover (Akaike weight of 0.99, $R^2 = 0.80$, Table 4). The agriculture cover, hunting pressure and categorical land-use models also indicated that the ratio of adult males to family groups was significantly higher in agricultural areas and lower in nature reserves (Table 4).

**Table 4:** Model-selection statistics of the effects of the land-use factors on the ratio of adult males to family groups in autumn. Models were ranked by AICc and model weight. Only the top 3 ranked models and the null model (Intercept only) are presented (the full table is presented as appendix 7 in the Supplementary Material). Agriculture (Agri), Nature reserves (Nature) and Hunting pressure (Hunting pr.).

| Model | Coefficient | Estimate | Std. error | *z* value | *P*-value | ΔAICc | Weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Built areas | | | | | | 0.00 | 0.989 | 0.80 |
| | Intercept | -2.217 | 0.681 | -3.254 | 0.001 | | | |
| | Built areas | 0.003 | 0.002 | 3.386 | <0.001* | | | |
| Land use | | | | | | 11.25 | 3.6E-03 | 0.39 |
| | Intercept | 0.693 | 0.500 | 1.386 | 0.165 | | | |
| | Nature/Agri | -1.386 | 0.621 | -2.230 | 0.025* | | | |
| Agri cover | | | | | | 11.39 | 3.3E-03 | 0.39 |
| | Intercept | -0.993 | 0.467 | -2.123 | 0.033* | | | |
| | Agriculture cover | 0.005 | 0.002 | 2.105 | 0.035* | | | |
| Intercept only | | | | | | 13.48 | 1.2E-03 | 0.00 |
| | Intercept | -0.196 | 0.281 | -0.699 | 0.485 | | | |

Additionally, we found that in autumn the number of occurrences of male yearlings roaming with family groups in agricultural areas was higher compared to nature reserves (Figure 5). Moreover, our results showed that in autumn the ratio of male yearlings roaming with a family group increased significantly with increasing agriculture cover (indicates hunting areas) and decreased with increasing nature-reserve cover (indicates no hunting areas), such that the agriculture-cover model was the most robust with an Akaike weight of 0.66, $R^2 = 0.44$ (Table 5).

**Figure 5:** The frequency of male yearlings in autumn roaming with and without family groups in nature reserves and agricultural areas.

**Table 5:** Model-selection statistics of the effects of the land-use factors on the ratio of male yearlings roaming with and without a family group in autumn. Models were ranked by AICc and model weight. Only significant models and the null model (Intercept only) are presented. Agriculture (Agri), Nature reserves (Nature) and Hunting pressure (Hunting pr.).

| Model | Coefficient | Estimate | Std. error | *z* value | *P*-value | ΔAICc | Weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Agri cover | | | | | | 0 | 0.604 | 0.44 |
| | Intercept | -0.921 | 0.509 | -1.807 | 0.070 | | | |
| | Agri cover | 0.008 | 0.004 | 2.177 | 0.029 * | | | |
| Nature cover | | | | | | 0.84 | 0.395 | 0.36 |
| | Intercept | 0.872 | 0.499 | -2.656 | 0.080 | | | |
| | Nature cover | -0.002 | 0.001 | -2.104 | 0.035 * | | | |
| Intercept only | | | | | | 6.98 | 0.011 | 0.00 |
| | Intercept | 0.040 | 0.285 | 0.143 | 0.886 | | | |

## Discussion

Various studies have investigated the effects of predation risk on animal's behaviour (Frid and Dill 2002; Kuijper et al. 2014; Marchand et al. 2014). Yet our approach of evaluating wild boars' vigilance behaviour by age and sex in relation to different land-use factors yielded surprising insights. The vigilance of the wild boars varies spatially, depending on different land-use factors. When analysing the vigilance behaviour of all individuals together, our results suggest that generally wild boars in agricultural areas, where hunting is permitted, perceive a greater predation risk than wild boars in nature reserves were hunting is prohibited. However, a more detailed analysis of this behaviour, considering age and sex, revealed a more complex picture. Adult females showed significantly higher vigilance in agricultural areas compared to nature reserves. On the other hand, adult males did not show any significant differences in vigilance between agricultural areas and nature reserves, and were observed significantly more in agriculture areas compared to females. Scillitani et al. (2010) found that, when chased by hunting dogs, only family groups (and not males) fled and showed larger resting ranges and more interspersed resting sites. Furthermore, Saïd et al. (2012) observed that females responded to hunting disturbance more than males, leading to a pronounced sexual difference during the hunting season. Moreover, they found that only females showed a decrease in bush use during the hunting season. This decrease might be explained by the increased hunting effort in the study area or by the increased movements between resting sites due to disturbance (Saïd et al. 2012). Thus our results are in line with the ones reported by Tolon et al. (2009), where wild boars spatially respond to hunting with respect to females. In contrast, where the male wild boar demonstrated no significant differences in vigilance, this resembles the results reported by Keuling et al. (2008). Due to the differential response of male and females, we attribute this to hunting activities, and not to land cover. Moreover, these differences between the sexes might be amplified as females with offspring respond more strongly to hunting (Saïd et al. 2012). This explanation may also apply to the different vigilance responses by the sexes found in our study.

When analysing yearlings' vigilance, our results showed that they generally perceive a greater predation risk in agricultural lands compared to nature reserves, similar to adult females. However, when we further explored the vigilance behaviour of male and female yearlings separately, we found that only male yearlings showed significantly higher vigilance in agricultural areas. Many studies have shown a decrease in individual vigilance with increasing group size (Pays et al. 2007; Pays et al. 2012), including studies of wild boar (Quenette and Gerard 1992; Podgorski et al. 2016). Thus, it could be hypothesised that male yearlings roaming solitarily or in a small group of unexperienced yearlings (Andrzejewski and Jezierski 1978; Truve and Lemel 2003) will demonstrate relatively higher vigilance compared with female yearlings roaming in large family herds (Nakatani and Ono 1995), which might provide them with a higher sense of security. Our study suggests that the basic social unit of boars is solitary males or family group led by females, similar to the observations of Nakatani and Ono (1995). However, in autumn, the ratio of adult males to family groups was significantly higher in agricultural areas compared to nature reserves. Moreover, buildings and infrastructure within agricultural lands increased this ratio even further. These results suggest that, during autumn, adult females may avoid agricultural areas, in general, and the built areas on agricultural lands, specifically, which are probably associated with higher risk due to higher human activities and hunting. These findings correspond with our behavioural findings that showed that adult females were significantly more vigilant in agricultural lands as opposed to adult males.

In Mediterranean landscapes, wild boars have lower availability of natural-food and water during the summer and autumn compared to northern Europe. Limited access to forage occurs mainly during this period due to the dry, hardened soil, and overall reduced, and limited natural availability of fodder. Such a food shortage may result in high natural mortality during this season (Woodall 1983; Caley 1993; Massei et al. 1997). Thus, wild boars are forced to extend their search for food and water in irrigated crop fields during this season (Woodall 1983; Baber and Coblentz 1986; Massei et al. 1997). As mentioned above, sexual differences in behaviour might result from females' stronger response to hunting. This may lead females to select safer habitats, such as nature reserves, even at the expense of higher resource abundance in agricultural areas during autumn, whereas males are more prone to risk and remain hidden in very dense vegetation plots in agricultural lands (Saïd et al. 2012).

Usually, at the stage of reaching sexual maturity around 1 year of age, male yearlings leave the maternal group (Andrzejewski and Jezierski 1978; Truve and Lemel 2003). However, we found some exceptions to this social pattern. Our results showed that in autumn there were significantly more male yearlings roaming with family groups in agricultural areas, while in nature reserves, significantly more male yearlings roamed solitarily or in all male groups. This finding corresponds with the behavioural results that showed that male yearlings were significantly more vigilant in agricultural areas compared to nature reserves. It has already been demonstrated that wild boars tend to reduce 'predation risk' by modifying their behaviour, choosing to aggregate in response to hunting disturbances (Saïd et al. 2012). Furthermore, Keuling et al. (2010) found that, under high culling pressure, male yearlings demonstrate relatively low dispersal rates from their natal home range, probably due to the higher risk of being hunted during dispersal. Therefore, we suggest that hunting increases the vigilance of yearling males, thus delaying their dispersal from their maternal herd. Furthermore, the high proportion of male yearlings in family groups in agricultural areas in autumn (mating season) may offer young males early access to reproductive females, even within the same social group (Poteaux et al. 2009). Thus we cautiously speculate that this may increase their reproductive potential. Our study design was set to assess vigilance behaviour and social structure in different land use types – nature reserves and agricultural areas – which represent different hunting regimes. Yet, we cautiously interpret our results, as hunting pressure is not the only difference between these two land use categories. Increased forage availability during the fall in the agricultural areas is also of a difference, for example.

Considering the vigilance of individuals by age and sex, this study provides a standard measure for wild boars' perception of predation risk (Sih 1980; Fortin et al. 2005; Hernandez and Laundre 2005; Erdtmann and Keuling 2020). This measure enabled us to quantify wild boars' risk perception and better understand how it affects their social structure. This study provides a detailed assessment of the important land-use features working together to shape wild boars' behavioural and social responses to human disturbance and hunting. Yet, our research design was incomplete; the study lacked comparative data from agricultural areas without hunting and nature reserves with hunting, as these combinations are not found in Israel. Therefore, we encourage further research that will include agricultural areas without hunting and nature reserves with hunting, if possible. As stated above, however, hunting is permitted in agricultural areas and prohibited in nature reserves throughout the year (during 12 months), thus it is confounded by land use category, which serves as a strong proxy for it. As is evident from the results, hunting was a consistently significant factor relating to vigilant behaviour, but not to social structure. We interpret this as hunting being a driver for altered individual behaviour, but not of a strong enough factor to disrupt social structure by itself. This is suggestive that hunting in combination with land use have a combined effect, significantly altering social structure. Thus, the methods applied herein provide direct insights into the most important factors affecting the vigilance and social structure of wild boars. In conclusion, the distinction between the age and sex of individuals enabled us to reveal the potential influence that vigilance behaviour has on the social structure of wild boars under hunting pressure. Additionally, our results support the behavioral and social consequences of human hunting. Thus, long-term implications of altered behavioral and social responses should be considered in future management protocols.

## Acknowledgments

We would like to thank Chen Azagui and Almog Hershko for their valuable contributions to the videos analyses, and Ben Rosenberg, Yonatan Harael, Liron Tal, Barak Barchiel and Lishay Ben Yanai from INPA for their invaluable advice. We are grateful to Liat Hadar and Amir Arnon for their support and encouragement.

## Declaration of Funding

This study was financed by a research grant from Ramat Hanadiv Project of the Rothschild Foundation.

## Conflicts of interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data that support this study will be shared if this manuscript will be accepted for publication.

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## Supplementary Material

**Appendix 1:** The total amount of wild boar individuals that were recorded in nature reserves and agriculture areas during the spring and autumn of 2016-2017, including the amount of unknown individuals that were not recognized by their age or sex (piglets sex was not recorded).

| Males | Females | Unknown sex (adults) | Yearlings | Unknown sex (yearlings) | Piglets | Unknown age and se |
|---|---|---|---|---|---|---|
| 351 | 479 | 50 | 456 | 122 | 661 | 50 |

**Appendix 2 (The complete set of alternative GLMs of Table 3):** Model-selection statistics of the effects of the land-use factors on the vigilance of all individuals (all sexes and ages together). Models were ranked by AICc and model weight. Only significant models and the null model (Intercept only) are presented. Agriculture (Agri), Nature reserves (Nature) and Hunting pressure (Hunting pr.).

| Model | Coefficient | Estimate | Std. error | *z* value | *P*-value | ΔAICc | Weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Nature cover | | | | | | 0.00 | 0.954 | 0.96 |
| | Intercept | 0.708 | 0.113 | 6.238 | <0.001* | | | |
| | Nature cover | 0.001 | 0.002 | 5.803 | <0.001* | | | |
| Land use | | | | | | 7.20 | 0.032 | 0.93 |
| | Intercept | 0.890 | 0.096 | -2.656 | <0.001* | | | |
| | Nature/Agriculture | 0.795 | 0.151 | 5.265 | <0.001* | | | |
| Agri cover | | | | | | 7.72 | 0.021 | 0.92 |
| | Intercept | 1.777 | 0.127 | 13.989 | <0.001* | | | |
| | Agriculture cover | -0.003 | 0.006 | -5.358 | <0.001* | | | |
| Hunting pr. | | | | | | 16.48 | 2.5E-04 | 0.83 |
| | Intercept | 1.588 | 0.110 | 14.427 | <0.001* | | | |
| | Hunting pressure | -0.249 | 0.057 | -4.375 | <0.001* | | | |
| Built cover | | | | | | 31.34 | 1.4E-07 | 0.34 |
| | Intercept | 1.420 | 0.106 | 13.367 | <0.001* | | | |
| | Built cover | -0.002 | 0.001 | -2.163 | 0.036* | | | |
| Intercept only | | | | | | 32.77 | 7.3E-08 | 0.00 |
| | Intercept | 1.260 | 0.073 | 17.200 | <0.001* | | | |

**Appendix 3:** Model-selection statistics of the effects of the land-use factors on adult females' vigilance. Models were ranked by AICc and model weight. Only significant models and the null model (Intercept only) are presented. Agriculture (Agri), Nature reserves (Nature) and Hunting pressure (Hunting pr.).

| Model | Coefficient | Estimate | Std. error | *z* value | *P*-value | ΔAICc | Weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Nature cover | | | | | | 0.00 | 0.795 | 0.90 |
| | Intercept | -0.700 | 0.242 | -2.890 | 0.003* | | | |
| | Nature cover | 0.003 | 0.006 | 4.739 | <0.001* | | | |
| Land use | | | | | | 3.37 | 0.154 | 0.86 |
| | Intercept | -0.440 | 0.208 | -2.115 | 0.034 | | | |
| | Nature/Agriculture | 1.330 | 0.296 | 4.504 | <0.001* | | | |
| Hunting pr. | | | | | | 5.27 | 0.062 | 0.83 |
| | Intercept | 0.836 | 0.204 | 4.100 | <0.001* | | | |
| | Hunting pressure | -0.509 | 0.118 | -4.288 | <0.001* | | | |
| Agri cover | | | | | | 15.09 | 4.2E-04 | 0.59 |
| | Intercept | 0.823 | 0.238 | 3.450 | <0.001* | | | |
| | Agriculture cover | -0.003 | 0.001 | -3.048 | 0.002* | | | |
| Built cover | | | | | | 14.96 | 4.5E-04 | 0.59 |
| | Intercept | 0.738 | 0.219 | 3.367 | <0.001* | | | |
| | Built cover | -0.007 | 0.002 | -2.894 | 0.038* | | | |
| Intercept only | | | | | | 21.71 | 1.5E-05 | 0.00 |
| | Intercept | 0.242 | 0.140 | 1.733 | 0.083 | | | |

**Appendix 4:** Model-selection statistics of the effects of the land-use factors on male and female yearlings' vigilance. Models were ranked by AICc and model weight. Only significant models and the null model (Intercept only) are presented. Agriculture (Agri), Nature reserves (Nature) and Hunting pressure (Hunting pr.).

| Model | Coefficient | Estimate | Std. error | *z* value | *P*-value | ΔAICc | Weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Agri cover | | | | | | 0.00 | 0.998 | 0.92 |
| | Intercept | 2.510 | 0.283 | 8.845 | <0.001* | | | |
| | Agriculture cover | -0.008 | 0.001 | -5.110 | <0.001* | | | |
| Land use | | | | | | 19.21 | 6.7E-05 | 0.57 |
| | Intercept | 0.945 | 0.186 | 5.077 | <0.001* | | | |
| | Nature/Agriculture | 0.866 | 0.288 | 3.005 | 0.002* | | | |
| Nature cover | | | | | | 19.31 | 6.4E-05 | 0.57 |
| | Intercept | 0.818 | 0.218 | 3.747 | <0.001* | | | |
| | Nature cover | 0.002 | 0.005 | 2.954 | 0.003* | | | |
| Built cover | | | | | | 22.64 | 1.2E-05 | 0.41 |
| | Intercept | 1.676 | 0.195 | 8.586 | <0.001* | | | |
| | Built cover | -0.004 | 0.001 | -2.504 | 0.012* | | | |
| Hunting pr. | | | | | | 23.55 | 7.6E-06 | 0.36 |
| | Intercept | 1.671 | 0.207 | 8.050 | <0.001* | | | |
| | Hunting pressure | -0.231 | 0.104 | -2.223 | 0.026* | | | |
| Intercept only | | | | | | 25.48 | 2.9E-06 | 0.00 |
| | Intercept | 1.362 | 0.140 | 9.727 | <0.001* | | | |

**Appendix 5:** Model-selection statistics of the effects of the land-use factors on male yearlings' vigilance. Models were ranked by AICc and model weight. Only significant models and the null model (Intercept only) are presented. Agriculture (Agri), Nature reserves (Nature) and Hunting pressure (Hunting pr.).

| Model | Coefficient | Estimate | Std. error | *z* value | *P*-value | ΔAICc | Weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Agri cover | | | | | | 0 | 0.974 | 0.83 |
| | Intercept | 2.397 | 0.420 | 5.705 | <0.001* | | | |
| | Agriculture cover | -0.009 | 0.002 | -4.065 | <0.001* | | | |
| Land use | | | | | | 7.57 | 0.024 | 0.67 |
| | Intercept | 0.405 | 0.263 | 1.539 | 0.123 | | | |
| | Nature/Agriculture | 1.504 | 0.461 | 3.259 | 0.001* | | | |
| Nature cover | | | | | | 9.61 | 0.011 | 0.60 |
| | Intercept | 0.245 | 0.313 | 0.783 | 0.433 | | | |
| | Nature cover | 0.005 | 0.008 | 2.965 | 0.003* | | | |
| Hunting pr. | | | | | | 11.95 | 2.5E-03 | 0.50 |
| | Intercept | 1.671 | 0.342 | 4.887 | <0.001* | | | |
| | Hunting pressure | -0.440 | 0.164 | -2.674 | 0.007* | | | |
| Built cover | | | | | | 12.15 | 2.2E-03 | 0.49 |
| | Intercept | 1.611 | 0.311 | 5.179 | <0.001* | | | |
| | Built cover | -0.007 | 0.002 | -2.626 | 0.008* | | | |
| Intercept only | | | | | | 16.48 | 2.5E-04 | 0.00 |
| | Intercept | 1.034 | 0.205 | 5.024 | <0.001* | | | |

**Appendix 6:** Summary table with the number of occurrences of each social group recorded in each site in nature reserves and agricultural areas during the two-year camera census efforts in the spring and autumn of 2016–2017. Nature reserves (Nature).

| Site | Land use | Family group | Group of subadults | Mixed group | Solitary adult female | Solitary adult male | Solitary subadult |
|---|---|---|---|---|---|---|---|
| 1 | Nature | 15 | 10 | 3 | 3 | 8 | 4 |
| 2 | Nature | 4 | 2 | 3 | 0 | 2 | 5 |
| 3 | Agriculture | 7 | 2 | 4 | 6 | 4 | 2 |
| 4 | Agriculture | 3 | 13 | 2 | 1 | 5 | 7 |
| 5 | Nature | 12 | 7 | 2 | 5 | 1 | 8 |
| 6 | Agriculture | 3 | 3 | 4 | 0 | 7 | 2 |
| 7 | Agriculture | 2 | 3 | 2 | 2 | 4 | 5 |
| 8 | Agriculture | 6 | 2 | 1 | 1 | 3 | 2 |
| 9 | Agriculture | 3 | 2 | 3 | 2 | 9 | 2 |
| 10 | Nature | 6 | 10 | 6 | 4 | 11 | 7 |
| 11 | Nature | 8 | 2 | 2 | 2 | 3 | 3 |

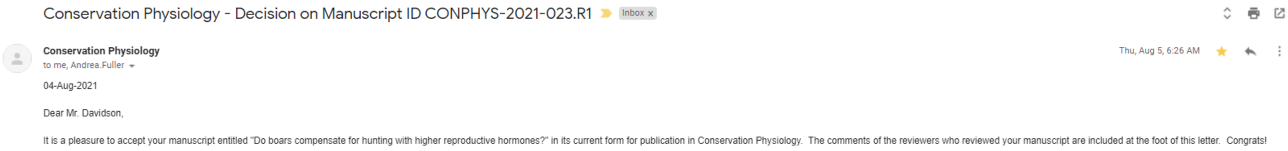
**Appendix 7 (The complete set of alternative GLMs of Table 4):** Model-selection statistics of the effects of the land-use factors on the ratio of adult males to family groups in autumn. Models were ranked by AICc and model weight. Only significant models and the null model (Intercept only) are presented. Agriculture (Agri), Nature reserves (Nature) and Hunting pressure (Hunting pr.).

| Model | Coefficient | Estimate | Std. error | *z* value | *P*-value | ΔAICc | Weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Built areas | | | | | | 0.00 | 0.989 | 0.80 |
| | Intercept | -2.217 | 0.681 | -3.254 | 0.001 | | | |
| | Built areas | 0.003 | 0.002 | 3.386 | <0.001* | | | |
| Land use | | | | | | 11.25 | 3.6E-03 | 0.39 |
| | Intercept | 0.693 | 0.500 | 1.386 | 0.165 | | | |
| | Nature/Agri | -1.386 | 0.621 | -2.230 | 0.025* | | | |
| Agri cover | | | | | | 11.39 | 3.3E-03 | 0.39 |
| | Intercept | -0.993 | 0.467 | -2.123 | 0.033* | | | |
| | Agriculture cover | 0.005 | 0.002 | 2.105 | 0.035* | | | |
| Hunting pr. | | | | | | 12.10 | 2.3E-03 | 0.34 |
| | Intercept | -0.637 | 0.362 | -1.758 | 0.078 | | | |
| | Hunting pressure | 0.502 | 0.246 | 2.038 | 0.041* | | | |
| Intercept only | | | | | | 13.48 | 1.2E-03 | 0.00 |
| | Intercept | -0.196 | 0.281 | -0.699 | 0.485 | | | |

# Chapter 4

## Do boars compensate hunting with higher reproductive hormones?

The manuscript was accepted for publication in Conservation Physiology.



Conservation Physiology - Decision on Manuscript ID CONPHYS-2021-023.R1

**Conservation Physiology**
to me, Andrea.Fuller

Thu, Aug 5, 6:26 AM

04-Aug-2021

Dear Mr. Davidson,

It is a pleasure to accept your manuscript entitled "Do boars compensate for hunting with higher reproductive hormones?" in its current form for publication in Conservation Physiology. The comments of the reviewers who reviewed your manuscript are included at the foot of this letter. Congrats!

# Statement of Authorship

## Principal Author

| | | | |
|---|---|---|---|
| Title of Paper | Do boars compensate for hunting with higher reproductive hormones? | | |
| Publication Status | ☐ Published ☐ Accepted for Publication<br>☑ Submitted for Publication | | |
| Publication Details | Submitted to Conservation Physiology | | |
| Name of Principal Author (Candidate) | Achiad Davidson | | |
| Contribution to the Paper | Conceived, designed and performed the research, analysed the data and wrote the paper (supervised by Uri Shanas and Dan Malkinson). | | |
| Certification: | This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper. | | |
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## Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the dissertation

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| Name of Co-Author | Uri Shanas | | |
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# Do boars compensate for hunting with higher reproductive hormones?

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## LAY SUMMARY

Predation risk usually impairs reproduction, through the stress-response mechanism. However, this study shows that progesterone levels were higher in female wild boars that live in regions of high hunting pressure and roam in a group. Such elevated reproductive hormones, which were associated with high hunting pressure, may lead to a higher reproductive potential in female wild boars.

Total word count: 7636

# ABSTRACT

The predation-stress hypothesis has been proposed as a general mechanism to explain the negative effect of predation risk on reproduction, through a chronic activation of the stress-response. However, in some cases, stress appears to augment the reproductive potential of mammals. Wild boar (*Sus scrofa*) populations are on a rise worldwide, despite the high hunting pressure that they are exposed to. This hunting pressure instigates, among other effects, earlier sexual maturity in juvenile females, leading to the shortening of wild boars' generation time. The mechanism that underlies this earlier sexual maturity under high hunting pressure has not been examined to date. To explore the physiological effects that hunting has on the reproductive system and whether the stress response is involved, we examined steroid hormone levels in the hair of female wild boars in northern Israel, comparing populations exposed to high and low hunting pressure. Furthermore, we compared steroid levels in the hair of female wild boars that were roaming alone or as a part of a group. We found no hormonal signs of stress in the hunted boars. Cortisol levels were low in both the high and low hunting-pressure groups. Yet, progesterone levels were higher in females that were exposed to high hunting pressure. Females roaming in a group also had higher progesterone levels compared to females that were alone, with no distinguishable differences in cortisol levels. These elevations in reproductive hormones that were associated with hunting may lead to a higher reproductive potential in female wild boars. They further show that high hunting pressure does not necessarily lead to chronic stress that impairs the reproductive potential of female wild boars. This data suggests that a reproductive-hormonal response may be one of the factors leading to the rapid wild boars population growth worldwide, despite the high hunting pressure.

## INTRODUCTION

Prey species commonly minimize predation risk through anti-predator behaviours (Lima and Dill, 1990). These responses usually include changes in vigilance behaviour (Brown, 1999; Lima and Bednekoff, 1999), foraging activity (Kotler *et al.*, 1994; Brown, 1999), space use (Keuling *et al.*, 2010; Saïd *et al.*, 2012; Thurfjell *et al.*, 2013), and physiology (Bateson and Bradshaw, 1997; Creel *et al.*, 2002; Gobush *et al.*, 2008). These adaptations facilitate an increase in fitness by enhancing immediate survival (Lima, 1998), but they often also incur physiological costs that can effect body condition (Hik, 1995) and reproduction (Sheriff *et al.*, 2009; Zanette *et al.*, 2011). The predation-stress hypothesis has been proposed as a general mechanism to explain the negative effects of predation risk on reproduction. The predation-stress hypothesis predicts that encounters with predators affect reproduction and survival through the chronic activation of the stress response (Clinchy *et al.*, 2013). The threat of predation causes an elevation of glucocorticoids (GCs) (Lima, 1998; Frid and Dill, 2002; Creel *et al.*, 2009), which can suppress reproduction (Munck *et al.*, 1984; Romero, 2004; Sapolsky, 2005) through their effects on the hypothalamic-pituitary-gonadal axis (Moberg, 1991; Romero, 2004).

The predation-stress hypothesis has been proposed relatively recently and thus has not been studied extensively (Creel *et al.*, 2009; Clinchy *et al.*, 2013; Dulude-de Broin *et al.*, 2020). In recent years, it has received more empirical support (Clinchy *et al.*, 2013; Dulude-de Broin *et al.*, 2020; Rey, 2020); however, there is some evidence that in certain systems, the predation-stress hypothesis does not apply. For example, the decrease in the reproduction of elk (*Cervus canadensis*) following the reintroduction of wolf (*Canis lupus*) in Yellowstone National Park (Creel *et al.*, 2007) was mainly tied to constrained foraging activity or efficiency, with no physiological ‘stress-related’ evidence, such as GC elevation (Creel *et al.*, 2009). Moreover, there is some evidence that stress may even elevate reproduction-related hormones in several species (Brandt *et al.*, 2009; Bryan *et al.*, 2015; Cattet *et al.*, 2017). Thus, the ecological conditions under which the predation-stress hypothesis is supported in different species are not fully understood (Creel *et al.*, 2009; Creel, 2018; Dulude-de Broin *et al.*, 2020).

Experimental studies have shown that animals cope with, and respond to, predators partly by activating their hypothalamic-pituitary-adrenal (HPA) axis, resulting in the release of GC hormones (Boonstra, 2013; Clinchy *et al.*, 2013). Chronic elevation of GCs (i.e., frequently recurring or constant over a long time span) can interrupt the hypothalamic-pituitary-gonadal (HPG) function, whereas short pulses of GC secretion normally do not (Moberg, 1991; Romero, 2004; Sapolsky, 2005). Bouts of human hunting may also cause chronic or short-term stress that can result in higher levels of GCs (Bateson and Bradshaw, 1997; Creel *et al.*, 2002; Bryan *et al.*, 2015), particularly if they occur during limited time periods during the year.

Reproductive hormones can provide additional insight into the effects of hunting on the social structure, behaviour and reproduction of animals. For example, progesterone is elevated in the females of many vertebrate species during pregnancy and the oestrus period and thus can serve as an indicator of long-term population-level reproductive activity (Anderson, 2009; Bryan *et al.*, 2015; Cattet *et al.*, 2017). Furthermore, progesterone in females might be elevated when social conditions are unstable and thus may reflect a stressful social environment (Brandt *et al.*, 2009; Bryan *et al.*, 2013, 2015). However, despite the importance of studying reproductive hormones in the context of conservation and management purposes (Creel *et al.*, 2007; Gobush *et al.*, 2008; Bryan *et al.*, 2015), only a few studies have tested the prolonged effects of hunting on reproductive hormones compared to stress hormones in wildlife (Koren *et al.*, 2019). Moreover, a number of recent studies have revealed that reproductive-hormone levels reflect meaningful biological and ecological patterns, such as social and physiological consequences arising from dietary constraints and human hunting (Bryan *et al.*, 2013, 2015; Koren *et al.*, 2019).

Over the past 40 years, the substantial population increases in wild boar (*Sus scrofa*) in agricultural, urban and suburban areas have intensified human-boar conflicts (Marsan *et al.*, 1995; Massei *et al.*, 2015; Linnell *et al.*, 2020). These conflicts have led to elevated economic costs due to disease spillover into livestock and humans, as well as damage to gardens and infrastructure in urban areas and to agricultural crops (Barrios-Garcia and Ballari, 2012; Massei *et al.*, 2015). Hunting is the most common and widespread management tool applied throughout the world to minimize conflicts with wild boars in agricultural areas (Gamelon *et al.*, 2011; Keuling *et al.*, 2013; Massei *et al.*, 2015). A study by Linnell *et al.* (2020) estimated that more than 3 million wild boars are hunted every year in Europe. Furthermore, the amount of harvested wild boars is constantly rising (Massei *et al.*, 2015). It has been previously shown that such high hunting pressure causes variations to the social structure of wild boar populations (Poteaux *et al.*, 2009; Bieber *et al.*, 2019), and instigates earlier sexual maturity, allowing juvenile females to reproduce earlier (Toigo *et al.*, 2008; Gamelon *et al.*, 2011; Servanty *et al.*, 2011). These consequences eventually causes wild boar generation times to shorten and may eventually lead to the higher reproduction and population growth of wild boars (Servanty *et al.*, 2009; Servanty *et al.*, 2011; Toigo *et al.*, 2008). However, the mechanisms that underlie the shortening of the wild boar generation time under high hunting pressure has not been examined to date.

In this study, we investigated the effects of hunting and social structure on the stress and reproductive hormones of female wild boars in northern Israel. Specifically, we tested cortisol and progesterone levels in the hair of female wild boars roaming alone or as part of a group in areas characterized by high and low hunting pressures. It has already been demonstrated that females tend to roam in bigger groups when predation risk is high, most likely because it provides them with a higher sense of security due to greater chances of predator detection (Roberts, 1996; Pays *et al.*, 2012; Podgórski *et al.*, 2016). Thus, we hypothesized that female wild boars roaming in a group would have lower stress hormones, and accordingly higher reproductive hormones, compared to solitary wild boars. Moreover, we hypothesized that in areas of high hunting pressure, female wild boars would have higher levels of stress hormones, and accordingly lower reproductive hormones, compared to areas of low hunting pressure.

## METHODS

### *The study area*

The study took place in the Carmel coastal mountain range in northern Israel (Figure 1), an area of approximately 600 $km^2$, with an elevation ranging from 0 to 546 m above sea level. The climate is Mediterranean, and the annual rainfall varies between 500 and 700 mm, falling mainly (80%) from December to March. The natural vegetation is a typical Mediterranean maquis (Neeman *et al.*, 1995; Hadar *et al.*, 1999), intermixed with cultivated areas.

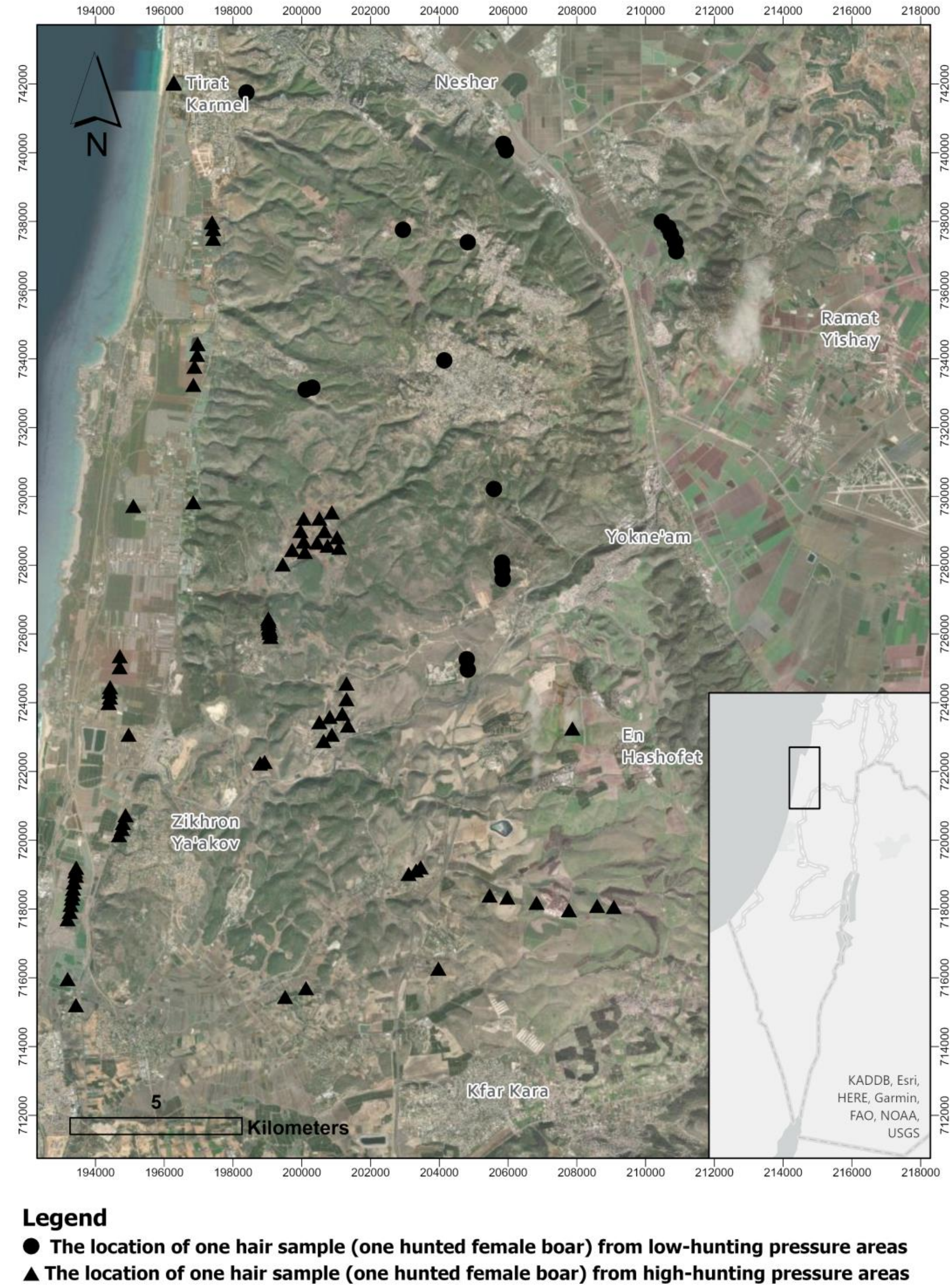

**Figure 1:** The study area in the Carmel coastal mountain range, Israel, including the high and low hunting-pressure agricultural areas where hair samples were collected.

Within the study area, the main predator of wild boars in Israel, the wolf, has been considered as locally extinct. However, there are other mortality causing factors, such as roadkill and especially hunting. To the best of our knowledge (given the ample food availability in the agricultural areas) roadkill and especially hunting, are the dominant exogenous stress factors in the study site. This region exhibits the highest hunting pressure in Israel, as well as the country's highest reported number of human–wild boar conflicts in agricultural landscapes (Lider, 2012) and urban areas (Malkinson, 2015). Hunting is prohibited in nature reserves and authorized in agricultural areas (given the required permits) throughout the year; there are no hunting seasons. To account for hunting pressure in the studied region, the agricultural areas were divided into polygons and each was assigned a hunting pressure from 1 (low) to 3 (high). Polygons were not identically delimited throughout the study area. Polygons were delineated according to estimated hunting regimes in the different areas, and were mainly marked around villages or towns of different sizes and shapes. Furthermore, polygons with different hunting pressures, were far enough from each other in order to minimize the probability that individuals did not move among them. Namely, the distance between polygons were much greater than the daily home-range sizes of wild boars in rural areas (1-1.6 km2) (Boitani *et al.*, 1994; Russo *et al.*, 1997; Morelle *et al.*, 2015). Because the INPA generally does not formally record the exact location of hunting events, we used the expert opinions of three different INPA ecologists and rangers and cross-validated them with local hunters' expertise to estimate the hunting pressure within each polygon. Then all polygons that were assigned with the values of two and under were categorized as low hunting-pressure areas and polygons that were assigned with values greater than 2 were categorized as high hunting-pressure areas. Hof HaCarmel Regional Council, is the only area within the study site that the INPA thoroughly records hunting events. Thus, we used Hof HaCarmel hunting records as a reference for the rest of the polygons in the study site. The hunting pressure in Hof HaCarmel was assigned by the INPA ecologists and rangers with a value of 3, Based on an average of 40 hunting campaigns/week that are carried out throughout the year. On average 870 boars/year are hunted in Hof HaCarmel which has a Jurisdiction of 190km$^2$. Other regions that were assigned with the value of 3 have similar hunting regimes. In low hunting pressure areas INPA rangers estimate that the average number of hunting campaigns is approximately 3 per week throughout the year. Despite differences in hunting regimes, habitats are quite similar throughout high and low hunting pressure areas - they both have agriculture areas in valleys and agriculture areas in mountainous regions (Figure 1). In both high and low hunting pressure areas, wild boars hide during the day in the dense Mediterranean maquis vegetation, and during the night they forage in the nearby agricultural areas. There are no official estimates of wild boars densities in the study region, or anywhere else in Israel (except for the average amount of hunted boars per year from Hof HaCarmel).

### *Hair-sample collection*

Mammalian hair, which integrates steroid hormones as it grows, can provide a valuable resource to investigate physiological responses to natural processes and potentially prolonged stressors, such as hunting (Macbeth *et al.*, 2010; Meyer and Novak, 2012; Bryan *et al.*, 2015). Levels of hormones in hair have been demonstrated to be correlated with measures in blood, saliva and faeces in several mammalian species (Accorsi *et al.*, 2008; Bennett and Hayssen, 2010; Morgan *et al.*, 2019). However, compared with other noninvasive sampling methods, the investigation of hair has several features that make this method advantageous or complementary to assess hormone levels (Gormally and Romero, 2020). For example, although steroids are often excreted as metabolites in urine and faeces, steroids remain intact in hair (Koren *et al.*, 2019). Furthermore, steroid hormones in hair appear to be stable for months to years or more (Macbeth *et al.*, 2010). Thus, unlike other steroid sampling techniques, steroid hormones in hair present opportunities to study the prolonged effects of stressors, such as hunting (Bryan *et al.*, 2015; Koren *et al.*, 2019; Gormally and Romero, 2020).

We provided paper envelopes to INPA rangers and expert hunters, who then returned them with hair samples of hunted wild boars enclosed. All samples were collected from fresh carcasses immediately after they were shot. The hair was cut from the hindquarters (posterior) of the wild boars with scissors, as closely as possible to the root. Tufts of hair (20–5,170 mg) were placed in dry paper envelopes and kept at room temperature for up to two years before hormonal assays were performed (Bryan *et al.*, 2015). The rangers and hunters provided the following information with each sample envelope: the date and location of the hunting event, the age and sex of the hunted boar, and whether the hunted individual was alone or a part of a group (Tables 1, 2). The hair samples were collected between 2016 and 2018 as part of an ongoing control program to mitigate wild boar damages to crops in agricultural areas. Due to an insufficient number of samples, we excluded the winter season from our seasonal analysis of the wild boars' hormones. For each hair-sample location, we assessed stress- and reproductive-hormone levels as dependent on the season, level of hunting pressure and social structure (Tables 1, 2).

**Table 1:** Summary of the number of samples collected and analysed and the available information regarding season and social structure of the samples.

| | Number of samples | Available seasonal data | Available social structure data |
|---|---|---|---|
| Progesterone | 95 | 62 | 48 |
| Cortisol | 133 | 100 | 55 |

**Table 2:** Sample sizes of females in group and solitary females.

| | Females in group | Solitary females |
|---|---|---|
| High hunting pressure | 32 | 5 |
| Low hunting pressure | 7 | 4 |

In the northern hemisphere, mammalian winter coats are composed of longer and denser hair than summer coats (Berman and Volcani, 1961; Mowafy and Cassens, 1976). It had been shown that the hair of domesticated pigs (*Sus scrofa domesticus*), in Wisconsin grew 54 mm in approximately 5 months during spring to autumn (Mowafy and Cassens, 1976). However, we do not have information about hair growth of wild boars in Israel (or other Mediterranean countries). Nevertheless, we do know that other mammals in Israel show continuous hair growth throughout the year (Koren *et al.*, 2019b).

### *Measurements of steroids in hair*

In the laboratory, we extracted and quantified steroid hormones from female wild boar using standard protocols (Fishman *et al.*, 2018). The mass of the samples varied depending on the availability. The entire hair in the taft was used for the steroid analysis. All hair samples were carefully weighed, and the mass was recorded, and then cut into smaller pieces and placed in a Petri dish (10 X 20 mm or 90 X 15 mm, De-groot Ltd., Rosh Haayin, Israel). Briefly, we washed hair samples twice with isopropanol (Romical Ltd., Beer Sheva, Israel), while we mixed them on an orbital rotator for 3 minutes. Next, we dried the samples for 12 hours, and then cut the hair into smaller pieces so that it would fit into the vials. (20 ml, Yoel Naim Ltd., Rehovot, Israel), we added 2 ml of methanol (Sigma-Aldrich Israel Ltd., Rehovot, Israel) and then the sample was sonicated for 30 minutes (MRC, model DC150H), followed by incubation overnight at 50°C while shaking. The next day, after the vial had cooled to room temperature, we transferred the methanol and steroids to a polypropylene Eppendorf tube (De-groot Ltd., Rosh Haayin, Israel), and centrifuged it in order to separate them from unwanted particles (Thermo Scientific, model microCL 178R) for 10 minutes at 13.3 RPM at 4°C. Then the methanol was transferred to a glass vial and evaporated under a stream of nitrogen at 45°C using a Techne Sample Concentrator (FSC496D). Samples were reconstituted in 10% methanol and 90% assay buffer (provided by the kit manufacturer), and steroids were quantified using commercial competitive Enzyme-Linked Immunosorbent Assay (ELISA; Salimetrics Europe, Newmarket, for cortisol and for progesterone, UK) kit. For progesterone, the manufacturer reported that antibody cross reactivity with other steroids was less than 0.192%. For cortisol, it was reported that antibody cross reactivity with dexamethasone was 19.2%, and less than 0.568% with all other steroids. Cortisol and progesterone were validated for female wild boar hair by conducting serial dilutions of separate hair pools, consisting of more than 12 random samples and testing for linearity (10–350 mg and 0.5–2 mg, respectively) and parallelism (slope covariance $P$ = 0.641 and $P$ = 0.361, respectively) with the kit standards provided. Intra-assay variability (CV) was 4.5% for cortisol and 9.1% for progesterone for six repetitions of the pool on the same plate. Inter-assay CV was 10.2% for cortisol and 10.09% for progesterone across five plates. Recovery was 90% for cortisol and 102.2% for progesterone, with results quantified by comparing hair samples spiked with a known amount of cortisol or progesterone to unspiked samples.

## Statistical Analysis of Hormonal Data

Data on cortisol and progesterone and concentrations were log transformed to achieve normality. Model assumptions of equality of variances (Levene’s test) and normality of residuals (Kolmogorov-Smirnov test) were met. For both cortisol and progesterone, we used a two-way analysis of variance (ANOVA) to assess interactions between hunting pressure and social structure. We applied Tukey's HSD tests post hoc. Furthermore, we used t-tests to compare differences in the cortisol and progesterone of female wild boars, between high and low hunting-pressure areas.

## RESULTS

### *Evaluating cortisol and progesterone levels of female wild boars*

The mean cortisol was $\bar{x}$ =2.0 pg/mg, *SD* = 1.6. Season ($F_{2,97}$ = 1.40, *P* = 0.250) and hunting ($t_{(24.77)}$ = 0.71, *P* = 0.483) did not have a significant effect on hair cortisol levels. Group structure did not have a significant effect on cortisol levels ($t_{(11.03)}$ = -0.02, *P* = 0.984). The mean progesterone was $\bar{x}$ =10.2 pg/mg, *SD* = 9.5. Season had a significant effect on hair progesterone levels ($F_{2,59}$= 3.31, *P* = 0.043), but a post hoc Tukey's HSD analysis revealed no significant interactions among the different seasons: spring-autumn (adjusted *P* = 0.930), summer-autumn (adjusted *P* = 0.114), summer-spring (adjusted *P* = 0.104). Land use (agriculture areas in valleys or Mount Carmel) did not have a significant effect on cortisol ($t_{(17.64)}$ = -1.04, *P* = 0.308) or Progesterone ($t_{(5.77)}$ = 1.59, *P* = 0.163). There was no significant correlation between cortisol and progesterone $r_{(93)}$ = 0.15, p = 0.127.

### *The effect of hunting and social structure on progesterone levels*

A two-way ANOVA showed that both hunting pressure ($F_{1,44}$ = 14.57, *P* = 0.001) and social structure ($F_{1,44}$ = 5.49, *P* = 0.023) had a significant effect on the progesterone levels of female wild boars (adjusted $R^2$ = 0.28; Table 3). Although both hunting and social structure had a significant and additive effect on progesterone levels, there was no interaction between them (F1,44 = 0.228, P = 0.63; sample sizes are presented in Table 2). A post hoc Tukey's HSD analysis of the social-structure data set indicated that adult females that were exposed to high hunting pressure had significantly higher progesterone levels compared to females exposed to low hunting pressure (*P* = 0.001; Figure 2). Furthermore, adult females that roamed as part of a group had significantly higher progesterone levels compared with solitary females (*P* = 0.026; Figure 3). In order to evaluate the relative effect of the estimates of social structure (-0.248; Table 3) and hunting (-0.307; Table 3), we standardized the values of the coefficients. The ratio between the standardized estimates of social structure and hunting was 0.874. This result indicates that hunting and social structure had almost the same relative effect on progesterone levels, with hunting slightly more influencing.

In order to complement the two-way ANOVA, and further evaluate the effect of hunting on progesterone levels with a bigger sample size, we also analysed the effect of hunting on the progesterone levels of 95 adult females (Table 1). We found that females exposed to high hunting pressure had significantly higher progesterone levels compared to females exposed to low hunting pressure ($t_{(42.51)} = 2.66$, $P = 0.010$; Figure 4). The results revealed no significant differences in progesterone levels among the different seasons. The average progesterone levels, however were higher in the high hunting pressure areas compared to the low hunting pressure areas (Appendix 1).

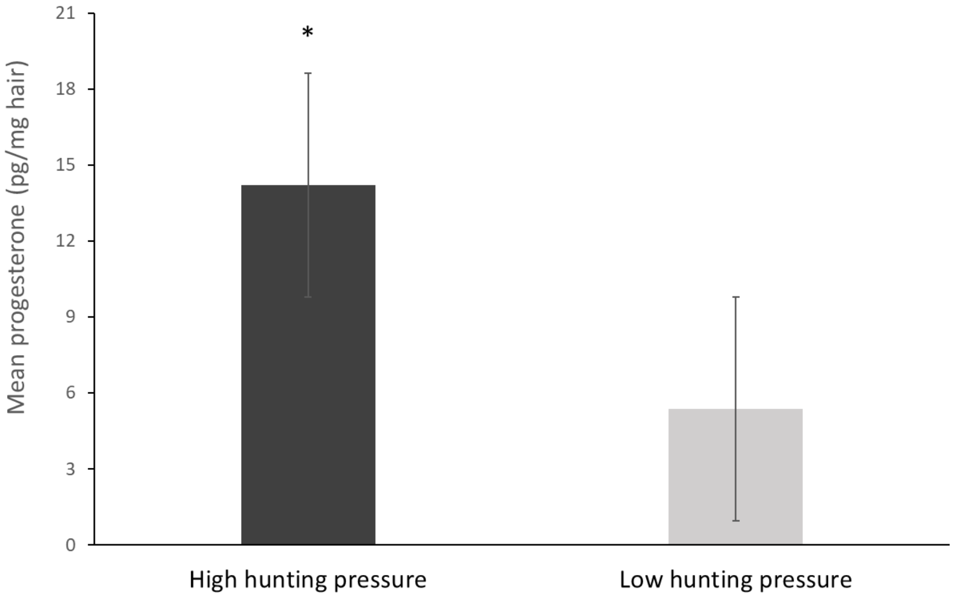

**Figure 2:** Mean ± SE hair progesterone concentrations (picograms per milligram of hair) collected from 48 hunted adult female wild boars (social-structure data set) in high and low hunting-pressure areas (high, *n* = 37; and low, *n* = 11). The asterisk denotes significant differences among populations (p=0.001).

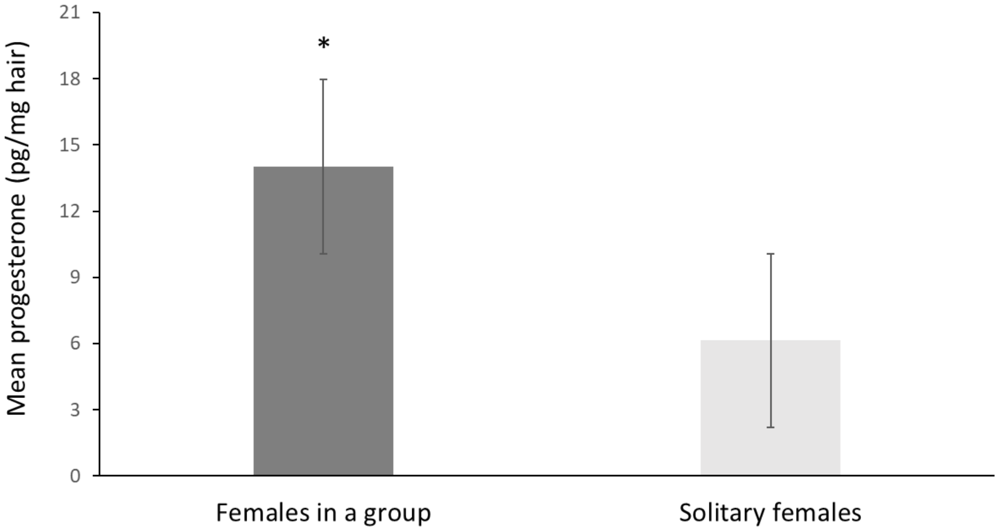

**Figure 3:** Mean ± SE hair progesterone concentrations (picograms per milligram of hair) collected from 48 hunted adult female wild boars (social-structure data set) that roamed as a part of a group or alone (group, *n* = 39; and solitary, *n* = 9). The asterisk denotes significant differences among populations (p=0.026).

**Table 3:** Coefficients and goodness-of-fit measure of the two-way ANOVA linear model relating progesterone levels to hunting pressure and social structure. Results are based on the social-structure data set (*n*=48 hunted adult female wild boars).

| Coefficient | Estimate | Std. error | *t* value | *P*-value | $R^2$ |
|---|---|---|---|---|---|
| | | | | | 0.28 |
| Intercept | 1.105 | 0.047 | 23.256 | <0.001* | |
| Hunting pressure | -0.307 | 0.097 | -3.151 | 0.002* | |
| Social structure | -0.248 | 0.105 | -2.364 | 0.022* | |

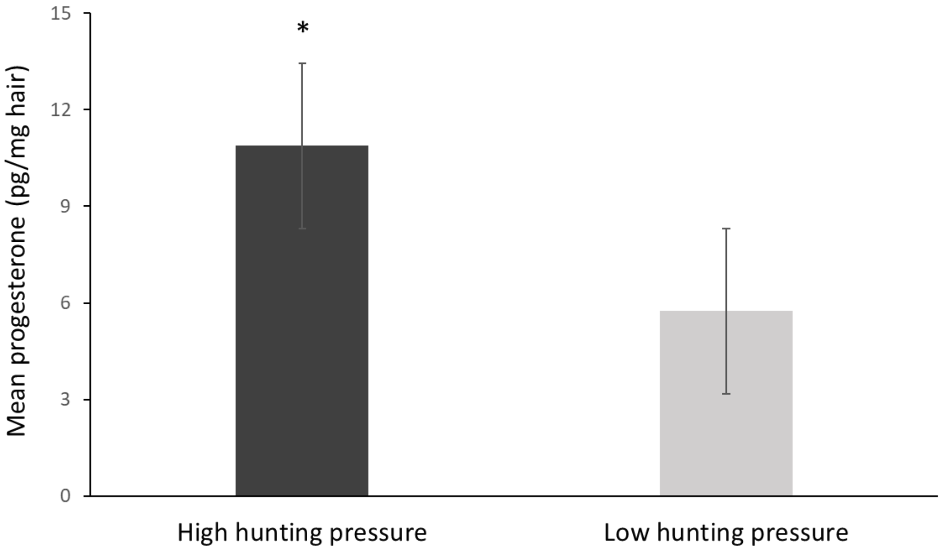

**Figure 4:** Mean ± SE hair progesterone concentrations (picograms per milligram of hair) collected from 95 hunted adult female wild boars (full data set) in high and low hunting-pressure areas (high, *n* = 78; and low, *n* = 17). The asterisk denotes significant differences among populations (p=0.01).

## DISCUSSION

Contrary to the predation-stress hypothesis and to our prediction, we did not find higher GC levels in female wild boars that were exposed to high hunting pressure. However, these females had higher progesterone levels, which may reflect higher reproductive efforts as a result of exposure to high hunting pressure (Bryan *et al.*, 2015). Additionally, we found that females in groups had significantly higher progesterone levels compared to solitary ones. Our results show an additive effect of hunting and social structure on the levels of reproductive hormones of female wild boars. Thus, the significantly higher progesterone levels we detected in female wild boars in high hunting-pressure areas may be linked to the social disruption caused by high hunting pressure (Poteaux *et al.*, 2009; Massei *et al.*, 2015; Bieber *et al.*, 2019).

Turner and Tilbrook (2006) suggested that cortisol levels need to be elevated in a sustained manner for a substantial period (greater than 4 days) in female domesticated pigs before reproduction is negatively affected and, even then, reproduction in some individuals appears to be resistant to its effects. Moreover, in recent years, evidence has accumulated on the positive role of short elevations in stress on the LH secretion and ovarian function of female pigs (Turner and Tilbrook, 2006; von Borell *et al.*, 2007; Madej *et al.*, 2009). This LH secretion forms the basic conditions for the activation of ovaries in terms of follicular growth, maturation and ovulation (Stančić *et al.*, 2012). For example, Paterson and Pearce (1989) found that female pigs that were exposed to short-term stress were more responsive to puberty stimulation and reached puberty earlier compared to "gently" handled gilts. Furthermore, Brandt *et al.* (2009) found that cortisol concentrations that were elevated in the short-term significantly increased progesterone concentrations in female pigs. Because domesticated pigs are essentially the same species as wild boars (*Sus scrofa*), it is expected that short-term stress can also enhance reproductive hormones, fertility and sexual puberty in wild boar populations.

Wild boars are exposed to high hunting pressure worldwide (Massei *et al.*, 2015; Linnell *et al.*, 2020). It has been previously demonstrated that this high hunting pressure significantly affects their behaviour; for instance, their dispersal patterns (Keuling *et al.*, 2010), and activity and spatial-usage patterns (Keuling *et al.*, 2008; Scillitani *et al.*, 2010; Thurfjell *et al.*, 2013). Furthermore, hunting may also cause wild boars to select safer habitats, even at the expense of decreased access to resources (Saïd *et al.*, 2012). Moreover, our unpublished research shows that hunting causes higher levels of vigilance behaviour in wild boars in general, and in females in particular (Davidson *et al.* 2021, in review). Thus, it is expected that these behavioural responses are caused by stress induced by hunting, among other factors. In the wild, it has been demonstrated that female wolves exposed to high hunting pressure have elevated progesterone and cortisol levels (Bryan *et al.*, 2015). Bryan *et al.* (2015) suggested that this increase in stress- and reproductive hormones may reflect an increased reproductive effort in response to hunting. As mentioned above, short-term stressors often do not have a negative effect and even may stimulate reproduction and enhance fertility of female pigs (Turner and Tilbrook, 2006; von

Borell *et al.*, 2007; Madej *et al.*, 2009). Thus, we suggest that repeated bouts of short-term stress caused by hunting campaigns may also stimulate higher levels of reproductive hormones in female wild boars.

Contrary to our prediction at the outset of the study, there was no difference in cortisol levels between female wild boars roaming in a group or alone. However, females roaming in a group did show significantly higher progesterone levels compared to solitary female wild boars. The proportion of time spent engaging in vigilant behaviour is associated with both short- and long-term stressors (Morgan and Tromborg, 2007), and factors such as group size and habitat characteristics can influence it (Chmura *et al.*, 2016). In many species, including wild boars (Quenette and Gerard, 1992; Podgórski *et al.*, 2016), individuals tend to decrease their vigilance behaviour by increasing their group size (Roberts, 1996; Pays *et al.*, 2007, 2012). Bigger groups provide individuals with a higher sense of security due to greater chances of predator detection and fewer chances of been preyed upon (Roberts, 1996; Pays *et al.*, 2012; Podgórski *et al.*, 2016). Furthermore, Saïd *et al.* (2012) and Scillitani *et al.* (2010) both found that hunting caused females with offspring to change their activity and spatial usage significantly more than males. These differences between sexes might result from females with offspring responding more strongly to hunting (Saïd *et al.*, 2012). Thus, it is expected that in high hunting-pressure areas, breeding females (with relatively high progesterone levels) with offspring will prefer to breed and raise their young in larger groups of females, as opposed to nonbreeding females (with relatively lower progesterone levels) with no offspring. This suggests a combined effect of social structure and hunting.

Furthermore, the mortality among individuals, especially adults, due to hunting has been considered a potential driver of variations in the social organization of wild boar populations. These variations may lead to the disassembly of family groups and thus to a chaotic social structure; disorientation among the remaining yearlings of the group may affect their social status and eventually reproduction (Poteaux *et al.*, 2009; Keuling *et al.*, 2010; Bieber *et al.*, 2019). Additionally, it had been shown that hunting may facilitate the breakup of wild boars' polygynous mating system, due to selective hunting of adult males, and thus may contribute to a higher number of males in the next generation and the early access to reproduction for young males, even within the same social group (Poteaux *et al.*, 2009). The consequent effects of hunting for social structure, social status and breeding strategies of wild boars may enhance the progesterone levels of female wild boars. Progesterone levels in female pigs are significantly elevated during the rut season (estrus) and pregnancy (Anderson, 2009). Thus, the significantly elevated progesterone levels that we found in females that were exposed to high hunting pressure, may indicate higher reproductive potential. Despite this, to the best of our knowledge there is no evidence of higher reproductive success in areas with higher hunting in our study site. Thus, we suggest that elevations in reproductive hormones that were found to be associated with hunting may lead to a higher reproductive potential (and not necessarily to reproductive success). There are many factors that affect reproductive success in rural areas. Thus, it is hard to make a direct link in wild populations between reproductive potential and success. For instance, we may not see an increased prevalence of juveniles in high hunting pressure areas because a lot of juveniles are being hunted in this areas.

The accumulated evidence from the literature together with our findings on the effects of hunting on the behaviour and social structure of wild boars, suggest that hunting stress combined with a disrupted social structure may have an additive effect on the progesterone levels of female wild boars (Poteaux *et al.*, 2009; Bryan *et al.*, 2015; Bieber *et al.*, 2019). Furthermore, our results indicate that hunting and social structure had almost equal additive effects on progesterone levels. Despite this, we did not find that hunting had a significant effect on the cortisol levels in the hair of female wild boars. Possibly, short bouts of GCs do not appear in wild boar hair, because they are quickly removed from the body. Additionally, cognitive and emotional aspects of avoiding predation are still unknown, thus predation risk effects may also occur through mechanisms that do not involve the stress response (Creel *et al.*, 2009).

Moreover, our results suggest that there are probably other factors affecting progesterone levels that were not tested in our research, such as sex ratios, genetic structure and other social factors that may affect wild boars' reproduction across several generations. Thus, we encourage further studies that will explore the possibility that other behavioural, social, genetic and reproductive factors may affect GC and progesterone levels of female wild boars.

Nevertheless, our findings highlight the importance of studying reproductive hormones for management purposes (Gobush *et al.*, 2008; Bryan *et al.*, 2013, 2015), especially because few studies have tested the prolonged effects of hunting on the reproductive hormones found in the hair of wildlife (Koren *et al.*, 2019). In conclusion, our study suggests that elevated reproductive hormones, which were associated with high hunting pressure, may lead to a higher reproductive potential in female wild boars. Furthermore, our study provides evidence that increased predation risk does not necessarily lead to chronic stress that impairs the reproductive potential of female wild boars. This response may be one of the reasons leading to the worldwide rapid population growth of wild boars, despite the high hunting pressure they are exposed to.

## FUNDING

This work was supported by a research grant provided by the Ramat Hanadiv Project of the Rothschild Foundation and the Sherman Foundation.

# ACKNOWLEDGMENTS

We would like to thank Dr. Devorah Matas from the Faculty of Life Sciences, Bar-Ilan University, for her advice and support, and Ben Rosenberg, Yonatan Harael, Liron Tal and Barak Barchiel from the INPA for their priceless advice and help in the collection of hair samples. We are grateful to Liat Hadar, Amir Arnon and Dror Ben-Ami for their support and encouragement.

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## SUPPLEMENTARY MATERIAL

**Appendix 1:** Mean values ± SD (*n*) of hair progesterone (picograms per milligram of hair) according to the different seasons and hunting pressures.

| | High hunting pressure | Low hunting pressure |
|---|---|---|
| Autumn | 7.5 ± 5.0 (*n*=10) | 6.9 ± 3.4 (*n*=7) |
| Spring | 6.7 ± 2.2 (*n*=7) | 4.1 ± 1.6 (*n*=3) |
| Summer | 11.1 ± 10.0 (*n*=28) | 6.1 ± 2.5 (*n*=7) |

# Chapter 5

## General Discussion

The work presented in this thesis provides a comprehensive study of the effects of hunting and different land-use types on the behavior, risk perception, social structure and physiology of wild boars in northern Israel .

## Risk perception and behavior responses

The results of the behavioral parts of the research suggest that hunting leads to higher risk perception in wild boars habituating non-urban landscapes. This is expressed by higher vigilance levels and lower foraging rates and efficiency in agriculture areas compared to nature reserves. Many prey species have evolved defense mechanisms that are induced by predation risk (Creel, 2018). These defenses entail behavioral plasticity in nature and they extend to response to human lethality in places where hunting is common (Montgomery et al., 2020). This is especially true for large mammals, given that these species have been disproportionately exploited over evolutionary time by humans (Montgomery et al., 2020). The inducible defenses of large mammals to human lethality usually include changes in spatial usage, movement, activity, flight distance, occupancy, foraging rates and vigilance levels. However, surprisingly, in the context of human lethality and its effects on large mammals in general, and specifically on wild boars, foraging rates and vigilance levels have been significantly less studied (Keuling et al., 2010; Said et al., 2012; Thurfjell et al., 2013; Montgomery et al., 2020).

The predator-sensitive food hypothesis predicts that predators constrain the foraging activity or efficiency of their prey, thus increasing energetic or nutritional constraints on their reproduction or survival (Sinclair and Arcese, 1995). There is considerable support for this hypothesis from many studied species (Lima and Dill, 1990), including ungulates (Tadesse and Kotler, 2012; Hayward et al., 2015). For instance, it had been shown that black-tailed deer (*Odocoileus hemionus*) in areas where they are exposed to hunting, avoided bait stations at the outset of hunting (Le Saout et al., 2014). To the best of my knowledge the only confirmation of the predator-sensitive food hypothesis and the effect of human disturbance on the foraging of a member of the Suina sub-order, comes from observations on the collared peccary (*Pecari tajacu*) that avoided food stations near human hiking trails and had lower foraging rates in habitats near human houses (Bleicher and Rosenzweig, 2018). Thus, the results of this study present the first evidence that the predation risk imposed by human hunting abates the foraging rates and efficiency of wild boars.

The results of this study further suggest that wild boars in urban areas perceive substantially lower risks of predation, while foraging, compared to wild boars in rural areas. Moreover, this perception of risk was independent of hunting that took place during the study and is permitted year around. These results were obtained during the end of the summer when hunting pressure reaches its peak in agricultural areas (Table 1). This is because, as mentioned in chapter 2, during the end of summer natural food and water availabilities are in their lowest, thus wild boars are drawn into irrigated orchards in the agricultural areas which offer them moist soil for burrowing and water for drinking. It is important to mention that although during the end of summer the water availability in nature reserves is in its lowest, wild boars inhabiting these areas still have access to drinking water through troughs and springs. During the course of this study, Haifa municipality employed a professional hunter which hunted annually 300 wild boars within Haifa's jurisdiction which is 60km$^2$ (an average of 5 boars/km$^2$). For comparison, as mentioned in chapters 3 and 4, at the same time, on average 870 boars/year were hunted in the Hof HaCarmel municipality which has a jurisdiction of 190km$^2$ (an average of 4.5 boars/km$^2$). This suggests that the hunting pressure in Haifa and the agricultural areas in Hof HaCarmel was quite similar. Furthermore, during the course of the study, in the city of Nesher no hunting took place. The lower risk perception perceived by urban boars, most likely originates from their habituation to human presence. The differences in human presence and activities between urban and rural areas are immense and have been previously shown to affect wild boars' space-use patterns and movement behavior (Podgórski et al., 2013; Stillfried et al., 2017). Accordingly, I suggest that lower neophobia of urban boars and habituation to humans override the effects of hunting. The results of this study further reveal substantial differences between the foraging behavior and risk perception of rural and urban boars.

| Winter | Spring | Summer | Autumn |
|---|---|---|---|
| 73.3 | 131.3 | 135.8 | 80.0 |

**Table 1:** The mean number of hunting events per month by season during 2016-2018 in the agricultural areas of Hof Carmel regional council.

Vigilance allows animals to monitor their surroundings for signs of danger associated with predators. Vigilance is costly, because it reduces time allocation to other fitness-enhancing activities (Beauchamp, 2019). Animals tend to allocate more time to vigilance when the risk posed by predators increases (Beauchamp, 2019). Hence, the increased vigilance levels wild boars showed in agriculture areas, compared to nature reserves, suggest that hunting imposes high predation risk in these areas. As mentioned above, prey can reduce risk imposed by hunting, by altering various behaviors. In general, antipredator responses are associated with a glucocorticoid (GC) stress response, and in other cases they are associated with trade-offs between food and safety (Creel, 2018). Because vigilance is supposed to increase the safety of an animal, Creel (2018) suggested that when predation risk is predictable animals will usually respond by using proactive responses such as increasing their routine vigilance. Vigilance behavior is usually expected to have two components: "routine vigilance" when the animal is simply monitoring its surroundings during spare time or "induced vigilance" when responding to a stimulus (Blanchard and Fritz, 2007). This suggests that the predation risk in agricultural areas in my study site is usually predictable. Indeed, park rangers and hunters usually hunt in the same locations, techniques and times (usually in the early night time and on weekends) (Ben Rozenberg, personal communication).

Studies on vigilance behavior usually make no distinction of the sex of the individuals, thus, knowledge on the differences between the vigilance behavior of males and females are scarce (Beauchamp, 2019). All the more so regarding differences in the vigilance behavior between different age classes (Beauchamp, 2019). The results of this study show significant differences in the vigilance behavior between males and females and male versus female yearlings, and thus they indicate the importance of studying age and sex specific vigilance behavior. The results, however, also suggest that social structure did not affect the foraging behavior of wild boars. This implies that when quantifying risk perception of wild boars, one should consider that vigilance and foraging are two surrogates of the response to fear. Furthermore, as the results of this study indicate, they are both good behavioral indicators that demonstrated that high hunting pressure causes higher risk perception in wild boars. Thus, because they are both different behavioral indicators they complement each other and thus provide a more complete picture of the effect of human hunting on the risk perception of wild boars. Furthermore, considering the vigilance of individuals by their age and sex, not only enabled me to quantify wild boars' risk perception, but also better understand how it affects their social structure.

## Social structure

This study shows that the vigilance response is not uniform across age and sex. For instance, adult males did not show any significant differences in vigilance between agricultural areas and nature reserves, as opposed to adult females. In ungulates, males are known to be more prone to adopting riskier behaviors (Laurian et al., 2000). In wild boars, it has also been shown that females respond more strongly to hunting than males, by changing their space use patterns, probably as a result of rearing offspring (Scillitani et al., 2010; Said et al., 2012). One important proactive response to predation risk includes movement to areas where detection or attack is less likely to occur (Creel, 2018). This provides further support for my earlier suggestion that the predation risk in agricultural areas in my study site is usually predictable, thus enabling females to shift their activity to safer habitats (nature reserves).

In addition to sex, age also had an impact on how wild boars respond to hunting. I found that male yearlings that were exposed to hunting in autumn, showed higher vigilance levels and roamed significantly more with family groups. This observation may have consequences on reproduction since the high proportion of male yearlings in family groups in agricultural areas during the autumn (mating season) offers young males early access to reproductive females, even within the same social group (Poteaux et al., 2009), thus increasing the overall reproductive potential of the group.

## Physiological responses

Contrary to my hypotheses, I did not find higher GC levels in female wild boars that were exposed to high hunting pressure. However, as described above, I did find that hunting causes higher vigilance levels and lower foraging rates and efficiency in rural wild boars. Furthermore, as mentioned above, numerous studies have shown that elevated hunting pressure significantly affects wild boar spatial behavior and activity (Keuling et al., 2010; Said et al., 2012; Thurfjell et al., 2013). I assume that the behavioral responses to hunting that I found in this study, result from the stress imposed by the hunting pressure in the rural sites. Animal's respond to stressors, by using physiological and/or behavioral adaptations that serve to neutralize the effects of the stressor and to reestablish homeostasis (Reeder and Kramer, 2005). As mentioned above, antipredator responses are associated with a GC stress response, and in other cases they are associated with trade-offs between food and safety (Creel, 2018). Thus, as mentioned above, it is possible that the predation risk in the agricultural sites in my study is usually predictable for wild boars. Therefore, it may be that wild boars responses to hunting are more proactive and thus are more associated with trade-offs between food and safety as I found in this study (e.g. vigilance and foraging). Moreover, the results of this study, highlight the importance of studying behavior together with the physiology of wildlife. For instance, addressing only GC levels, important insights gained in this study regarding the vigilance and foraging behavior of wild boars would have been overlooked.

Contrary to my hypothesis, I found that females that were exposed to higher hunting pressure had higher progesterone levels. This result can find support from a study on female wolves that were exposed to high hunting pressure and had elevated progesterone and cortisol levels (Bryan et al., 2015). The authors suggested that this increase in stress and reproductive hormones may reflect increased reproductive efforts in response to hunting. As mentioned in chapter 4, short-term stressors often do not have a negative effect but may even stimulate reproduction and enhance fertility and sexual puberty of domesticated female pigs (Turner and Tilbrook, 2006; von Borell et al., 2007; Brandt et al., 2009). Because domesticated pigs (*Sus scrofa domesticus*) are essentially the same species as wild boars, it is possible that short-term stress, caused by hunting campaigns, may also stimulate higher levels of reproductive hormones, fertility and sexual puberty in female wild boars.

Additionally, I found that social structure also had a significant effect on progesterone levels. Namely, females in groups had significantly higher progesterone levels compared to solitary ones. To survive and reproduce, animals must also have mechanisms to cope with different stressors caused by environmental conditions. For example, essential changes in the social environment has already been shown to enhance stress responses in many animals (Reeder and Kramer, 2005). As Bryan et al. (2015) found in wolves, it is expected that the significant changes caused by hunting to the social structure, social status and breeding strategies of wild boars, may among others, enhance the progesterone levels of female wild boars. Thus, my findings suggest that hunting stress and possibly a disrupted social structure have an additive effect on the progesterone levels of female wild boars. Moreover, these results provide evidence that increased hunting stress does not cause chronic stress, but positively impacts reproductive hormones in female wild boars.

## Further research

The results of this study raise an interesting question – do urban boars show lower GC levels compared to rural boars? In this study I did not manage to obtain a sufficient amount of hair samples from urban boars. Thus, I encourage further research that would explore GC levels also in urban boars. According to my findings, it is plausible to hypothesize that urban boars may show lower GC levels compared to rural boars. Furthermore, the differences that I found in the vigilance behavior between males and females, imply that males might show lower GC levels than females. Thus, I encourage further research that will study the differences in GC levels between males and females (and the reproductive hormones of males and how they are affected by hunting pressure).

The results of this study further showed that higher proportion of male yearlings are found in family groups in agricultural areas during the autumn (mating season). As mentioned in the introduction, under high hunting pressure male yearlings show lower dispersal rates possibly because they have higher probabilities being shot during dispersal, thus having a strong pressure to remain in their natal group (Keuling et al., 2010). Furthermore, the selective hunting of adult males (Milner et al., 2007; Toigo et al., 2008; Poteaux et al., 2009), may ease the pressure of young males to leave their natal group and thus lead to an early access of reproduction for young males, even within the same social group (Poteaux et al., 2009). Therefore, it is possible that the yearlings that do not disperse may cause a "boar effect" on the female yearlings. The “boar effect” is a vastly-studied phenomenon in domesticated pigs caused by a contact between a male boar and young females that eventually causes the Induction of synchronized estrus and advanced first pubertal estrus in those young female pigs (Stančić et al., 2012). To date the "boar effect" was only studied in domestic pigs, and to the best of my knowledge has never been investigated in wild boars. Because domesticated pigs are essentially the same species as wild boars, it is expected that the boar effect phenomenon exists also in wild boars.

In conclusion, this study presents evidence that increased predation risk, caused by human hunting, leads to: higher risk perception (e.g. increased vigilance behavior and reduced foraging), variations in social structure and higher reproductive hormones in rural wild boar populations. The results further suggested that urban boars show significantly lower risk perception compared to rural boars possibly due to habituation of urban boars to humane presence. Additionally, according to Montgomery et al. (2020), and up to date, it seems that my research extends the known behavioral responses of large mammals to human lethality as studied in other areas of the world. Yet, because my experiments were conducted in natural conditions, they were observational by nature and not controlled experiments. Nevertheless, this study provides important insights regarding the effects of hunting on the behavior, social structure and physiology of wild boars. The results provide evidence that high hunting pressure causes significant changes to the behavior and social structure of wild boars, however it is not associated with chronic stress, but positively impacts reproductive hormones in wild boars. This response may be one of the reasons leading to the worldwide rapid population growth of wild boars, despite the high hunting pressure they are exposed to, and provides a better understanding of the biology of wild boars.

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# השפעת ציד ושימושי קרקע שונים על ההתנהגות, המבנה החברתי והפיזיולוגיה של חזירי הבר באזורים עירוניים, חקלאיים וטבעיים בישראל

**אחיעד דוידסון**

## תקציר

חזיר הבר (*Sus scrofa*) הוא יונק אומניבור גדול החי בדרך כלל במגוון רחב של בתי גידול ותנאי אקלים. זהו אחד ממיני היונקים עם התפוצה הרחבה ביותר בעולם, ומבין הפרסתנים תפוצתו היא הרחבה ביותר. תחום התפוצה הטבעי שלו משתרע ממזרח רוסיה, יפן ודרום-מזרח אסיה, ועד למערב אירופה ואגן הים התיכון. חזירי בר שמקורם בחזירי בית שהתפראו, הופצו על-ידי האדם בחלקים מאמריקה הצפונית, אמריקה הדרומית, אוסטרליה וניו זילנד. אפשר למצוא חזירי בית שהתפראו גם באיים כמו גלפגוס ואלדברה.

מבנה גופו של חזיר הבר הוא צר ומותאם לריצה וללחימה. גופו מכוסה בשיער קשיח ובעור עבה, המגנים עליו בעת חדירה לתוך סבכי שיחים. אורך גופו מגיע עד 180 ס"מ, גובהו 102-30 ס"מ באזור הכתף ומשקלו 200-50 ק"ג. הזכרים גדולים יותר מן נקבות, גופם ארוך יותר ומשקלם רב יותר. פרוותם של חזירי הבר עשויה שערות נוקשות וגסות שצבען חום-אפור עד שחור, אולם הגורים נולדים מפוספסים בפסי אורך חומים וצהובים לסירוגין, אשר דוהים בהדרגה ונעלמים כליל בגיל ארבעה חודשים. תוחלת החיים הממוצעת של חזירי הבר בשביה היא עד עשרים שנה.

חזירי הבר הם מין פוליגיני וטריטוריאלי, ופוטנציאל הרבייה שלהם הוא הגבוה ביותר מבין הפרסתנים: גידול האוכלוסייה השנתי של חזירי הבר עשוי להיות גבוה מ 100%. כמו כן, גיל ההתבגרות המינית שלהם מוקדם יותר, ואורך הדור שלהם קצר יותר בהשוואה לפרסתנים אחרים בגודל ובעלי משך חיים דומה. המבנה החברתי הבסיסי של חזירי הבר מורכב מעדרים של נקבות עם גורים וצעירים, המונים 30-6 פרטים. העדרים תלויים בעיקר בנוכחותן של הנקבות הבוגרות, שמובילות את הקבוצה ואחראיות ללכידותה. אינטראקציה בין זכרים ונקבות בוגרים נדירה ביותר מחוץ לעונת הרבייה. במהלך עונת הרבייה, כמות האינטראקציות עולה באופן משמעותי, וזכרים בוגרים מצטרפים באופן זמני לעדרי הנקבות בתקופת הייחום בסתיו. כך נוצרים עדרים מרובים ומעורבים בעונה זו.

ההיריון נמשך כארבעה חודשים וההמלטה מתרחשת בחודשי האביב (מרס-יוני). מספר הגורים בשגר נע בדרך כלל בין שלושה לשמונה. הגורים נולדים פקוחי עיניים, מכוסי שיער ובעלי כושר תנועה. תקופת ההנקה נמשכת כשלושה חודשים, אולם כבר מגיל שבוע-שבועיים, הגורים מסוגלים לאכול גם מזון מוצק, ומגיל שבועיים הם מצטרפים לאם בחיפושיה אחר מזון. הגורים נשארים עם עדרי הנקבות במשך כשנה וככל שהם גדלים, כך הקשר שלהם עם אמם הולך ומתנתק, והם נהיים עצמאיים יותר ויותר. רוב הנקבות הצעירות נוהגות להישאר באזור שבו נולדו, ולעתים קרובות הן אף נשארות בעדר שבו גדלו עם אמן. לעומת זאת, הזכרים הצעירים בדרך כלל מגורשים על-ידי הזכרים הבוגרים הטריטוריאליים, בערך בין גיל 9 ל 14 חודשים, ויוצרים עדרים של זכרים צעירים עד שהם מגיעים לבגרות מלאה בסביבות גיל 4-3 שנים, אז הם כבר חזקים ומנוסים מספיק כדי להילחם על טריטוריות משלהם.

תזונתם של חזירי הבר מגוונת מאוד. היכולת שלהם להסתגל למגוון גדול של סוגי מזון מאפשרת להם להתקיים כמעט בכל אזור בתחום תפוצתם. חזירי הבר הם אופורטוניסטים אוכלי-כול, והם אוכלים כל סוג של חומר אורגני אך בעיקר חומר צמחי (~ 90% מהתזונה) כגון שורשים, בלוטים, אגוזים, חומר צמחי ירוק ויבולים חקלאיים. יתר תזונתם

מורכבת ממגוון גדול של פטריות ובעלי חיים, כגון תולעים, חלזונות, פרוקי רגליים, דגים, ציפורים, ביצי ציפורים וגם יונקים קטנים ופגרים.

בישראל, כמו במדינות רבות אחרות באירופה ובאסיה בעשורים האחרונים, אוכלוסיות חזירי הבר גדלו והתפשטו, במיוחד בסביבות אזורים חקלאיים ועירוניים. התוצאות של הגידול באוכלוסיות אלה כוללות עלויות כלכליות גבוהות הנובעות ממגיפות המועברות לבע"ח ולבני אדם ומנזקים לגנים באזורים עירוניים ולגידולים חקלאיים. לדוגמה, ההערכה היא שבשנה אחת באירופה נזקי החקלאות שנגרמים מחזירי בר הם כ 80 מיליון אירו. אחד מכלי הממשק הנפוצים והנרחבים ביותר המשמשים לבקרת גידול באוכלוסיית חזירי הבר הוא צייד. לאחרונה העריכו כי באירופה יותר מ 3 מיליון חזירי בר ניצודים מדי שנה. עם זאת, למרות לחץ הציד הגבוה אליו חשופים חזירי הבר, מספרם ממשיך לגדול בעולם כולו. בישראל ההערכה היא שבמועצה אזורית חוף הכרמל חזירי הבר גורמים לנזקי חקלאות בשווי של מאות אלפי שקלים בשנה. בתגובה לנזקי החקלאות הללו, ניצודים כל שנה כ 1,000 חזירי בר במועצה אזורית חוף כרמל.

מחקרים שהתקיימו באירופה והתפרסמו בשנים האחרונות הראו כי לחץ ציד גבוה גורם לנקבות צעירות להתרבות מוקדם יותר, וכתוצאה מכך משך הדור שלהם מתקצר (נקבות נהיות פוריות בסביבות גיל שנה במקום גיל 2-3 שנים). תופעה זו יכולה לגרום לשיעורי רבייה גבוהים יותר ועשויה להיות אחת הסיבות העיקריות המובילות לצמיחה מהירה של אוכלוסיות חזיר הבר. מחקר זה מנסה להשוות ולהעריך את השפעות הציד על הפיזיולוגיה, התנהגות, החששנות, אופן שיחור המזון, והמבנה החברתי של חזירי הבר בארבעה שימושי קרקע שונים באזור הכרמל: אזורים עירוניים עם ובלי ציד, אזורי חקלאות עם לחץ ציד גבוה ושמורות טבע ללא ציד.

במסגרת פרק המחקר הראשון של הדוקטורט ביקשתי לבחון את ההשערה שצייד פוגע בשיחור המזון של חזירי בר. בכדי לחקור את דפוסי שיחור המזון ותפיסת הסכנה של חזירי הבר תחת השפעות משולבות של ציד ושימושי קרקע שונים הנחתי מתקני האכלה שהכילו 300 גרם תירס מעורבב עם 600 גרם חתיכות של צינורות פלסטיק. התירס המעורבב עם הפלסטיק כוסה ברשת וטי ברזל על מנת לגרום לכך שלחזירים יהיה יותר קשה לברור את התירס ככל שכמות התירס פוחתת, ובכדי ליצור אצלם תגובה של הכנסת האף לתוך המתקן בדומה לנבירה בקרקע. מתקני ההאכלה, הוצבו בארבעה סוגים שונים של שימוש קרקע: אזורים עירוניים עם (חיפה) וללא ציד (נשר), ואזורים כפריים (שטחים חקלאיים עם ציד ושמורות טבע ללא ציד). התוצאות העידו כי חזירים החיים באזורים חקלאיים, החשופים ללחץ ציד גבוה, אכלו פחות תירס מהמתקנים באופן מובהק והראו תפיסת סכנה גבוהה משמעותית לעומת חזירי הבר משמורות הטבע. באופן מפתיע התוצאות הראו גם שתפיסת הסכנה של חזירי בר מאזורים עירוניים בזמן שיחור מזון הייתה נמוכה בהרבה לעומת חזירי בר באזורים כפריים (חזירי העיר אכלו באופן מובהק הרבה יותר תירס מחזירי הכפר וגם לקח להם באופן מובהק הרבה פחות זמן להתחיל לאכול ממתקני ההאכלה) ללא קשר לרמת הצייד לה הם חשופים באזורים העירוניים. תוצאות אלו מעידות על הביטואציה (התרגלות לנוכחות האדם) חזקה מאד של חזירי הבר בחיפה ונשר לבני אדם.

על מנת לבחון את השפעות הציד על התנהגות החששנות והמבנה החברתי של חזירי הבר, התקנתי מצלמות המופעלות ע"י חיישני תנועה לאורך שבילי תנועה קבועים של החזירים. השערת המחקר שנבחנה במסגרת פרק זה היא שצייד יגרום לרמות חששנות גבוהות יותר ולשינויים במבנה החברתי של חזירי הבר. ממצאי פרק זה מצביעים על הבדלים

משמעותיים בהתנהגות החששנות של חזירי הבר בין שטחים חקלאיים לשמורות טבע. באזורים חקלאיים, נקבות בוגרות היו חששניות באופן משמעותי בהשוואה לזכרים בוגרים. בהתאמה לכך באזורים אלה מצאתי באופן משמעותי יותר זכרים בוגרים ופחות עדרי משפחה המובלים ע"י נקבות בוגרות. תוצאות אלו מעידות שנקבות שחוששות יותר מזכרים (כנראה בעיקר מכיוון שיש להן גורים), מעדיפות בשל כך להסתובב ולשחר למזון בשמורות הטבע שם לא מתקיים צייד. יתר על כן, זכרים צעירים היו חששניים יותר באופן משמעותי בשטחים חקלאיים בהשוואה לנקבות צעירות. בהתאמה לכך, מצאתי שזכרים צעירים נטו יותר באופן משמעותי להסתובב עם עדרי משפחה באזורים חקלאיים בהשוואה לשמורות טבע, שם הם נטו יותר להסתובב לבד או בקבוצות של זכרים צעירים. תוצאה זו מעידה על כך שכנראה עקב הצייד האינטנסיבי באזורי החקלאות הזכרים הצעירים חוששים לעזוב את עדרי המשפחה שנותנים להם תחושה של בטחון עקב הכמות הגדולה של הפרטים שנמצאים בעדר. כמו כן, ייתכן כי הזכרים הצעירים חוששים לעזוב את עדרי המשפחה מחשש שיפגעו מצייד, אם כי הנחה זו לא נבחנה ישירות במסגרת הדוקטורט. כמוזכר למעלה, זכרים צעירים אמורים לעזוב את עדרי המשפחה בסביבות גיל שנה. הימצאות הזכרים הצעירים בקרב עדרי המשפחה לאחר גיל שנה עשויה להעלות את פוטנציאל הרבייה של הנקבות בעדרי המשפחה באמצעות תופעה הנקראת boar effect. תופעה זו מאופיינת בירידה בגיל הבגרות המינית של הנקבות עקב הימצאות של זכרים בעדר שמפרישים פרומון שנמצא ברוק שלהם ועשוי לגרום לנקבות להקדים את גיל הבגרות המינית. מעבר לכך, תוצאות אלו, מעידות שקיים קשר בין התנהגות של חששנות לבין המבנה החברתי של חזירי הבר, ככל הנראה עקב השפעת הצייד ומאפיינים נוספים שמבדילים בין שמורות הטבע ואזורי החקלאות באזור הכרמל.

השערה נוספת שנבחנה במסגרת הדוקטורט היא מידת הקשר בין ציד לבין תגובה פיזיולוגית של חזירי הבר, כפי שהיא באה לידי ביטוי במאזנים הורמונליים. על מנת לבחון את ההשפעות הפיזיולוגיות של ציד, השוויתי בין רמות הורמוני רבייה (פרוגסטרון) וסטרס (קורטיזול) בשיער נקבות חזירי בר מאוכלוסיות שנחשפו ללחץ ציד גבוה לבין אלו שנחשפו ללחץ ציד נמוך משמעותית. יתר על כן, בדקתי את רמות הורמוני הרבייה והסטרס משיער של נקבות חזירי בר שהסתובבו לבדן או כחלק מקבוצה. לא מצאתי הבדלים ברמות הקורטיזול בין חזירים שהיו חשופים ללחץ צייד גבוה לנמוך. עם זאת, דגימות השיער הראו כי רמות הפרוגסטרון היו גבוהות יותר אצל נקבות שהיו חשופות ללחץ ציד גבוה. כמו כן, גם בנקבות שהסתובבו בקבוצה היו רמות פרוגסטרון גבוהות יותר בהשוואה לנקבות שהסתובבו לבדן. רמות גבוהות של פרוגסטרון באזורי לחץ צייד גבוה עשויות להעלות את פוטנציאל הרבייה של נקבות חזירי הבר ואף לגרום לירידה בגיל הבגרות המינית שלהן. זאת מכיוון שפרוגסטרון הוא ההורמון המרכזי שאחראי על הייחום וההריון בנקבות חזירי בר.

לסיכום, מחקר זה מציג עדויות לכך שלחץ צייד גבוה באזורי חקלאות ככל הנראה גורם ל: פגיעה בשיחור מזון, רמות גבוהות יותר של חששנות ותפיסת סיכון, שינויים במבנה החברתי ורמות גבוהות יותר של הורמוני רבייה בחזירי בר בשטחים פתוחים. מאידך אין ללחץ הציד השפעה על התנהגות שיחור המזון ותפיסת הסיכון באזורים עירוניים. כמו כן, לחץ הצייד הגבוה אינו גורם לסטרס כרוני בחזירים בשטחים חקלאיים. התגובות הללו, מחד עליה ברמות הפרוגסטרון ומאידך רמות נמוכות של סטרס, עשויות להסביר את הצמיחה המהירה של אוכלוסיות חזירי הבר ברחבי העולם, למרות לחץ הציד הגבוה אליו הם חשופים. ממצאים אלה מספקים לנו הבנה טובה יותר על הביולוגיה של חזירי הבר ויכולים לסייע בתוכניות ממשק עתידיות שמטרתן למתן קונפליקטים בין בני אדם לחזירי בר.

# השפעת ציד ושימושי קרקע שונים על ההתנהגות, המבנה החברתי והפיזיולוגיה של חזירי הבר באזורים עירוניים, חקלאיים וטבעיים בישראל

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בהנחיית: פרופ' אורי שיינס

פרופ' דן מלקינסון

חיבור לשם קבלת התואר "דוקטור לפילוסופיה"

דוקטורט פרסומים

אוניברסיטת חיפה

הפקולטה למדעי הטבע

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