UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PERSONALITY AND VIGILANCE BEHAVIOUR IN ALPINE MARMOT (MARMOTA MARMOTA)

THESIS
PRESENTED
AS A PARTIAL REQUIREMENT
FOR THE MASTER IN BIOLOGY

BY
CATERINA FERRARI

MAY 2010

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PERSONNALITE ET COMPORTEMENT DE VIGILANCE CHEZ LA MARMOTTE ALPINE (MARMOTA MARMOTA)

MÈMOIRE
PRÉSENTÉE
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN BIOLOGIE

PAR
CATERINA FERRARI

MAI 2010

AVANT-PROPOS

I present this thesis in a form of a scientific paper. The article, titled "Personality and vigilance behaviour in Alpine marmot (*Marmota marmota*)", is a study about individual differences in behavioural and physiological responses and its effect on individual vigilance in Alpine marmot.
Authors of the article will be Caterina Ferrari, Cristian Pasquaretta (University of Pavia), Achaz Von Hardenberg (Alpine Wildlife Research Centre, Gran Paradiso National Park, Aosta) and Denis Rèale (UQAM). CF and CP performed all the open-field tests; CF and Nicole Martinet (University of Turin) collected data on vigilance behaviour. Statistical analyses and drawing up of the paper was made by CF under the supervision of DR and AVH. DR and the Gran Paradiso National Park in the person of AVH gave financial and logistic support during the field work.

This thesis contains appendix A that is a brief description of the Gran Paradiso National Park.

ACKNOWLEDGMENTS

First of all I want to thank Denis Réale and Achaz von Hardenberg, my supervisor and cosupervisor, that gave me the possibility to collaborate to this project, support me with their advices and their enthusiasm.

A special thank to Cristian Pasquaretta, for the work made together, under the sun or under the rain. Bruno Bassano and Giuseppe Bogliani have been a clear reference in all the step of this project.

Thanks to the Gran Paradiso National Park that allow and support us to develop the "Alpine marmot project"; I sincerely thanks all the guards of the Parks.

I am very grateful to Neeltje Boogert, Caroline Grou, Pierre Olivier Montiglio, Adi Boon and to all the members of GRECA (Groupe de Recherche en Écologie Comportementale et Animale, UQAM) for their help, their advices and their friendship. I thanks Claudio Carere for his advices on the collection of physiological parameters.

This work has been possible thanks to the collaboration of many people of the marmot team: Elena Castoldi, Francois Dumont, , Luigi Ranghetti, Lino Zubani, Mariaceleste Labriola, Massimiliano Luppi, Nicole Martinet Laura Busia, Simone Tommasina.

Personally I would like to thank my family and my friends for their support and friendship during these years.

I dedicate this work to *friendship* and *passion*.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

TABLE PAGE

LISTE DES ABRÉVIATIONS

BLUP	Best Linear Unbiased Predictors
df	Degree of freedom
e.g.	For example (from Latin *exempli gratia)*
et al.	and others (from Latin *et alii*)
Fig.	Figure
ID	Identity
i.e.	That is (from Latin *id est*)
Loglik	Log-likelihood
LR	Log-likelihood ratio
LRT	Log-likelihood ratio test
ML	Maximum Likelihood
na	Not available
np	Not provided
pers. obs.	Personal observation
REML	Restricted Maximum Likelihood
Vs.	Versus

RÉSUMÉ

De plus en plus d'études démontrent la notion que le comportement des individus diffère selon les situations et à travers le temps. Ce phénomène se nomme personnalité de l'individu. Il est fort probable que les traits de personnalité jouent un rôle pertinent dans l'écologie de l'individu et les chercheurs tentent de comprendre quelles sont les causes de ces différences individuelles. À cette fin, il est nécessaire d'avoir diverses approches et on procède actuellement, en laboratoire et sur le terrain, à des recherches effectuées selon l'approche de l'optimalisation afin de vérifier si les variations, la répétabilité et l'hérédité ont une incidence sur les traits de personnalité. Les mesures biologiques de réponses physiologiques et endocriniennes peuvent nous aider à comprendre les mécanismes qui sont à la base des variations comportementales.

L'étude de la personnalité réalisée avec des contraintes dans l'utilisation du temps nous permet de vérifier comment certains traits de personnalité influencent l'histoire de vie des individus. Nous avons étudié la personnalité dans un contexte d'anti-prédation où l'animal doit faire face à un compromis entre se nourrir ou rester vigilant car il risque d'être attaqué à tout moment. La présente recherche vise à déterminer si la personnalité de la marmotte Alpine (*Marmota marmota*) diffère d'un individu à l'autre et si, compte tenu de leur personnalité, les marmottes utilisent différentes stratégies contre les prédateurs. La marmotte Alpine constitue un bon modèle afin d'étudier les stratégies anti-prédateurs et les comportements de prises de risques. Les marmottes vivent en groupes et ces derniers habitent des terriers interreliés possédant plusieurs points d'accès. Les marmottes cherchent leur nourriture à l'extérieur de leur terrier et pendant qu'elles s'alimentent, elles surveillent l'environnement afin de s'assurer qu'il n'y a pas de risques d'attaques de la part de prédateurs. Notre recherche a été effectué dans une zone où habitent un grand nombre de marmottes Alpines ainsi que deux espèces de leurs prédateurs naturels, soit l'aigle royal (*Aquila chrysaetos)* et le renard roux (*Vulpes vulpes)*. Au cours des été 2007, 2008 et 2009, nous avons étudié 12 groupes familiaux habitant deux secteurs situés à diverses latitudes au sein du Parc National Gran Paradiso (Italie). Nous avons capturé et marqué 122 individus d'âges et de sexes différents et nous avons procédé à des tests d'*open-field* sur 105 de ces individus. Dans la plupart des cas, les tests ont été effectués au moins à deux reprises au cours d'années différentes. Grâce à ces tests *d'open-field*, nous avons pu mesurer le niveau d'activité pour chacun des individus et nous avons découvert une très forte incidence d'habituation sur ce trait. Les mesures des paramètres physiologiques lors de la manipulation nous ont fourni une mesure biologique de la pro-activité pour chacun des individus ce qui nous a permis de constater qu'un individu dominant avait un rythme cardiaque plus élevé que celui proposé dans la théorie. On a également noté que l'âge, le poids et leur interaction avaient une incidence sur la pro-activité des individus mais que cette tendance diffère selon la classe d'âge. Grâce à ces mesures, nous avons obtenu un indice fiable sur la personnalité des individus ainsi que des preuves permettant d'affirmer que cette espèce possède une stratégie d'adaptation (*coping style)*: les individus plus actifs avaient un rythme cardiaque plus élevé. Nous avons effectué d'autres analyses en utilisant ces valeurs individuelles de personnalité. Le deuxième objectif visé par la présente étude était de valider les résultats sur la personnalité au sein du cadre écologique du comportement antiprédateur. À cette fin, nous avons effectué sur le terrain des observations focales lorsque des marmottes marquées faisaient preuve de vigilance en s'alimentant et nous avons considérer la fréquence et la durée des cas de vigilance comme constituant des paramètres du comportement de vigilance. Nous avons constaté que la personnalité jouait un rôle sur le comportement de vigilance mais que certains des résultats allaient à l'encontre de la théorie; nous suggérons que de contrôler pour l'indice du risque pourrait clarifier nos résultats.

Mot clés :activité;comportement antiprédateur; *open-field*; personnalité; *Marmota marmota*

SUMMARY

Recently several studies and empirical evidence have shown that individual differ in their behaviour across situation and over time; such phenomenon is named personality or temperament. Personality traits are likely to play a relevant role in individual's ecology and researchers are investigating on mechanistic and remote causes at the bases of these differences. To this end different approaches are needed and research, with the optimality approach as a fundamental reference, is developed both in the laboratory and in the field where researchers test for variation, repeatability and hereditability in personality traits. Biological measures of physiological and endocrinological responses can provide knowledge about mechanism at the bases of variation in behaviour.

The study of personality within a context characterised by a time budget conflict provide the opportunity to investigate how different traits influence individual's life history; we studied personality in an antipredator context wherein animals constantly experience a time budget conflict between the necessity to feed and the risk of being preyed upon. This research aims to estimate whether individuals of Alpine marmot (*Marmota marmota*) consistently differ in their personality, and if, according to their personality, they vary in their antipredator strategies.

Alpine marmots represent a good model for the study of antipredator strategies and risk taking behaviour; they live in social groups that occupy a burrow system with several entrances. Marmots move around their burrows in search for food resources. While they are foraging they scan their surroundings to detect potential predator attacks. The fieldwork-area is characterised by a high density in Alpine marmots and of the two main species of marmots' natural predators, the golden eagle (*Aquila chrysaetos*) and the red fox (*Vulpes vulpes*).

During the summer 2007, 2008 and 2009, we have been working on 12 family groups inhabiting two area at different latitude within the Gran Paradiso National park (Italy); we trapped and marked 122 individuals of different age and sex and we performed open–field test to 105 of these; for most of them the test has been repeated at least twice during different years. By means of the open-field test we measured individual level in activity and we found an high effect of habituation in this trait. By measuring physiological parameters during handling we provided a biological measure of individual proactivity and we found that dominant individual are characterized by higher hearth rate, according to the theory; age , weight and their interaction also affect individuals proactivity but the tendency is different according to the age class. These measures gave us a reliable index of individual's personality and provided evidence of the existence of coping style in this species: individual more active show higher level in hearth rate. We used individual value of personality in further analysis. The second goal of this study was to validate personality result within the ecological framework of antipredator behaviour; to this aim we collected focal observations of vigilance events during foraging activity in marked marmots in the field and we estimate frequency and duration of vigilance events as parameters of vigilance behaviour. We found that personality affect vigilance behaviour but some results are in contrast with the theory; we suggested that correcting for index of risk could clarify our results.

Key words: Activity; antipredator behaviour; open-field; personality; *Marmota marmota*

INTRODUCTION

Darwin in 1859 explained the theory of evolution in his most important work "On the Origin of Species by Means of Natural Selection"; this theory states that natural selection, acting on single organisms, drives the process of evolution and can explain the great biological diversity existing between taxa and across species (Darwin, 1859). Thanks to the knowledge acquired on the genetics of adaptation, we are now aware that natural selection acts on different alleles of a gene, favouring the optimal phenotype corresponding to the current environmental conditions experienced by the population, and penalizing those deviating from that optimal (Wright and Dobzhansky, 1946). Knowledge of the theory of evolution and of genetics are the references for evolutionary biologists who, since the first half of 1900s, have been investigating of biological diversity and adaptations within and across species, and mechanistic (*i.e.* proximal) and remote (*i.e.* ultimate) causes that explain these different adaptations.

THE STUDY OF PERSONALITY

i-Optimal approach and individual differences

The optimal approach in behavioural ecology suggests that individuals should behave at the optimal level in each situation. Following this approach, animals are expected to show an unlimited plasticity in their reactions, behaving as if they were maximising the cost/benefit ratio across different situations (Charnov, 1976; Krebs and Davies, 1993).

Considering the optimal level of a certain behaviour in a given situation, values at the extremes or around the optimum have been long considered as "noise" from an adaptive point of view, being just rough material for natural selection (Wilson, 1998). By the late 1980s until nowadays, several authors focused their research on the significance and the mechanisms of these behaviours different from optimality and how these deviations from optimality can be explained under the evolutionary point of view (Wilson, 1988; Wilson, *et al.* 1994; Boissy, 1995; Gosling and John, 1999; Dall, Houston and McNamara, 2004; Dingemanse and Réale, 2005; Stamps, 2007).

Many works have provided evidence that conspecifics can often differ consistently in their behavioural reaction towards novel and challenging situations, over time and across situations (Koolhaas, *et al.* 1999; Dingemanse, *et al.* 2004; Carere, *et al.* 2005; Wilson and Godin, 2009). These results indicate that individuals in a population generally show limited behavioural variation and can not systematically express phenotypes close to the optimal levels when coping with different situations (Sih, Bell and Johnson, 2004). These individual differences consistent over time and across situations have been named temperament, personality, coping style, or behavioural syndromes, and represent an interesting issue in evolutionary biology since they are likely to play a significant role in an individual's life history (Réale, *et al.* 2007). From an evolutionary point of view in which it would be more advantageous for individuals to be more flexible and to express the optimum level in every situation, the maintenance of individual consistency in natural populations is, however, not well explained yet and researchers investigate how this variation can arise and be maintained by natural selection (Sih, *et al.* 2004; Réale, *et al.* 2007; Wolf, *et al.* 2007).

In this work we want to estimate if individuals of the same species (Alpine marmot, *Marmota marmota*) differ consistently in their reaction when facing a stress caused by novelty or challenge. We first analyse individual behavioural and physiological differences to a novel environment test and a handling test (referred to as personality or coping style thereafter). We then determine if individuals show different personality profiles by successively studying individual variation in vigilance behaviour, and to what extend such variations are affected by personality traits.

We measured individual personality using reliable, experimental methods; using repeated tests on 105 individuals we estimated the repeatability of their behaviour. We evaluated the ecological role of personality within the context of vigilance behaviour; individuals often show variations in their anti-predator strategy and we suggest that individual personality could explain a part of this variation.

ii-Personality traits and behavioural syndromes

Personality describes the fact that individuals of the same species consistently differ in their behaviour over time and across situations (Budaev, 1997; Gosling, 2001; Groothuis and Carere, 2005; Réale, *et al.* 2007). Personality traits are generally characterized by some phenotypic variation, and are repeatable and heritable (Réale, *et al.* 2007). Consistent differences are often polarized into two extreme phenotypes along an axis that are generally defined with different labels in the literature. For example, Koolhaas *et al.* (1999) classified coping styles into "proactive" and "reactive" individuals, based on their behavioural reaction to a stressor; Drent refers to passive or active individuals (Drent, *et al.* 2003). Réale *et al.* (2007) consider a temperament or personality trait as a characteristic of an organism shared by all or some of the individuals of a species that can vary among these individuals, and they assume continuous phenotypic variation for these traits, divided into five main categories: shyness-boldness, exploration-avoidance, activity, sociability and aggressiveness.

A suite of personality traits correlated consistently across situations are referred to as coping style or behavioural syndromes (Sih, *et al.* 2004). Behavioural syndromes have been reported in several species of mammals, birds and fish: generally, activity and exploration tend to be correlated positively with risk-taking, and aggressiveness (Coleman, 1998; Brick and Jakobsson, 2002; van Oers, *et al.* 2004). For example, a behavioural syndrome have been described in sunfish (*Lepomis macrochirus*), where individuals correlated positively across situations in their activity level and risk-taking behaviour (Wilson and Godin, 2009). Exploration, aggressiveness and risk-taking have been shown to be tightly correlated in population of sticklebacks (*Gasterosteus aculeatus aculeatus*) with high predation risks, whereas those traits were not correlated in populations with low predation risks, suggesting that natural selection may favour different behaviour types in different environments (Bell, 2005; Dingemanse, *et al.* 2007).

iii- Method of study

Direct observation of the behaviour of animals in the wild is rarely sufficient to measure the personality of individuals, and researchers generally study variation in behavioural responses within an experimental and controlled context. This way it is possible to investigate behavioural traits within a large sample of individuals in a constant environment (Réale, *et al.* 2007).

A reliable method to measure individual differences in several species is the new-environment test, that is generally an open-field test for rodents. An individual is placed in an empty, novel arena and its behaviour is scored within a new environment during a fixed interval of time (Archer, 1973; Gould, Dao and Kovacsics, 2009). This test provides information on the way each individual reacts to a novel, and potentially stressful situation. Previous studies on wild animal populations pointed out that activity and explorative behaviour can be measured in an open-field test, and that they are generally highly correlated and therefore not clearly distinguishable (Boon, Réale and Boutin, 2007; Martin and Réale, 2008). Boldness, the way an individual reacts to a risky situation, can be measured using individual trappability in the field, reaction towards handlers, or with the tonic immobility test (Jones, 1982; Erhard, Mendl and Christiansen, 1999; Réale, *et al.* 2007). Aggressiveness, the tendency to attack conspecifics is experimentally measured by the reactions and the aggressive displays of a focal individual during the mirror image stimulation test or during dyadic encounters in an arena test (Sih, Kats and Maurer, 2003; Boon, Réale and Boutin 2007; Wilson, *et al.* 2009).

An important step of a study of personality in an ecological context is to validate the ecological relevance of activity and others traits measured in the open-field test by correlating these measures with the behaviour of individuals in nature (Réale, *et al.* 2007). Measures of personality traits in the open-field are expected to reflect an animal's behaviour in the wild and its reaction towards challenging and novel situations in its natural environment; for example the score of activity/exploration measured in experimental context on great tits (*Parus major*) correlated with dispersal rate of the same individuals in the wild (Dingemanse, *et al.* 2003).

Researchers also investigated physiological and hormonal changes prior to or after a stress or a social defeat, providing a biological validation of the variation in the behaviour observed in the population. Individual differences tend to covary with different individual biological and hormonal responses, and physiological activity has been suggested to form the basis of individual behavioural variation (Benus, *et al.* 1991; Koolhaas, *et al.* 1999; Groothuis and Carere, 2005). The proactive-reactive syndrome describes patterns of individual differences in physiological change.

Proactive animals (generally bold, active, superficial explorers, and aggressive animals) show low Hypotalamic-Pituitary-Axis (HPA) reactivity (low plasma corticosterone response), high sympathetic reactivity (high plasma noradrenaline levels), low parasympathetic reactivity (leading to an increased heart rate) and, higher level of testosterone. Proactive individuals respond to a stress by fleeing or fighting, are characterized by strong territorial control and aggressiveness. In contrast, reactive individuals (generally shy, slow, thourough explorers, and less aggressive animals) are characterised by high HPA-axis reactivity, low sympathetic reactivity and high parasympathetic reactivity. Reactive individuals respond to a stress by freezing and conservation behaviour (Koolhaas, *et al.* 1999). When coping with a stress, proactive individuals tend to actively manipulate the source of stress. They also tend to develop routines very quickly. They thus should be favoured in a stable environment (Benus, *et al.* 1991). In contrast reactive individuals react to a stress by a passive confrontation. They are very sensitive to cues in the environment rarely develop routines. They should thus be favoured in a more variable environment (Koolhaas, *et al.* 1999).

iv-Personality in an ecological context

The study of behavioural syndromes within an ecological context allow researchers to estimate the action of natural selection upon different behavioural types. Personality traits and behavioural syndromes play a significant role in most relevant fields of an animal's ecology: effects of different personality profiles have been found for example in the use of territory (Civantos, 2000), dispersal dynamics (Dingemanse, 2002), and the establishment of a dominance hierarchy (Verbeek, Boon and Drent, 1996). Personality is likely to affect individual fitness in some species: for example aggressiveness in female red squirrels (*Tamiasciurus hudsonicus*) affects offspring survival during years of low food resources (Boon, Réale and Boutin, 2007). In bighorn sheep (*Ovis Canadensis*) bolder ewes were favoured during years of higher predation pressure, suggesting that personality is subjected to natural selection (Réale and Festa-Bianchet, 2003; Dingemanse and Réale, 2005). Sociability in lizards (*Lacerta vivipara*) influence dispersal dynamics and individuals less tolerant to the presence of conspecifics tend to disperse when the population density becomes high. Furthermore social and asocial lizards showed different fitness outcomes when living in populations of low or high density: asocial lizards have higher survival compared to social ones when the density is low; on the other hand in high density populations social lizards have higher reproductive success (Cote and Clobert, 2007;Cote, Dreiss and Clobert, 2008).

In a prey-predator context, natural selection could act differently according to differences in personality traits: on one hand individuals who forage boldly and take consistently more risk are likely to find fresh and rich resources, but on the other hand such a behaviour increases the chance of encountering predators. We thus expect bolder individuals to adjust their anti-predatory strategy according to the higher risk of predation. Shy and less active individuals on the contrary may behave in a safer way so that they reduce predation risks, but may as a consequence incur some foraging costs (Sih, Bell and Johnson, 2004; Sih, Kats and Maurer, 2003)

VIGILANCE BEHAVIOUR

Predation is one of the major selective pressures acting on wild animal populations through which natural selection drives the evolution of various anti-predator strategies in prey species such as group living, cryptic coloration or optimization of reactions when a predator is detected (Holmes, 1984; Mateo, 1996;Longland and Price, 1991; Ruxton, 2004). Animals have thus to trade the primary necessity of feeding to get energetic resources with the need to be vigilant and avoid or escape predator attacks (Brown, Kotler and Valone, 1994).

In most species, foraging and vigilance are mutually exclusive, hence being vigilant include both direct and indirect costs: the cost in energy used to be vigilant and the loss of feeding opportunities (Krause and Godin, 1996; Brown and Kotler, 2004). However, it has been shown that in some species an individual can be partly vigilant, while chewing or handling food (Bednekoff and Lima, 2005; Makowska and Kramer, 2007). The cost of being vigilant and the risk of starvation, therefore, force individuals to adjust their vigilance to the level of risk of the situation. As a consequence starving individuals should take more risks or reduce there vigilance to increase their time spent foraging (Damsgard and Dill, 1998; Höjesjö, Johnsson and Axelsson, 1999). An anti-predator strategy common to different species consists in frequent scanning of the surroundings while foraging or carrying out other activities. These sequences of head-ups and head-downs provide an efficient way for an individual to detect potential predators in the surroundings and at the same time to get the necessary amount of food (Lima and Dill, 1990).

By varying the frequency and the duration of scan events animals are able to adjust their vigilance level to the situation (Bednekoff and Lima, 2002). More frequent and slightly longer vigilant bouts provide more information about a potential threat approaching, but a further extension of the duration would reduce the time spent foraging without necessarily increasing probability of detecting a predator. However, an individual that perceives a potential danger in the surroundings increases the duration of the vigilance scan (Beauchamp, 2008; Bednekoff and Lima, 1998). This trade-off between vigilance and foraging explains why adults Belding's ground squirrels (*Spermophilus beldingi*) living in a more risky site showed higher rate in vigilance than squirrels living in an area of lower risk (Mateo, 2007). In the same way Alpine marmots living in a site close to the forest and characterized by a low visibility adjust their vigilance by increasing the frequency of scans rather than their duration (Ferrari, Bogliani and von Hardenberg, 2009).

i-Factors affecting predation risk and vigilance behaviour

Vigilance behaviour can be affected by both extrinsic and intrinsic factors. Both factors could be responsible for individual plasticity (*i.e.* an individual changes its vigilance behaviour depending on rapid changes in its environment) and individual consistent differences in vigilance (*i.e.* some individuals are consistently more vigilant than others independent of the environmental conditions).

Differences in risk of predation and in vigilance behaviour could be influenced by several external factors. Living in a group has been extensively shown to affect an individual's vigilance level in gregarious species; for example, vigilance levels in spice finches

(*Lonchura punctulata*) decreased with increasing group size (Beauchamp and Livoreil, 1997). The position of an individual in a group has important consequences on its probability of being the target of predation (Hamilton, 1971). Being in the centre of the group or at close distance from conspecifics provides safer conditions. In the teal (*Anas crecca*) proximity to other conspecifics reduces the level of vigilance of an individual (Poysa, 1994). Tall vegetation generally decreases visibility, and favours the approach of potential predators, thus leading some prey species to increase their vigilance behaviour (Bednekoff and Blumstein, 2009). Finally, environmental characteristics, such as the slope of the meadow, or the distance to a refuge are other factors that affect the risk for prey species and therefore their vigilance (Armitage, 1991; Devereux, *et al.* 2008; Frid, 1997). For example head-raising rates increase with distance to the burrow in Eastern chipmunks, *Tamias striatus* (Trouilloud, Delisle and Kramer, 2004).

Among intrinsic factors, sex, age, body condition can have several effects on vigilance behaviour. For example, it has been shown that variation in body mass was related to vigilance in Belding's ground squirrels and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*). Juvenile squirrels were less vigilant than adults, and this difference was attributed to their higher nutritional needs (Arenz and Leger, 2000; Bachman, 1993). Variation in vigilance between males and females have been reported for several mammal taxa: males of many primate species are more vigilant than females (Koenig, 1998; Buchanan-Smith, 1999) as it was shown also in some ungulates species (Prins and Iason, 1989). In giraffe (*Giraffa camelopardalis*), males were more vigilant but only during the wet season; in fact, females showed higher vigilance during the dry season (Ginnett and Demment, 1997; Cameron and du Toit, 2005). These differences are commonly attributed to the intra-specific competition or to the different absolute energy requirements between the two sex (especially in species with marked sexual dimorphism) (Pays and Jarman, 2008).

In some species, vigilance level can vary during the year according to the mating season; the necessity to fight against conspecifics, to defend or acquire a territory, or the possibility to mate can increase the individual level of vigilance; females may increase their vigilance to defend their offspring against predators. For example, during the breeding season elk stags (*Cervus elaphus*) increase their vigilance to avoid sudden aggressions from other males; females increased their vigilance after the calving season when the possibility to have a dangerous encounter with predator was higher (Lung and Childress, 2007).

Independent of other effects, individuals of the same species may show behavioural differences in their level of vigilance. We are aware that individual variation around the mean value of a behaviour can be, at least partially, explained by individual and its personality. In a previous work on Alpine marmots, for example, we have shown that individuals inhabiting an area surrounded by the forest and with poor visibility (factors that potentially increase the risk of being surprised by a predator) have a higher frequency of vigilance events. At the same time individuals living in the same area differed considerably in their level of vigilance (see App. A FIGURE A.1; A.2); we suggest that this variation can be partially explained by individual effects. Our scope in the present study is to investigate if variation in vigilance behaviour follows variation in an individuals temperament.

As we resumed above, individuals often differ consistently in their aggressiveness, activity and boldness (or risk taking behaviour), and these traits are generally positively correlated with dominance (Verbeek, Boon and Drent, 1996;Dall, *et al.* 2004; Fox, *et al.* 2009). We expect that individual variation in personality traits has a significant effect in vigilance behaviour.

The way vigilance behaviour should vary with personality is not completely clear: in a hypothetical simplified situation, where the risk is constant and uniformly distributed, we would expect bolder individuals to show lower vigilance level compared to shy ones; this is not easily the case in nature, where risk varies with to several different factors (as we resumed above). In a situation where risk is not uniform and varies with different external factors, we can imagine two main possible scenarios:

1) bolder and more dominant individuals could conquer and defend a safer area, and thus could show a lower vigilance level against predator; despite that, vigilance against possible conspecific intruders could lead dominants individuals to show a high level of vigilance.

2) In another scenario we may expect that bolder individuals tend to take higher risks, for example foraging further from the refuge or during particular times (Sih, Kats and Maurer, 2003); in this case bold individuals should adjust their vigilance level to the degree of risk, otherwise they would probably suffer high mortality. Effects of personality traits on the level of risk taken by an animal in a predatory context have been provided, for example, in a study on bluegill sunfish (*Lepomis macrochirus*): individuals more active in a new environment were also more prone to approach a novel object and more willing to remain

in the arena when confronted with a simulated risk of predation (Wilson and Godin, 2009).

Because personality traits are repeatable we expect that individuals differ consistently in their vigilance and risk-taking behaviour across situations. In streamside salamanders (*Ambystoma barbouri)*, for example, individuals that take more risks in a less risky situation also tend to take a higher risk within a more risky one (Sih, Kats and Maurer, 2003). In this species early exposition to chemical cues of predators and physiological constrains prevent salamanders from being optimal in every situation (Sih, Kats and Maurer, 2003). When individuals show different strategies, natural selection could act by favouring alternatively different behavioural types according to environmental variations (for example based on the presence –absence of predators) and this would maintain individual variation within a population (Sih, *et al.* 2004). The study of the ecological role of personality is thus a necessary step: in our project on Alpine marmots we aim to integrate the study of personality and the study of vigilance behaviour in nature.

ALPINE MARMOT AS A CASE OF STUDY

Alpine marmots are large diurnal burrow-dwelling rodents inhabiting the high alpine and subalpine meadows in the mountainous regions of west and central Europe. This species lives in social groups of up to 20 individuals and is one of the most social species of rodents (Arnold, 1988; Perrin, Allainé and Le Berre, 1993). Alpine marmots spend half of the year hibernating below ground, and members of each groups hibernate together in one hibernaculum (Arnold, 1990b).

Each family is generally composed of one dominant pair of adults and of their offspring of various ages, or of unrelated younger individuals (*e.g.* in the case of reconstituted families or when the family tolerates the presence of an immigrant) (Arnold, 1990a). In general, offspring and unrelated younger individuals are subordinates and are inhibited in their reproduction by the dominant pair (see below). The dominant pair defends the territory occupied by the whole family against intruders trough aggression (Arnold, 1990b). However, territorial defence is not restricted to the two dominant individuals, and it is possible to observe younger individuals involved in the defence of the family territory.

This species does not show any evident sexual dimorphism (Arnold, 1990a). Mass and size do not vary between sexes, but only among different age classes. Alpine marmots grow until three years of age, when they reach their adult size and mass (Arnold, 1990b). Individuals reach sexual maturity between the second and the third summer, but the possibility to mate is generally determined by their social status within the group: only dominant females reproduce and dominant males have a higher reproductive success than subordinates males (Arnold 1990a; Hacklander, Mostl and Arnold, 2003). However several authors documented many cases of extra-pair paternity in this species, showing that subordinates can occasionally successfully reproduce (Arnold, 1990a; Cohas, Yoccoz and Allainé, 2007). Dominant individuals inhibit reproduction in subordinates through frequent aggressions, dominant display and hormonal action (Arnold and Dittami, 1997; Hacklander, Mostl and Arnold, 2003). Most members of a family disperse during their third summer; they move outside of their natal territory to evict the dominant individual from another territory, or enter in a group where the dominant position is vacant. Dispersing individuals generally leave their natal site at the beginning of the summer and during this period it is common to observe agonistic and aggressive interactions between territorial individuals and intruders (Arnold, 1990a). Alternatively individuals avoid dispersing and remain in the natal site as subordinates and eventually reaching the dominant status (Arnold, 1990b; Allainé, 2000). Remaining in the family territory gives delayed benefits to these individuals at a cost of delayed reproduction (Allainé, *et al.* 2000).

Marmots live in hibernacula under the ground and dig a burrow system with several entrances surrounding a core area. Burrows are essential for winter hibernation, and the presence of young subordinates (*i.e.* mainly the males) increases the chance of survival of the pups of the year (Allainé; 2004). Burrows are also part of the anti-predator strategy for the family and provide a shelter when a potential threat is detected. In general a system is composed of a couple of main burrows and several refuge burrows (Bassano, *et al.* 1991). The main burrow is longer, contains multiple entrances, and is often protected by natural elements. Marmots spent most of their time around these main burrows, where they sleep, nest and hibernate. Refuge or escape burrows are spread over the whole home-range of a family. Each escape burrow usually has only one entrance and is used for shorter periods than the main burrow.

Marmots are herbivores and feed selectively among plants species (Barash, 1973; Armitage, 1979). Their impact on food distribution is stronger in the core area near their burrow and decreases with distance from the refuge (Holmes, 1979; Wood, 1973). For this reason they have to move further away from the core area to find fresh food resources, thereby increasing their vulnerability to potential attacks by predators (Holmes, 1984). Furthermore, a marmot that forages away from its family refuge, increases its chances of experiencing aggressive encounters with neighbours from other families.

While foraging, Alpine marmots scan the surroundings as part of the anti-predator strategy; this behaviour allows individuals to be aware of any dangerous change in the environment and to gain a satisfying amount of energy (Blumstein, 1998). When they perceive a danger marmots use alarm calls to warn conspecifics about the threat (Armitage, 1962; Blumstein, 1998).

The main terrestrial predator in the Alps is the fox (*Vulpes vulpes*), which approach the prey quietly and attempt an attack. In our study site, successful attacks by foxes on adults are very rare, but foxes have been frequently observed catching pups directly from the burrow (C. Ferrari *pers. obs.*). The main avian predator in this area is the golden eagle (*Aquila chrysaetos*), that possibly prey upon every age class. Although attacks by eagle have not been observed during the summer season, we think it may play an important role early in the spring when marmots emerge from the burrow and the snow still covers the whole area surrounding burrow entries.

Scanning behaviours, burrow systems and social alarm constitute a major part of the anti predator strategy in this species; Alpine marmots can vary their risk-taking behaviour by foraging at different distances from the closest burrow or in different environmental conditions and they are expected to adjust their vigilance level by varying the frequency and duration of vigilance events.

OBJECTIVES OF THIS RESEARCH

This research aims to investigate how personality affects vigilance behaviour in a wild population of Alpine marmots, living in the Gran Paradiso National Park, in Italy. The first objective of this study is to evaluate individual behavioural consistency in the open-field test and in the behavioural reactions towards handlers, and to correlate this variation with variation in physiological parameters characterising different coping styles. I expect that more active/explorative individuals in the open-field will show a higher increase in heart rate, breathing rate and temperature when handled. Results in support of my prediction will help me validate the differences in behaviour found in the open-field test.

The second objective of this study, was to link differences in personality among individual marmots with their vigilance in the field during foraging activity. I used linear mixed models to quantify the variance explained by the individual (*i.e.* repeatability) and to test the effect of personality traits and others factors on vigilance behaviour. I expect differences in proactivity to be positively correlated with differences in vigilance rate and with individual characteristics such as social status, age, sex and area inhabited.

CHAPTER I

PERSONALITY AND VIGILANCE BEHAVIOUR IN ALPINE MARMOT (Marmota Marmota)

Caterina Ferrari, Cristian Pasquaretta, Achaz von Hardenberg and Denis Réale

ABSTRACT

Several studies provided evidence that individuals of the same species differ consistently in their behaviours and that behaviour in one context is correlated with behaviour in other contexts; these suites of consistent individual differences in behavioural traits have been referred to as personality or coping style. The study of the ecological role of personality allow researchers to estimate the action of natural selection upon different personality types. The aim of this study is to evaluate whether individual Alpine marmots (*Marmota marmota*) show consistent differences in their personality and if, according to their personality, individuals differ in their vigilance behaviour. We collected data during captures and field observations on 122 marmots during the summers of 2007 to 2009 in the Gran Paradiso National Park, Italy. We measured the individual level of proactivity during handling and the individual level of activity during open-field tests. We analysed the data using Linear Mixed Models to account for individual and environmental differences, and to estimate the repeatability of individual measurements. We found that Alpine marmots differ in their behavioural responses during handling and during the open field tests, marmot identity explaining 45% and 33% of the phenotypic variance in behaviour, respectively. These two measures were also highly positively correlated. Vigilance behaviour differed among individual marmots and results suggest that age, status and individual personality were the best predictors for these variation. Our study provides evidence that one can use just one of the methods (*i.e.* measures of heart rate or measures of the activity level during the open-field test) to obtain a reliable measure of coping style in this species, a significant result for the study of personality in wild animal populations.

Key words: activity, coping style, heart rate, personality, vigilance, *Marmota marmota*

I-1. INTRODUCTION

In predator-prey systems, individuals of potential prey experience a time budget conflict between the necessity to forage and the necessity to detect predators (Sih, Bell and Johnson, 2004). As a consequence, animals have to trade off foraging activity with vigilance behaviours and often have to choose between foraging in a more or less risky situation (Lima, 1985). They are thus expected to adjust their vigilance level according to predation risk (Brick and Jakobsson, 2002; Lopéz, *et al.* 2005). A common anti predator strategy in herbivorous species consists of a sequence of head-down/head-up movements to detect potential predators in their surroundings while they are foraging. By doing so they can both gain enough energy and detect potential predators (Lima and Dill, 1990). In most of these species, individuals vary in their vigilance behaviour by varying the time spent vigilant and the frequency of vigilance events according to the level of risk. Different extrinsic or intrinsic factors can affect the vigilance of an individual in the short or long term. For example, environmental characteristics are responsible for differences in vigilance behaviour in two populations of marmots: individuals inhabiting an area characterized by low visibility and proximity to the forest were more vigilant than individuals living in alpine meadows with great visibility (Ferrari, Bogliani and von Hardenberg, 2009). Adults of Belding's ground squirrel living in sites with high predation risk spend more time alert than those living in sites with lower predation risk (Mateo, 2007). Individuals decrease their vigilance with increasing group size (Frid, 1997; Bednekoff and Lima, 1998; Beauchamp, 2003; Fernández-Juricic, *et al.* 2007). Social and breeding status (Haskins, Sih and Krupa, 1997;Aureli, Preston and de Waal, 1999; Lung and Childress, 2007), or energy needs (Damsgard and Dill, 1998) also influence the time an individual spends vigilant.

When behavioural differences between individuals are consistent over time and across situations they are referred to as personality or temperament traits (Budaev, 1997; Gosling, 2001; Groothuis and Carere, 2005). Correlations between personality traits have been described for several species and are referred to as a behavioural syndromes or coping style. In this work we will use the terms personality and coping style.
Personality traits have been shown to play a significant role in some salient aspects of individuals' life history such as habitat use, dispersal and social behaviour (Civantos,

2000; Armitage and Vuren, 2003; Dingemanse, *et al.* 2003; Sih, Kats and Maurer 2003; Dall, 2004), and to be under natural selection (Réale and Festa-Bianchet, 2003; Dingemanse and Réale, 2005; Quinn, *et al.* 2009).

In situation where animals have to choose between different mutually exclusive activities, differences in personality traits are likely to affect an individual's behaviours. For example in situations differing in their level of risks animals have to balance their foraging activity with vigilance. In this context personality may influence the foraging and vigilance behaviour and the risk individuals are willing to take. Bold and active individuals are expected to take more risks. Indeed in many species individual activity tends to positively covary with boldness and risk-taking (Verbeek, Drent and Wiepkema, 1994; Lopéz, *et al.* 2005; Wilson and McLaughlin, 2007). For example, Wilson and Godin (2009) recently showed that the most active individuals of bluegill sunfishes (*Lepomis macrochirus)* were also the boldest in a series of experimental tests. Also, the most active individuals of zebrafish (*Danio rerio*) were the ones with a higher tendency to approach a predator (Moretz, Martins and Robison, 2007). Finally, when facing the conflict between hiding or foraging, some individuals of streamside salamander larvae *(Ambystoma barbouri*) tend to take more risks by being consistently more active both in the presence and absence of predators (Sih, Kats and Maurer, 2003). Based on those differences in risk-taking among individuals of a population we tested if differences in personality can as well explain a part of the difference in vigilance between individuals (see Drent, van Oers and van Noordwijk, 2003; Sundström, *et al.* 2004). We predict that vigilance behaviour in Alpine marmots differs according to individual personality, with more active and bold individuals taking a higher risk reflected in a higher vigilance level. In addition, we predict that vigilance levels vary according to the social status of the individuals with dominants showing higher level due to both predation risk and social stress.

The model species in this study is Alpine marmot, a rodent inhabiting alpine meadows in the European Alps (Allainé, *et al.* 1994). This species provides an ideal subject for our study since it is easily observable during its daily activity, it is possible to trap and mark the individuals and it has a relatively complex social structure (Allainé, 2000).

We measured marmot personality traits as the reactions of individuals to a novel environment using the open field test (Gould, Dao and Kovacsics, 2009). Open-field tests have recently been applied in the wild (Boon, Réale and Boutin, 2008; Martin and Réale, 2008). Measures in the open-field and reaction towards handlers are assumed to provide reliable indices of individual personality/coping styles. However, it is needed to validate these measures by evaluating their correlation with some physiological responses to challenging conditions. Consistent individual behavioural differences have also been found to be linked with differences at the physiological level (Koolhaas, *et al.;* 1999; Kralj-Fiser, *et al.* 2007). For example, proactive individuals (*i.e.* bold, active and aggressive animals) show a higher reaction of the sympathetic nervous system, leading to an increase in heart rate and noradrenaline concentration in the blood. These individuals tend to actively cope with the source of stress through a "*flight or fight*" response. In contrast, reactive individuals (*i.e.* passive, shy, and lowly aggressive animals) show the opposite physiological patterns and tend to react by freezing (Koolhaas, *et al.* 1999). We thus expect that active marmots in the open-field will be the least docile during handling, and will show higher increase in heart rate, breathing rate, and temperature when handled.

I.2. METHODS

Model species and study site

Alpine marmots are large, diurnal, burrow-dwelling rodents inhabiting high alpine and subalpine meadows in Europe. The basic social unit is a family group of 2-20 individuals composed of a territorial dominant breeding pair, mature subordinates of 2-4 years, subadults (or yearlings) and pups (Perrin, Allainé and Le Berre, 1993). Alpine marmots spend half of the year hibernating underground inside the family burrow (Arnold, 1988; Perrin, Allainé and Le Berre, 1993). They dig a burrow system with several entrances surrounding a core area.

The study area was located in Orvielles (Valsavarenche, Aosta, Gran Paradiso National Park, North Western Italian Alps, 45°34'N/ 7°11'E). In the area, marmots reach a high density and they are active from mid-April to mid-October (Bassano, *et al.*1991). The alpine meadow is rich in Coloured fescue (*Festuca varia)* and Alpine meadow grass *(Poa alpina).* However, marmots feeds selectivity among plant species: for example in the Alps, according to the vegetative period, they prefer to feed on red clover (*Trifolium pratense*) friendly thistle (*Carlina acaulis*) black vanilla orchid (*Nigritella rhellicanii*) and dandelions (*Taraxucum alpinum*) (C. Ferrari, *pers. obs.*). The impact of a marmot's foraging activity on vegetation and food distribution is stronger in the core area near its refuge (Wood, 1973). Thus an individual has to move further away from its burrow entrance to satisfy its energy needs, but by doing so it increases the risk of being attacked by a predator (Holmes, 1984), or of experiencing agonistic encounters with marmots from neighbouring territories. One of the main anti-predator strategies of this species consists of scanning the surroundings while foraging, grooming or playing, and fleeing into a burrow as soon as a potential danger is detected (Armitage, 1962; Blumstein, 1998). Alternatively when the predator is detected at a distance a marmot will emit alarm calls. Marmots generally emit one single alarm responding to an aerial stimulus, and multiple alarms in response to terrestrial threat (Blumstein and Arnold, 1995). As a result, marmots can flee in their burrow, or mob the predator. Natural predators such as golden eagles (*Aquila chrysaetos*) and red foxes (*Vulpes vulpes*) also reach a high density in this region.

Capture protocol

We trapped marmots at two sites with similar marmot densities but different environmental characteristics and human disturbance levels:

- Low site (2000m above sea level): delimited by a mixed conifer forest (European larch *Larix decidua,* pine *Pinus silvestris* and Norway spruce *Picea abies*). Here the anthropogenic disturbance is higher since the mountain house (our logistic base) is located in the middle of the area and the touristic path crosses the marmots' territory. During the summer tourists frequently stop along the path.

- High Site*:* (2200-2500m above sea level). Characterized by an open alpine meadow (mainly *Festuca varia* and *Poa alpina).* Here the touristic trail is further from most family territories and the human impact is reduced.

We live-trapped a total of 122 individuals from May to July in 2007, 2008, and 2009, using 19 Tomahawk traps (150x30x30) and horse fodder (*Omolene*) as food bait. Once we trapped a marmot, two people transferred it to a handling bag and transported it to the working site (average time from the capture to first manipulation = 17 ± 5 minutes). We used the following standard protocol for all marmots wherein no more than three persons worked simultaneously, including one operator who kept the marmot quiet inside the handling bag during the whole operation. The hormonal analysis required that we strictly followed this sequence. We also noted the time at the beginning of each action.

1. Blood sample and physiological parameters (within 2 minutes of handling);
2. Marking procedure;
3. Body-mass and biometric measures
4. Open-Field (OF) and mirror image stimulation (MIS) tests (3+3 minutes);
5. Blood sample and physiological parameters (immediately after OF/MIS tests);
6. Release of the animal.

1) Blood samples were collected to measure an individual's hormonal response to acute stress for future work. Two samples were necessary to measure the increase in glucorticoids following the stress of handling (Mostl, 2002; Carere, *et al.* 2003). Samples were stored with Eparin, centrifuged in the next 48 hours and kept refrigerated until analyses. After each blood sample was taken (*i.e.* the first one just after capture and a second one after the open-field test), heart and breathing rates were measured simultaneously by counting the number of heart beats using a stethoscope and the number of breaths during 15 seconds. Anal temperature was measured using a digital thermometer. These measures were used to evaluate an individual's physiological reactions to handling and to the challenge presented by the open-field test (Carere and van Oers, 2004). We analyzed a total of 189 physiological measures on 105 different individuals.

2) We marked the marmot for individual recognition using a unique microchip transponder under the skin (Mod. Bayer Animal Coder), two plastic coloured ear tags (Mod. Minirototag, 5cm length) with different colour combinations and fur bleaching to help in visual recognition at a distance.

3) For each individual we used a calliper and a ruler to measure to the nearest mm:

a) Anogenital distance;

b) Total length from the nose to the base of the tail;
c) Chest circumference;
d) Length of posterior feet, from the heel to the base of the middle finger;
e) Tail length, from the base to the tip.

We determined sex by measuring ano-genital distances; a distance between 0.1mm and 1 cm indicates a female, while a male is characterised by a larger distance that increases with age (Zelenka, 1965). We measured body mass rounded to the nearest mg, measured with a field-scale, and we assessed age based on this measure and information from previous captures for individuals captured first as pups or juveniles. We divided age in three classes: pups (born during the summer), subadults (one year old), and adults (two years old or more). In our sample the mean weight was: 0.52 ± 0.2 kg for pups, 1.69 ± 0.4 kg for subadults, and 3.41 ± 0. 7 kg for adults.

During the season we assessed an individual's social status (dominant *vs.* subordinate) primarily based on its reproductive status and next on its interactions. Dominant individuals often showed territorial displays (approaching a conspecific with fast wagging movements of the tail) and frequently started agonistic interactions against subordinates and intruders (Armitage, 1975; Hacklander and Arnold, 1999; Allainé, 2000). During agonistic interactions one individual typically chased the other one, and they fought by biting, scratching and jostling each other. When we were not sure of the status of an individual, we referred to it as subordinate. Pups and juveniles occupied a subordinate position. In a given territory all the adults (two years of age and more) except two, referred to as the dominant pair, will be subordinate.

Open field test

The open-field test has been used in many studies to quantify the reaction of rodents to an novel environment (Archer, 1973; Gould, Dao and Kovacsics, 2009). Measures of movement patterns during an experimental test (*e.g.* open field test) are commonly interpreted as an individual's index of both activity and exploration (Boon, Réale and Boutin, 2007; Réale, *et al.* 2007) and have been shown to be representative of an individual's explorative behaviour in the wild (Boon, Réale and Boutin, 2008; Dingemanse and De Goede, 2004).

We performed a total of 182 open-field tests on 105 Alpine marmots of different sex and age. The test was repeated at least twice on 52 individuals. Tests were conducted in the field in May, June and July in 2007, 2008 and 2009. After the first step of the capture protocol (mean time elapsed = 10 ± 6 minutes) marmots were gently pushed from the handling bag inside the open-field arena. The arena consisted of a playpen (94.5 x 102 cm) adapted by adding white plastic panels on the ground and on each side, and covered by a plastic net as a lid (see FIGURE 1.1). A little door on the side allowed us to transfer the animal in and out of the arena.

We recorded the marmot's behaviour during 3 minutes while remaining silent and not visible to the marmot during the duration of the test. After the open-field test, we performed a Mirror Image Stimulation test (MIS) during 3 more minutes by placing a mirror within the arena; results from MIS are not shown in this work. Marmot behaviours during the test were scored using the software The Observer (Noldus Inc.). For this purpose we adapted the ethogram on red squirrels (*Tamiasciurus hudsonicus*) from Boon, Réale and Boutin (2007). See TABLE 1.1 for a description of the scored behaviours.

TABLE 1.1. Behaviours recorded on Alpine marmots during the open-field test. Ethogram was based on the work of Boon, Réale and Boutin (2007) on red squirrels. Walking, destroying, jumping and up posture were used to compute the time spent active by marmots in the open-field test.

Behaviour	Description
Walking	The marmot walks or runs inside the arena. Also includes animals constantly moving their head looking around.
Destroying	The marmot digs and bites the floor, the sides of the box or the net-lid.
Jumping	The marmot jumps on the walls.
Up posture	The marmots is in a rearing position or climbs against the walls . Also includes animals constantly moving their head looking around.
Immobility	The marmot stands or lies with four paws on the ground, and does not move its head.

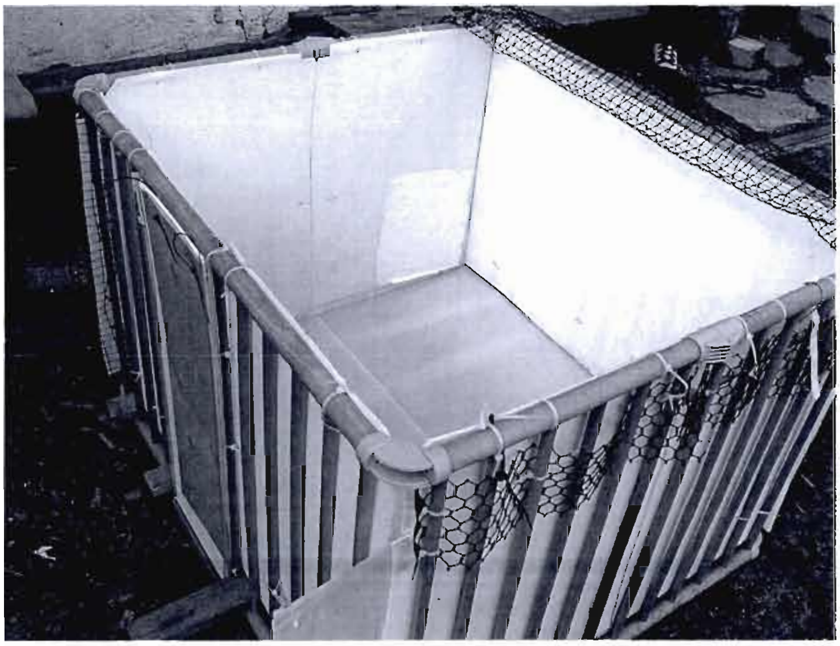

FIGURE 1.1: Open-field arena; Alpine marmots were gently transferred inside the arena through the door on the left side. During the test a plastic net was fixed on the superior part of the arena to prevent the possibility of escape.

Vigilance observations

We observed Alpine marmots with a scope (Swarosky 30x75) during their foraging activities (7:00 am-1:00 pm and 2:30 pm-6:00 pm), from June to September 2007, 2008 and 2009. We kept a minimum distance of 200m from the focal marmot. We recorded vigilance behaviour of individual marmots on a voice recorder as described in previous work on marmots (Blumstein, 1996). We located and determined the identity of a foraging marmot, and then waited for one minute before starting an observation session to avoid recording behaviour during or straight after any particular situation or disturbance (*e.g.* predator visits to the area, agonistic interactions with other marmots, disturbance by tourists). We then recorded the beginning and the end of each vigilance event (head-up) and foraging event (head-down) during the following 120 seconds. In this study we only considered occurrences of head-ups and head-downs and excluded half way-postures (but see Makowska and Kramer, 2007). We only collected focal observations on juveniles and adults. We analyzed data of 646 vigilance observations related to 43 different individuals.

We used the software EthoLog 2.0 (Ottoni, 2000) to digitalise all the records from the voice recorder. For each focal observation we calculated the percentage of time spent vigilant, the frequency of vigilance bouts (number of vigilance bouts/120 seconds) and the mean duration of vigilance bouts (Martin and Bateson, 1993). All the focal observations and data extraction were carried out by the same two people after a period of training (C. Ferrari and N. Martinet).

I.3. STATISTICAL ANALYSIS

For all the analyses we used R 2.8.1 version (R Development Core Team 2008) with the nlme package, following the model building approach suggested by Pinheiro and Bates (2001) and Zuur *et al.* (2009) for all the Linear Mixed Effects (LME) models.

Physiological parameters

Prior to analyses heart rate and breathing rate were square-root transformed and the body mass of each marmot at the day of capture was centred on its mean.

For each physiological parameter we used linear mixed models and tested for the significance of random effects by comparing different models including or excluding each of these random terms, while keeping the same fixed effect structure. We used the following models with random effects: a model including marmot identity only, a model including family only and a more general model with both marmot's identity nested in its family identity. All these models were run using a Restricted Maximum Likelihood (REML) procedure and compared using a Log-likelihood Ratio Test (LRT) (Pinheiro and Bates, 2001). Age, dominance status, sex, body mass at the day of capture and the interaction between age and body mass were included as fixed effects in the models.

For each physiological parameter we then fitted a model with the best random structure using Maximum Likelihood (ML) estimation and we simplified it using a stepwise backward procedure by removing all non-significant fixed effects to obtain the selected model. We used the value of alpha at 0.05 as a criterion to exclude or keep a fixed effect.

Repeatability (r), defined as the variance due to the individual, of the physiological parameters was assessed by the formula: $r = V_i / (V_i + V_r)$; where V_i represents the estimate of variance due to the individual, and V_r is the residual variance. When the random structure included marmot's identity nested in family we added the value of family variance in the formula [*i.e.*, $r = (V_i + V_f)/(V_i+V_f+V_r)$], where V_f is the estimate of family variance. We tested if V_i or V_f were significantly different from 0 by comparing the final model fitted using REML with a linear model without the random term (*i.e.* individual or family identity) using a likelihood ratio test with one degree of freedom (Pinheiro and Bates, 2001).

We tested for correlations between the physiological parameters using Spearman rank correlation tests.

Open field test

An explorative Principal Component Analysis (PCA) was performed on three categories of behaviour scored during open field test: "Movement", including destroying, walking and jumping, "Up posture" and "Still". Results from the PCA suggested a division between activity-related behaviours and inactivity-related ones (see TABLE I.1 for description of behaviours). Thus, to avoid complications due to the use of one component and to its interpretation (Réale, *et al.* 2007), we decided to use the sum of the percentage of time spent in all behaviours related to activity inside the open field ("Walking", "Destroy", "Jump", "Up", see TABLE I.1) in further analysis. This composite variable will be referred to as Activity, and we use it as a response variable in a linear mixed model including sex, age, site, month and number of open-field trials performed as fixed effects. The random structure and fixed effects best fitting the data, as well as the repeatability of Activity and its significance, were obtained as described in the section on physiological characteristics.

Correlation between behavioural variables

We used Best Linear Unbiased Predictors (BLUPs) for random effects within the final mixed models to estimate individual behavioural profiles. The BLUPS method provides estimates of random effects independent of other terms in the model, standardized to a mean of zero (Kruuk, 2004); recently a critical review of this method pointed out some potential limit in the use of this estimates, especially when used for predicted breeding values (Hadfield, *et al.* 2009). However, simulation analyses have shown that they provide good estimates of phenotypic values for an individual (Martin Pers. Comm.). The models of heart rate and activity with significant repeatability and including only significant fixed effects were used to calculate BLUPs. We will use the term "Heart rate" to indicate the BLUPs value of this variable; heart rate measures will be used to refer to raw measures. "Activity" will be used to indicate the BLUPs value.
We used the Spearman rank correlation test for correlations among BLUPs of physiological data and Activity. A positive correlation among these traits would suggest

the existence of a proactive-reactive syndrome (Benus, *et al.* 1991; Koolhaas, *et al.* 1999).

Vigilance observations

For each focal observation on vigilance behaviour during foraging we calculated the following parameters:

- percentage of time spent vigilant: the ratio of time spent vigilant during a focal observation to the total duration of the focal;
- rate of vigilant events: the ratio of the number of vigilant bouts to the total duration of the focal observation;
- mean duration of each vigilant event: the ratio of the total time spent vigilant to the number of vigilance bouts.

We tested for correlations among these variables using Spearman pair-wise correlations. A positive correlation between vigilance parameters would allow us to consider only one parameter in further analysis.

Using vigilance rate as a response variable and providing the same fixed-effect structure, we tested for the best random structure as described above. Fixed effects were Heart rate, Activity, age, social status, zone, month, sex, plus the interactions between Heart rate and status, Activity and zone, and Activity and status. The model with the best random structure was then fitted using a Maximum Likelihood (ML) procedure to test for the significance of the fixed effects. The model was simplified in a stepwise manner by removing all non-significant terms to obtain the selected model and alpha value fixed at 0.05. Vigilance parameters were log-transformed prior to analyses.

I.4. RESULTS

Physiological parameters

The effect of marmot ID was negligible, and family group explained 17% of the total variance of body temperature (TABLE 1.2). None of the random terms could explain a significant part of the phenotypic variance in breathing rate (TABLE 1.2). Since repeatability of these measures was null (breathing rate) or low (temperature), we did not consider them as indices of individual personality for further analyses. Repeatability of Heart rate was high and significant (r = 47%). The likelihood ratio test between models with different random structures suggested that we keep the more general model with ID nested in family (TABLE 1.2).

The final model on Heart rate included dominance status, age, body mass and the interaction between age and body mass as significant fixed effects (TABLE 1.3). Heart rate decreased with age, pups having higher heart rates (mean value and standard deviation 71.25 ± 10.92) than sub-adult (mean value and standard deviation 64.26 ± 12.96) and adult individuals (mean value and standard deviation 53.56 ± 12.52) (FIGURE 1.2). Dominant individuals had significantly lower heart rates (mean value and standard deviation 49.51 ± 10.85) than subordinate ones (mean value and standard deviation 64.21 ± 13.22)(FIGURE 1.3).

Overall heart rate decreased with body mass (TABLE 1.2). However, heart rate changed differently with body mass depending on the age class: heart rate increased with body mass in pups, while it decreased in sub-adults and adults (FIGURE 1.4).

TABLE 1.2: Likelihood ratio test for the best random structure in models with body temperature, breathing or heart rate as response variable in the marmot Orvielles population, Gran Paradiso National Park, Italy. All models were run using the Restricted Maximum Likelihood (REML) procedure and included the same fixed effects: age, dominance status, sex, body mass at the day of capture and the interaction between age and body mass. Rates were square-root transformed prior to analyses.

Response variable	**Model number**	**Random term**	**V_i**	**V_f**	**V_r**	**k**	**Random effect tested**	**Loglik**	**test**	**LRT**	**d.f.**	**P**
Body temperature	1	ID	0.17	na	1.50	8	Family	-217.919	1 vs 3	7.775	1	0.005
	2	**Family**	**na**	**0.28**	**1.41**	**8**	**ID**	**-214.031**	2 vs 3	0.000	1	0.999
	3	Family/ID	$2.4\ 10^{-6}$	0.28	1.41	9		-214.031				
Breathing rate	1	ID	0.05	na	0.32	10	Family	-172.607	1 vs 3	2.354	1	0.124
	2	family	na	0.04	0.34	10	ID	-171.829	2 vs 3	0.800	1	0.371
	3	Family/ID	0.03	0.03	0.31	11		-171.429				
Heart rate	1	ID	0.28	na	0.34	10	Family	-209.777	1 vs 3	7.988	1	0.004
	2	Family	na	0.17	0.47	10	ID	-208.334	2 vs 3	5.103	1	0.023
	3	**Family/ID**	**0.16**	**0.15**	**0.35**	**11**		**-205.782**				

V_i: Estimate of individual variance

V_f: Estimate of family variance

V_r: Estimate of Residual variance

na: not available; Models in bold are the selected models.

TABLE 1.3: Coefficients of fixed effects (β and their standard errors s.e.) for the mixed model on heart rate in Alpine marmots, Orvielles Gran Paradiso National Park, Italy. Marmot id was nested within family group as random terms. Body mass, sex, social status, age class and the interaction between body mass and age class were included as fixed effects.

Fixed effects	**β ± s.e.**	**F**	**d.f.**	**P**
Intercept	9.065 ± 0.587	237.974	1,85	<0.0001
Body mass	1.071 ± 0.392	7.445	1,75	0.007
Age	Np	7.542	2,75	0.001
Social status §	0.756 ± 0.183	16.962	1,75	0.000
Body mass x Age	Np	4.291	2,75	0.017
Rejected terms				
Sex†	-0.204 ± 0.131	2.458	1,84	0.120

† Male was the reference value for the variable 'sex' in the model;
§ Dominant is the reference value for the variable 'social status' in the model;
Np = not provided (see figures 1.2 and 1.3).

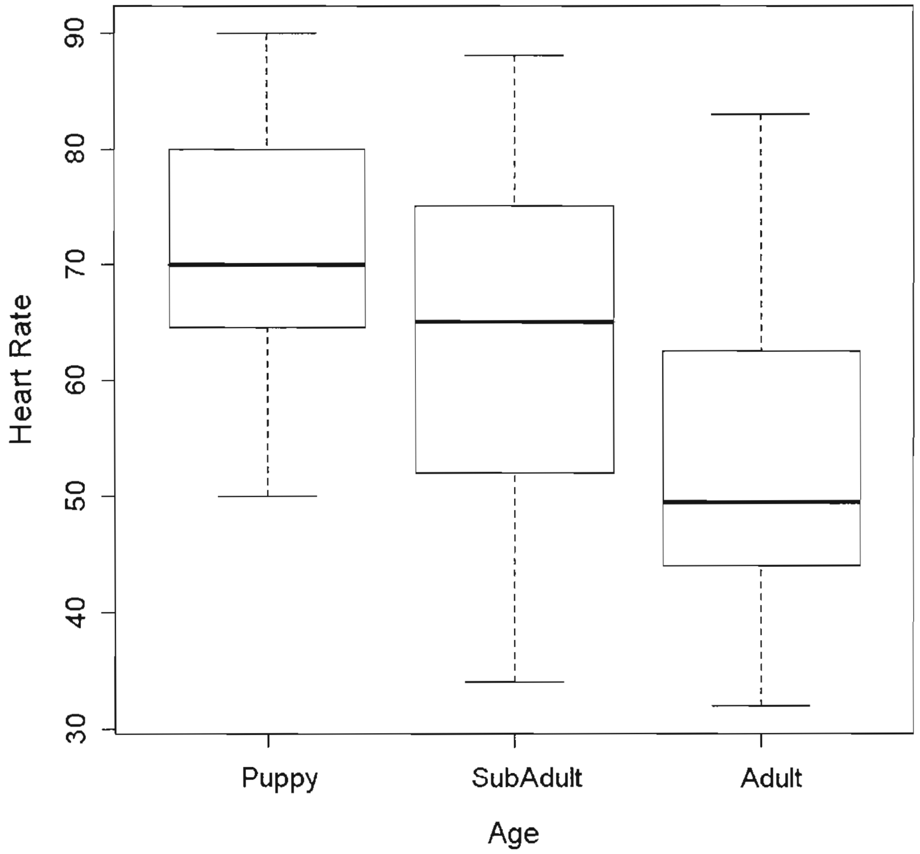

FIGURE 1.2: Boxplot of the effect of age on heart rate during handling in Alpine marmots.

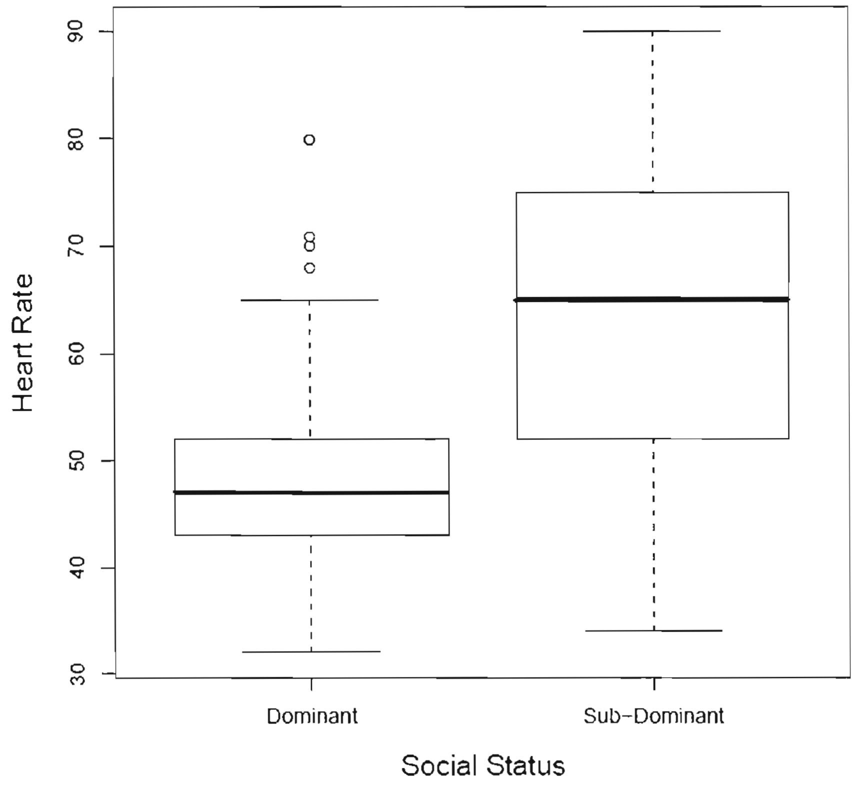

FIGURE 1.3: Boxplot of the effect of social status on heart rate during handling in Alpine marmots.

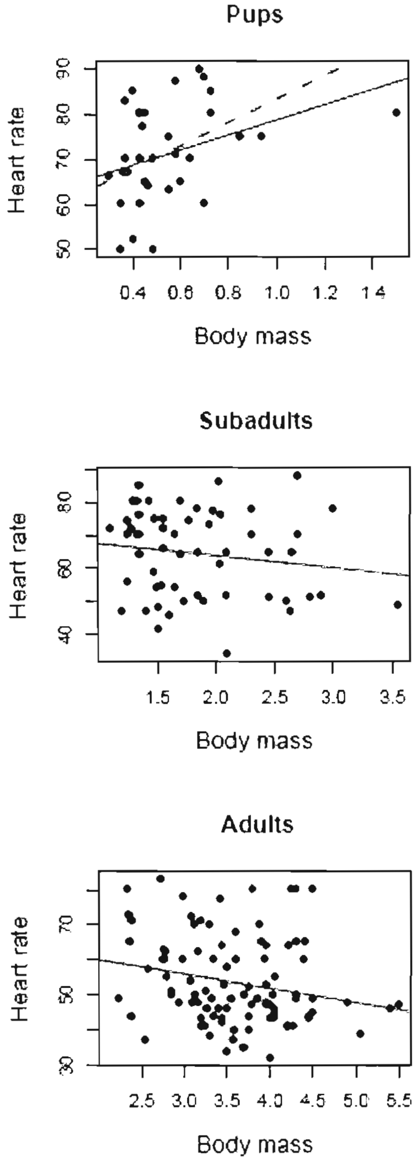

FIGURE 1.4: Scatter plots of the effect of body mass on individual heart rate during handling, for three different age classes in Alpine marmots at Orvielle, Gran Paradiso National Park, Italy. Lines indicate the tendency within the age class. In pups the dashed line indicate the tendency when the individual on the extreme right was removed from database.

Raw measures of heart rate, breathing rate and body temperature were all positively and significantly correlated with each other (breathing rate and heart rate: $r_s = 0.29$; $P < 0.0001$; heart rate and temperature: $r_s = 0.17$; $P = 0.05$; breathing rate and temperature: $r_s = 0.48$; $P < 0.0001$; FIGURE 1.5).

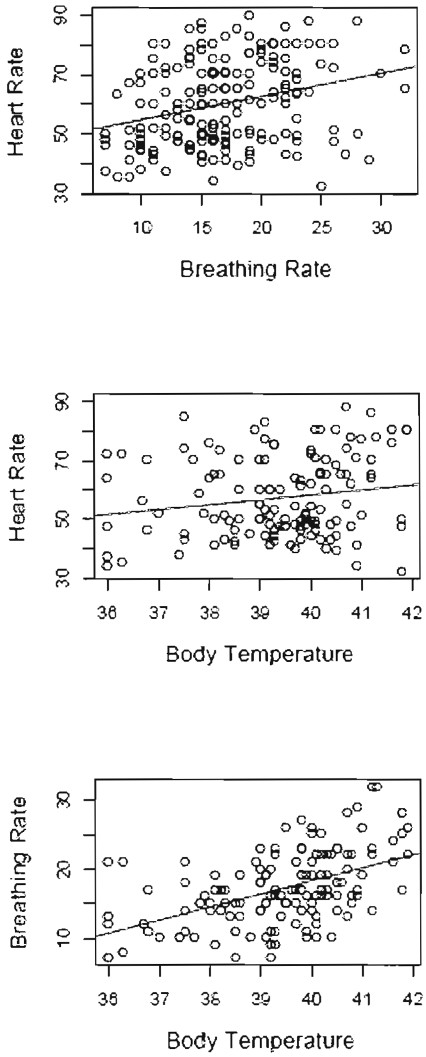

FIGURE 1.5: Correlations between raw measures of physiological parameters measured during handling in Alpine marmots, Orvielle, Gran Paradiso National Park, Italy. Each circle represents the value for one marmot.

Open field tests

In the Principal Component Analysis of behavioural data from the open-field the first component explained 69 % of the total variance in the data. Following the Kaiser-Guttman criterion Component 1 was the only suitable component to retain (Kaiser 1991). Component 1 regrouped "Movement" behaviour (destroy + walking + jump) positively associated with "Up posture", and opposed these variables to "Still" behaviour on the same axis. We thus calculated an index of Activity in the open field based on cumulative sum of destroy + walking + jump + up posture.

The best random structure in the full model of Activity during the open-field test included marmot ID, but not family ID (TABLE 1.4). Repeatability of Activity was 38 %. Marmots decreased their activity with number of trials. All other fixed effects were not significant and were removed from the model (TABLE 1.5; FIGURE 1.6).

TABLE 1.4: Likelihood ratio tests for models on Activity with different random structures in Alpine marmots_in Alpine marmots of the Orvielle, Gran Paradiso National Park, Italy. Models were fitted using a REML procedure and included the same fixed effects: sex, age, zone, month and number of open-field tests performed by the individual.

Model number	**Random term**	**V_i**	**V_f**	**V_r**	**k**	**Random effect tested**	**Loglik**	**test**	**LRT**	**d.f.**	**P**
1	**ID**	**0.03**	**na**	**0.05**	**15**	**Family**	**-43.052**	1 vs 3	0.061	1	0.803
2	Family	na	5.6e-03	0.8	15	ID	-46.026	2 vs 3	5.885	1	0.015
3	Family/ID	0.03	0.02	0.05	16		-43.083				

V_i: Estimate of individual variance; V_f: Estimate of family variance; V_r: Estimate of Residual variance
na: not available; the model in bold is the selected model.

TABLE 1.5: Coefficients of fixed effects (β and their standard errors s.e.) for the mixed model on Activity in Alpine marmots. Marmot ID was included as random term. Number of trials sex, age, zone, month and age were included as fixed effects in the initial model.

Fixed effects	**β ± s.e.**	**F**	**d.f.**	**P**
Intercept	0.545 ± 0.029	331.228	1,105	<.0000
Number of trials	np	9.165	3,50	<.0000
Rejected terms				
Sex‡	0.007 ± 0.055	0.018	1,103	0.890
Zone§	0.031 ± 0.060	0.269	1,104	0.604
Month	np	1.091	5,43	0.379
Age	np	2.215	2,48	0.120

‡ Female is the reference value for the variable 'age' in the model
§ Zone at higher altitude is the reference value for the variable 'zone' in the model

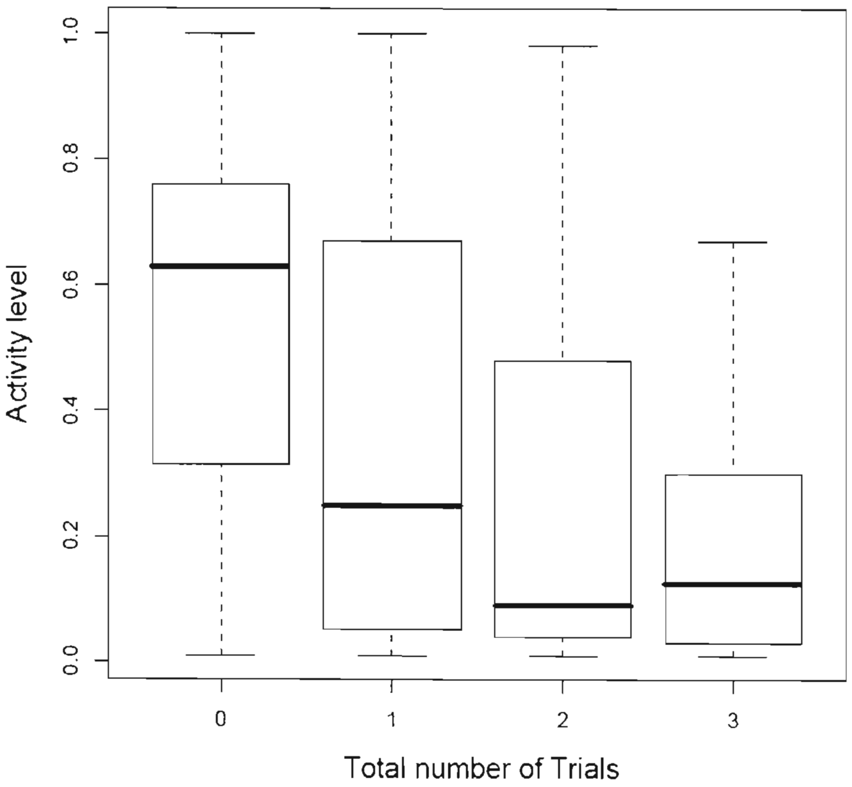

FIGURE 1.6: Boxplot of the effect of number trials on activity in the open-field test in Alpine marmots. For most of marmots trials were repeated during the subsequent summer.

Correlation between behavioural variables

BLUPs of Activity and BLUPs of Heart rate were positively correlated ($r_s = 0.59$; $P < 0.0001$; FIGURE 1.7).

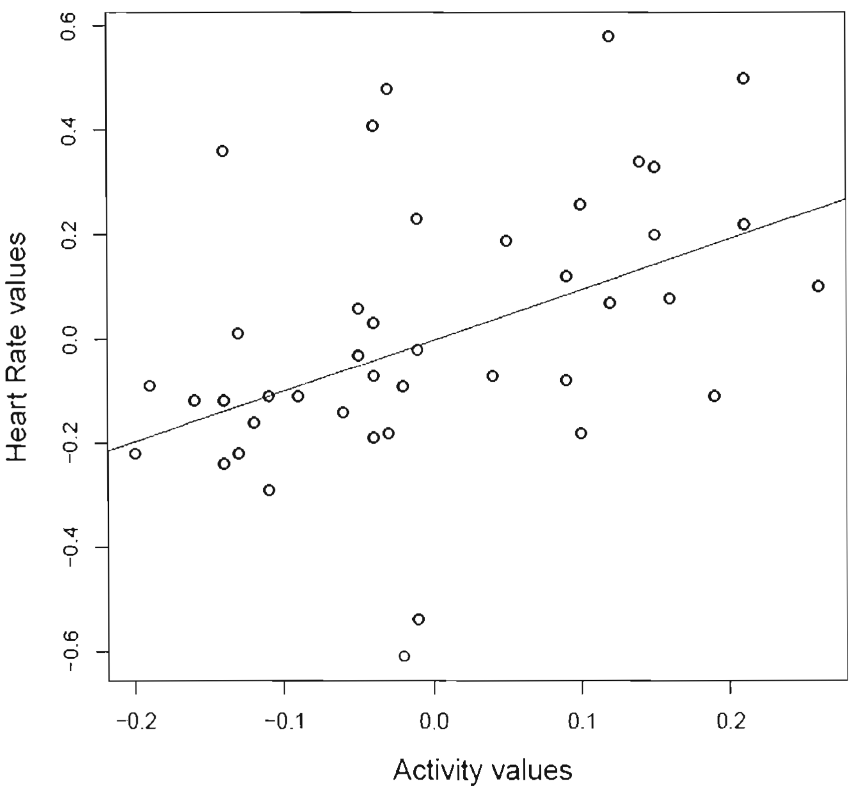

FIGURE 1.7: Correlation between individual values of Activity during the open-field and of Heart rate Alpine marmots. Each dot represents a combination of BLUPs value of Activity and Heart rate for one marmot.

Vigilance data

Percent of time spent vigilant by a marmot was positively correlated with both its vigilance rate and the mean duration of vigilant events (rho = 0.71; P < 0.0001; rho = 0.69; P < 0.0001, respectively). There was no significant correlation between vigilance rate and mean duration of vigilance (rho = 0.07; P = 0.082). Following Cresswell, *et al.* (2003) and Jones, Krebs and Whittingham (2007) we decided to use rate of vigilant events as an index of vigilance behaviour.

Once all the fixed effects were considered, the likelihood ratio test between models with different random structures showed that marmot ID was not significant and that family ID had a small and almost significant effect (2%) on vigilance rate (TABLE 1.6).

The final model of vigilance rate included age, Heart rate, dominance status, month and the interaction between Heart rate and dominance status as fixed effects (TABLE 1.7; note that only subadults and adults were used in these analyses). Sub-adult individuals had a higher rate of vigilance than adults. Marmots decreased their vigilance as time progressed over the season (mean and standard deviation of rate of vigilance June = 3.368 ± 2.406; July = 2.705 ± 2.183; August= 2.833 ± 1.992; September = 2.704 ± 2.166). The relationship between Heart rate and vigilance rate differed according to social status: vigilance decreased with Heart rate in subordinates, but increased with Heart rate in dominants (FIGURE 1.8). Sex, zone, Activity, and the interaction between Activity and zone and Activity and social status were not significant and were removed from the model (TABLE 1.7).

TABLE 1.6: Likelihood ratio test for linear mixed models on vigilance rate with different random structure in Alpine marmots. Fixed effects structure was identical for all the models: BLUPs of Heart rate, BLUPs of Activity level, age, dominance status, zone, month, sex plus the interactions between Heart rate and status, Activity and zone and Activity and status. All models were run using a REML procedure.

Model	Random term	V_i	V_f	V_r	k	Random effect tested	Loglik	Test	LRT	d.f.	P
1	ID	0.006	na	0.23	15	Family	-467.701	1 vs 3	3.633	1	0.056
2	Family	na	0.005	0.23	15	ID	-467.146	2 vs 3	2.525	1	0.112
3	**Family/ID**	**0.006**	**0.004**	**0.23**	**16**		**-465.884**				

V_i: Estimate of individual variance; V_f: Estimate of family variance; V_r: Estimate of Residual variance.The model in bold is the selected model.

TABLE 1.7: Coefficients of fixed effects (β and their standard errors s.e.) for the mixed model on vigilance rate in Alpine marmots. Marmot ID nested in family group was included as random terms. The final model included as fixed effects: age class, month, Heart rate, social status and the interactions between Heart rate and social status.

Fixed effect	β ± s.e.	F	d.f.	P value
Intercept	1.443 ± 0.065	489.475	1,597	<.0001
Age	0.117 ± 0.051	5.133	1,597	0.021
Month	np	3.941	3,597	0.0084
HR	0.780 ± 0.199	15.287	1,30	0.0005
Status $^{\Omega}$	-0.158 ± 0.058	7.291	1,30	0.011
HR:Status $^{\Omega}$	-1.12 3± 0.236	22.594	1,30	<.0001
Rejected terms				
Sex‡	-0.008 ± 0.055	0.022	1,27	0.881
Activity	0.487 ± 0.317	2.355	1,28	0.136
Zone§	0.084 ± 0.056	2.188	1,9	0.173
Act:Zone§	-0.794 ± 0.460	2.979	1,28	0.095
Act:Status $^{\Omega}$	-0.351 ± 0.571	0.377	1,26	0.544

$^{\Omega}$ Dominant is the reference category for the variable "status" in the model.

‡ Female is the reference value category for the variable "sex" in the model.

§ Zone at higher altitude is the reference category for the variable "zone" in the model.

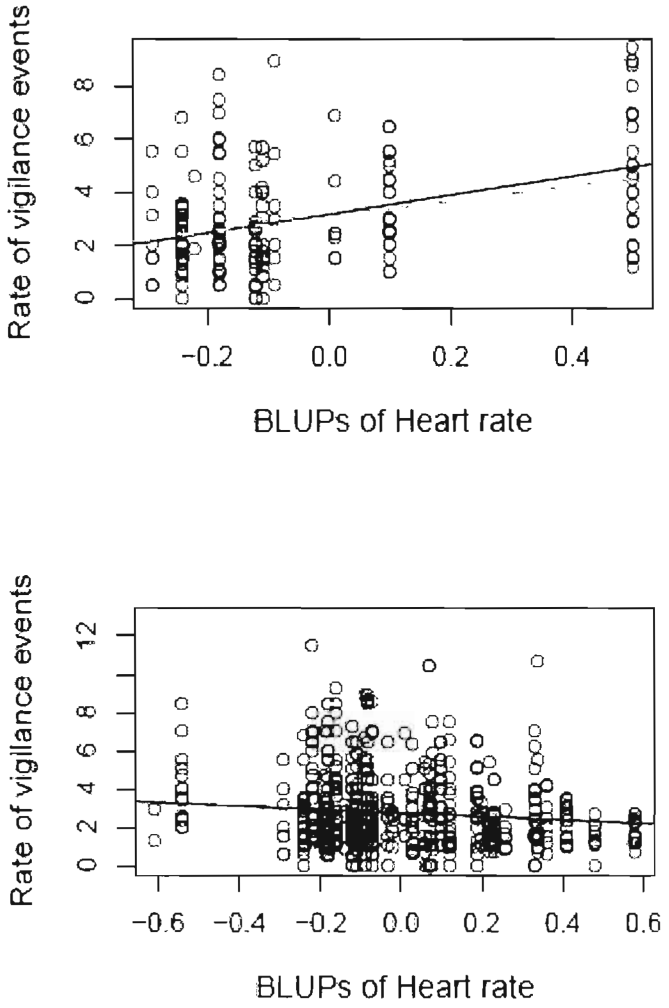

FIGURE 1.8 : Relationship between Heart rate and vigilance rate in dominant (top) and subordinate (bottom) individuals of Alpine marmots. In the top graph, the black line represents the regression line for the whole dataset and the dashed line represents the regression line when values for the most extreme individual (*i.e.* HR > 0.4) were excluded. In the bottom graph, the tendency did not change if the two individuals on the extreme left were excluded from the database.

I.5. DISCUSSION

Coping style in the Alpine marmot

Our results provide evidence that alpine marmots consistently differ in their personality or coping style. In the literature, physiological parameters have been used as reliable indices of individual coping styles (Carere, 2004), and have been proposed to be a potential mechanism underlying variation in behaviour (Benus, *et al.* 1991). The first step to a study looking at consistent correlations among traits in wild animals is to make sure that each trait measured is representative of the individual studied, and thus that traits show some consistency over time (*i.e.* repeatability). In our study Heart rate was highly repeatable (r = 45%), while temperature was lowly repeatable (r = 17%), and breathing rate not repeatable (r = 12%). Heart rate, therefore, is a robust measure of an individual's response to the stress triggered by capture and handling. Low or null repeatability of temperature and breathing rate might have been due to higher measurement errors for these traits than for heart rate. Alternatively temperature or breathing rate could be more plastic than heart rate in response to particular, unmeasured environmental variables. For example, breathing rate may strongly depend on the fighting activity prior to the measure. It is important to note that the positive correlation between heart and breathing rate, and body temperature follows the predictions of coping style studies (Koolhaas, *et al.* 1999; Carere and Oers, 2004).

It should be noted that we defined a family as a group of marmots, where most of the members are assumed to be related to each other. Some individuals, however, are not genetically related to the others as they are probably immigrants from other territories. This can happen for example when one or both individuals of the dominant pair die and are replaced by adults coming from other territories (C. Ferrari *pers. obs.*). This suggests that actual family effects on a trait could be underestimated by our definition of family and our approach.

Dominants had lower Heart rates than subordinate individuals. This result has also been found in other social species, wherein subordinates are generally more stressed and show a higher value of hormonal baseline (Louch and Higginbotham, 1967; Eisermann, 1992;

Sgoifo, *et al.* 2005). If subordinate Alpine marmots are generally more stressed we would have to assume that heart rate is plastic and depends on the different environmental conditions related to social status by individuals (Aureli, *et al.* 1999). Alternatively it is possible that the ability to reach a high dominance position could be affected by the proactivity of an individual. In our study, heart rate of marmots under stressful conditions is positively related to activity in the open-field, and both are indicators of high proactivity (Koolhaas, *et al.* 1999). Assuming that highly proactive individuals should reach high dominance status (*i.e.* Dingemanse and De Goede, 2004), the negative relationship between dominance and heart rate in the marmots is therefore surprising, and could possibility be explained if less proactive individuals have a higher chance to reach a dominant, reproductive status than highly proactive ones. Further work is necessary to figure out whether proactive individuals have a lower chance of becoming dominant, or if heart rate plasticity is affected by dominance status.

The relationship between Heart rate and body mass differed according to age class: in pups Heart rate increased with body mass. Heart rate, however, decreased with body mass in subadults and adults. The general lower heart rate of bigger animals is commonly observed in animals (Lindstedt and Calder, 1981; Hurst, ØRitsland and Watts, 1982), which explains the differences between age classes in Heart rate and the negative trend with body mass within a particular age class observed for subadults and adults. Two explanations can be provided for the positive link between Heart rate and body mass in pups. The first is that proactive pups with a higher heart rate also had a high growth rate and, therefore, a large body mass at a given age. The second is that survival is related to proactivity, so that only the most proactive pups reach a certain body mass.

Activity during the open-field test

Estimates of activity level and explorative behaviour have been used to measure individual personality traits in previous works on birds and mammals, both in the laboratory and in nature (Armitage, 1986; Némoz-Bertholet and Aujard, 2003; Carere, *et al.* 2005), and have been shown to reliably predict the behaviour of an individual in the wild (Verbeek, *et al.* 1994; Dingemanse, *et al.* 2003; Boon, Réale and Boutin, 2007).

In our study, we found that marmots differ in their activity level during the open field test and that this trait is significantly consistent over time between individuals (r = 33%). Repeatability of activity level found in this marmot population is comparable to other studies on personality in other Sciurids (Boon, Réale and Boutin, 2007; Martin and Réale, 2008; Montiglio, 2009). Activity in the open field is strongly affected by the number of open-field trials conducted on the individual. A strong effect of habituation to the test has also been found in studies on red squirrels and chipmunks (Boon, *et al.* 2008; Martin and Réale, 2008). Following our results, two open-field tests per individual would be enough to measure activity level in the Alpine marmot. Individual characteristics were accounted for in the model of activity level, but they were all removed during model selection. This suggests that individual differences in behaviour in an open-field test could not be explained by differences in age, sex, environmental and seasonal differences. Again this result is in accordance with others studies on personality among wild animal populations (Boon, Réale and Boutin, 2008; Martin and Réale, 2008). Furthermore, as we have outlined in the introduction, these studies have shown that activity and explorative behaviours measured during the open-field test are not clearly distinguishable (Boon, Réale and Boutin, 2007; Réale, *et al.* 2007; Martin and Réale 2008). Thus, we consider our measure of activity during the open-field test a reliable index of explorative behaviour in the wild, suggesting that the more active individuals in the open-field test could be fast and superficial explorers (individuals that show faster exploration performance compared to individuals with low speed of exploration)(Marchetti and Drent, 2000; Carere, *et al.* 2005) in their natural habitat, maybe going further from the burrow to forage.

Correlation between behavioural variables

We found a strong positive correlation between individuals' heart rate and their activity in the open-field, providing evidence for a behavioural syndrome in Alpine marmots. This result confirms the predictions that proactive individuals will have a higher activity level and be superficial explorers (Benus, *et al.* 1991;Korte, *et al.* 1998;Koolhaas, *et al.* 1999). The strong correlation between heart rate and activity, two different measures of individual coping style, is also important from a methodological point of view for the study of animal personality: in view of our results, future studies on the marmot could use only one of these measures as a reliable indicator of an individual's coping style. Generally the amount of data one can collect in the field is constrained by time, human resources and other practical limitations. When we perform an open-field test, for example, we need to carry the arena to the site of marmot capture, and we need some time to perform the test on each individual. This open-field test procedure limits the number of individuals and the field sites we can work on and can potentially have a higher impact on some particularly stressed individuals; minimizing the potential impact of stress and manipulation load exerted on animals should be one of the goals in every study using animals. Furthermore, heart rate was the most repeatable of all the traits measured in our study and should not be affected by habituation to repeated captures and handlings. It should thus provide a more accurate measure of personality in the long term. According to our study the measure of heart rate is highly consistent and, since it is more practical in term of time and materials, could be used as a reliable measure of personality.

Vigilance behaviour

Various different parameters of vigilance behaviour were positively correlated and consequently we decided to use vigilance rate as an individual's index of vigilance behaviour. According to the literature, this parameter is a reliable index of anti-predator strategy, since it allows individuals to detect any approaching threat (Bednekoff and Lima, 2002; Cresswell, *et al.* 2003; Jones, Krebs and Whittingham, 2007).

Alpine marmots differ in their vigilance behaviour according to their age, heart rate, and social status. Once these fixed effects were included in the model repeatability was very low (r=4%), meaning that most of the variation among individuals in vigilance is explained by their age, heart rate and social status. In this model only heart rate remained as significant predictors of vigilance, while Activity in the open field was rejected from the model. This is possibly due to a collinearity problem: by including two effects that are strongly correlated, one of them could be excluded by the other since they explain the same part of the variance. Heart rate is the most consistent trait, which could explain why only this predictor was maintained in the model. It is important to note that when only Activity was included in the model it was positively related to vigilance rate in the same way as Heart rate (results not shown). Furthermore when both were included in the model, heart rate and activity were positively associated with vigilance rate, even if activity was not significant. This suggests that different indices of coping styles (*i.e.* either heart rate or activity), had the same effects on vigilance rate.

At first, we expected proactive individuals to be less vigilant than more reactive individuals. We found the opposite, with dominant individuals having higher level of vigilance. However, we did not include any measure of risk in the model and, therefore, we cannot assess if individuals are taking different degrees of risk and adjusting their vigilance level accordingly. According to the literature we would expect that proactivity is positively correlated with risk-taking behaviour (Brick and Jakobsson, 2002; van Oers, *et al.* 2004;Wilson and Godin, 2009); so we can assume that proactive Alpine marmots generally take more risks. In marmots, a good measure of risk is the distance from the closest burrow and distance from the boundaries of the family territory during foraging (Holmes, 1984). Thus, we suggest that proactive individuals may forage further from burrow entries, showing a higher level of vigilance as an adjustment to the level of risk of the situation. This explanation is supported by the high correlation between heart rate and activity that we described above and by the fact that measures of activity are generally correlated with explorative behaviour (Dingemanse, *et al.* 2003; Wilson and Godin, 2009). Further analyses are needed to test this hypothesis.

Contrary to our expectation, we found that dominant animals were more vigilant than subordinates and increase their vigilance with their proactivity. Vigilance rate decreased with individual activity among the subordinates. This result suggests that we should consider different types of risks when considering the vigilance of individuals with different social status. In Alpine marmots, the dominant couple defends the territory against intruders and often against neighbours (Arnold, 1990). Thus, the dominant individual should pay attention not only to predators but also to conspecifics, and this could explain the higher level of vigilance that we found in dominant individuals. Similar results have been found in other species where dominant individuals are more aware of what conspecifics are doing in order to be ready to defend their territory (Cameron and du Toit, 2005; Lung and Childress, 2007). Really proactive individuals may thus spend a long time checking for conspecifics inside or outside of their territories, which can explain the positive relationship between vigilance and heart rate in dominant individuals. Thus in this work other factors potentially stressful should be considered. It should be noted, however, that in this work we identified individuals as "dominants" based primarily on their own reproductive status and, in the case of no reproduction, based on

their rate of agonistic interactions (see Introduction). When we were not sure about the dominance of an individual, we referred to it as "subordinate". It is known that in this species typically only the dominant couple reproduces and that other individuals disperse in an attempt to mate and form a new family (Arnold, 1990; Hacklander and Arnold, 1999). As dispersal was not the focus of this study, we do not have data on how and if individual coping style affects the possibility to mate after dispersal.
Vigilance decreases throughout the season, from June to September; potential factors that could explain a change in vigilance throughout the season are variation in social and/or predator pressure, different degrees of human disturbance and different nutritional needs according to change in the vegetation. We suggest that vigilance could decrease as a result of the constant decrease in conspecific agonistic interactions from June to September (Arnold, 1990; Ranghetti, 2009). Marmots could decrease their vigilance according to a lower rate in agonistic encounters and aggressive interactions.

Overall, this study suggests that Alpine marmots vary consistently in their response to a stressful situation and that these differences are also observable in individuals' anti-predator strategies. Measures on individual risk taking behaviour could further improve our understanding of marmot vigilance behaviour. In future analyses, we will investigate how the level of glucocorticoids vary with individual coping style.

CHAPTER 1 LITERATURE CITED

Allainé, D. 2000.«Sociality, mating system and reproductive skew in marmots: Evidence and hypotheses ». *Behavioural Processes*. vol. 51, no 1-3, p. 21-34.

Allaine, D., I. Rodrigue, M. Le Berre and R. Ramousse. 1994.«Habitat preferences of alpine marmots, *Marmota marmota* ». *Canadian Journal of Zoology*. vol. 72, no 12, p. 2193-2198.

Archer, J. 1973.«Tests for emotionality in rats and mice: a review ». *Animal Behaviour*. vol. 21, no 2, p. 205-235.

Armitage, K. B. 1962.«Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*) ». *Animal Behaviour*. vol. 10, no 3-4, p. 319-331.

---. 1975.«Social behavior and population dynamics of marmots ». *OIKOS*. vol. 26, no 3, p. 341-354.

---. 1986.«Individuality, social behaviour and reproductive success in yellow-bellied marmots ». *Ecology*. vol. 67, p. 1186-1193.

Armitage, K. B. and D. H. Vuren. 2003.«Individual differences and reproductive success in yellow-bellied marmots ». *Ethology Ecology and Evolution*. vol. 15, no 3, p. 207-233.

Arnold, W. 1988.«Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*) ». *Journal of Comparative Physiology - B Biochemical, Systemic, and Environmental Physiology*. vol. 158, no 2, p. 151-156.

---. 1990.«The Evolution of Marmot Sociality: I. Why Disperse Late? ». *Behavioral Ecology and Sociobiology*. vol. 27, no 4, p. 229-237.

Aureli, F., S. D. Preston and F. B. M. de Waal. 1999.«Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): A pilot study ». *Journal of Comparative Psychology*. vol. 113, no 1, p. 59-65.

Bassano, B., E. Macchi, P. Durio, M. Tarantola and A. Vita. 1991. « Caratteristiche ecologiche degli insediamenti di marmotta alpina (*Marmota marmota*) ». *Proceedings of the 1st International Symposium on Alpine Marmot Marmota marmota and on genus Marmota.* (Saint Vincent, Aosta-Italy, October 28-30).

Beauchamp, G. 2003. «Group-size effects on vigilance: A search for mechanisms». *Behavioural Processes*. vol. 63, no 3, p. 111-121.

Bednekoff, P. A. and S. L. Lima. 1998. «Re-examining safety in numbers: Interactions between risk dilution and collective detection depend upon predator targeting behaviour». *Proceedings of the Royal Society B: Biological Sciences*, vol. 265, no. 1409, p.2021-2026

Bednekoff, P. A. and S. L. Lima. 2002.«Why are scanning patterns so variable? An overlooked question in the study of anti-predator vigilance ». *Journal of Avian Biology*. vol. 33, no 2, p. 143-149.

Benus, R. F., B. Bohus, J. M. Koolhaas and G. A. Oortmerssen. 1991.«Heritable variation for aggression as a reflection of individual coping strategies ». *Experientia*. vol. 47, no 10, p. 1008-1019.

Blumstein, D. T. and W. Arnold. 1995. « Situational specificity in alpine-marmot alarm communication». *Ethology*. vol.100, no1, p. 1-13.

Blumstein, D. T. 1996.«How much does social group size influence golden marmot vigilance? ». *Behaviour*. vol. 133, no 15-16, p. 1133-1151.

---. 1998.«Quantifying predation risk for refuging animals: A case study with golden marmots ». *Ethology*. vol. 104, no 6, p. 501-516.

Boon, A. K., D. Réale and S. Boutin. 2007.«The interaction between personality, offspring fitness and food abundance in North American red squirrels ». *ecology letters*. vol. 10, no 11, p. 1094-1104.

---. 2008.«Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus* ». *OIKOS*. vol. 117, no 9, p. 1321-1328.

Brick, O. and S. Jakobsson. 2002.«Individual variation in risk taking: The effect of a predatory threat on fighting behavior in *Nannacara anomala* ». *Behavioral Ecology*. vol. 13, no 4, p. 439-442.

Budaev, S. V. 1997. «"Personality" in the Guppy (*Poecilia reticulata*): a correlational study of exploratory behavior and social tendency». *Journal of Comparative Psychology*. vol. 141, no.4, p.399-411.

Cameron, E. Z. and J. T. du Toit. 2005.«Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis* ». *Animal Behaviour*. vol. 69, no 6, p. 1337-1344.

Carere, C., T. G. G. Groothuis, E. Mostl, S. Daan and J. M. Koolhaas. 2003.«Fecal corticosteroids in a territorial bird selected for different personalities: Daily rhythm and the response to social stress ». *Hormones and Behavior*. vol. 43, no 5, p. 540-548.

Carere, C. and K. Oers. 2004.«Shy and bold great tits (*Parus major*): body temperature and breathe rate in response to handling stress ». *Physiology & Behavior*. vol. 82, p. 905-912.

Carere, C., P. J. Drent, L. Privitera, J. M. Koolhaas and T. G. G. Groothuis. 2005.«Personalities in great tits, *Parus major*: Stability and consistency ». *Animal Behaviour*. vol. 70, no 4, p. 795-805.

Civantos, E. 2000.«Home-range ecology, aggressive behaviour, and survival in juvenile lizards, *Psammodromus algirus* ». *Canadian Journal of Zoology*. vol. 78, no 9, p. 1681-1685.

Cresswell, W., J. L. Quinn, M. J. Whittingham and S. Butler. 2003.«Good foragers can also be good at detecting predators ». *Proceedings of the Royal Society B: Biological Sciences*. vol. 270, no 1519, p. 1069-1076.

Dall, S. R. X. 2004.«Behavioural biology: Fortune favours bold and shy personalities ». *Current Biology*. vol. 14, no 12, p.470-472.

Damsgard, B. and L. M. Dill. 1998.«Risk-taking behavior in weight-compensating coho salmon, *Oncorhynchus kisutch* ». *Behavioral Ecology*. vol. 9, no 1, p. 26-32.

Dingemanse, N. J., C. Both, A. J. Noordwijk, A. L. Rutten and P. J. Drent. 2003.«Natal dispersal and personalities in great tits (*Parus major*) ». *Proceedings of the Royal Society B: Biological Sciences*. vol. 270, no 1516, p. 741-747.

Dingemanse, N. J. and P. De Goede. 2004.«The relation between dominance and exploratory behavior is context-dependent in wild great tits ». *Behavioral Ecology*. vol. 15, no 6, p. 1023-1030.

Dingemanse, N. J. and D. Réale. 2005.«Natural selection and animal personality ». *Behaviour*. vol. 142, no 9, p. 1159-1184.

Drent, P. J., K. van Oers and A. J. Noordwijk. 2003.«Realized heritability of personalities in the great tit (*Parus major*) ». *Proceedings of the Royal Society of London - Biological Sciences*. vol. 270, no 1510, p. 45-51.

Eisermann, K. 1992. «Long-term heartrate responses to social stress in wild European rabbits: Predominant effect of rank position».*Physiology and Behavior*. vol.52, no1, p. 33-36.

Fernández-Juricic, E., G. Beauchamp and B. Bastain. 2007. «Group-size and distance-to-neighbour effects on feeding and vigilance in brown-headed cowbirds». *Animal Behaviour*, vol. 73, no 5, p. 771-778.

Ferrari, C., G. Bogliani and A. von Hardenberg. 2009.«Alpine marmots (*Marmota marmota*) adjust vigilance behaviour according to environmental characteristics of their surrounding ». *Ethology, Ecology & Evolution*. vol. 21, no 3-4. *In press*.

Frid, A. 1997.«Vigilance by female Dall's sheep: interactions between predation risk factors ». *Animal Behaviour*. vol. 53, no 4, p. 799-808.

Groothuis, T. G. G. and C. Carere. 2005. «Avian personalities: Characterization and epigenesis». *Neuroscience and biobehavioral reviews*. vol. 29, no. 1 SPEC. ISS, p. 137-150.

Gosling, S. D. 2001. « From mice to men: What can we learn about personality from animal research? ». *Psychological Bulletin*. vol. 127, no 1, p 45-86.

Gould, T. D., D. T. Dao and C. E. Kovacsics. 2009.«The open field test ». *Neuromethods*. vol. 42, p. 1-20.

Hacklander, K. and W. Arnold. 1999.«Male-caused failure of female reproduction and its adaptive value in Alpine marmots (*Marmota marmota*) ». *Behavioral Ecology*. vol. 10, no 5, p. 592-597.

Hadfield, J. D., A. J. Wilson, D. Garant, B.C. Sheldon and L.E.B. Kruuk. 2009.«The Misuse of BLUP in Ecology and Evolution ». *American Naturalist*. vol. 175, no 1, p. 116-125.

Haskins, K. E., A. Sih and J. J. Krupa. 1997.«Predation risk and social interference as factors influencing habitat selection in two species of stream-dwelling waterstriders ». *Behavioral Ecology*. vol. 8, no 4, p. 351-363.

Holmes, W. G. 1984.«Predation risk and foraging behaviour of the hoary marmot in Alaska ». *Behavioral Ecology and Sociobiology*. vol. 15, p. 293-301.

Huntingford, F. A. 1976.«The relationship between anti-predator behavior and aggression among conspecifics in the three spined stickleback, *Gasterosteus aculeatus* ». *Animal Behaviour*. vol. 24, no 2, p. 245-260.

Hurst, R., N. A. ØRitsland and D. P. Watts. 1982. « Body mass, temperature and cost of walking in polar bears»*Acta Physiologica Scandinavica*. vol. 115, no. 4, p. 391-395

Jones, K. A., J. R. Krebs and M. J. Whittingham. 2007. « Vigilance in the third dimension: head movement not scan duration varies in response to different predator models». *Animal Behaviour*. vol. 74, no. 5, p. 1181-1187.

Kaiser, H. F. 1991.«Coefficient alpha for a principal component and the Kaiser-Guttman rule ». *Phycological Reports*. vol. 68, no 3, p. 855-858.

Koolhaas, J. M., S. M. Korte, De Boer S.F., Der Vegt B.J., Reenen C.G., Hopster H., De Jong I.C., Ruis M.A.W. and B. H.J. 1999.«Coping styles in animal: current status in behavior and stress-physiology ». *Neuroscience and biobehavioral reviews*. vol. 23, no 7, p. 925-935.

Korte, S. M., W. Ruesink and H. J. Blokhuis. 1998.«Heart rate variability during manual restraint in chicks from high- and low-feather pecking lines of laying hens ». *Physiology and Behavior*. vol. 65, no 4-5, p. 649-652.

Kralj-Fiser, S., I. B. R. Scheiber, A. Blejec, E. Moestl and K. Kotrschal. 2007.«Individualities in a flock of free-roaming greylag geese: Behavioral and physiological consistency over time and across situations ». *Hormones and Behavior*. vol. 51, no 2, p. 239-248.

Kruuk, L. E. B. 2004.«Estimating genetic parameters in natural populations using the 'animal model' ». *Philosophical Transactions of the Royal Society B: Biological Sciences*. vol. 359, no 1446, p. 873-890.

Lima, S. L. 1985.«Maximizing feeding efficiency and minimizing time exposed to predatos: a trade-off in the black-caped chickadee ». *Oecologia*. vol. 66, no 1, p. 60-67.

Lima, S. L. and L. M. Dill. 1990.«Behavioral decisions made under the risk of predation: a review and prospectus ». *Canadian Journal of Zoology*. vol. 68, no 4, p. 619-640.

Lindstedt, S. L. and W. A. Calder. 1981. «Body Size, Physiological Time, and Longevity of Homeothermic Animals». *The Quarterly review of Biology*. vol.56, no 1, p.1-16

Lopéz, P., D. Hawlena, V. Polo, L. Amo and J. Martin. 2005.«Sources of individual shy-bold variations in antipredator behaviour of male Iberian rock lizards ». *Animal Behaviour*. vol. 69, no 1, p. 1-9.

Louch, C. D. and M. Higginbotham.1967.«The relation between social rank and plasma corticosterone levels in mice ». *General and comparative andocrinology*. vol. 8, no 3, p. 441-444.

Lung, M. A. and M. J. Childress. 2007.«The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park ». vol. 18, no 1, p. 12-20.

Makowska, I. J. and D. L. Kramer. 2007.«Vigilance during food handling in grey squirrels, *Sciurus carolinensis* ». *Animal Behaviour*. vol. 74, no 1, p. 153-158.

Marchetti, C. and P. J. Drent.2000. «Individual differences in the use of social information in foraging by captive great tits». *Animal Behaviour*. vol. 60, no. 1, p. 131-140.

Martin, J. G. A. and D. Réale. 2008a.«Animal temperament and human disturbance: Implications for the response of wildlife to tourism ». *Behavioural Processes*. vol. 77, no 1, p. 66-72.

---. 2008b.«Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus* ». *Animal Behaviour*. vol. 75, no 1, p. 309-318.

Martin, P. and P. Bateson.(1993).«*Measuring Behavior: An introductory guide.*».(Cambridge).

Mateo, J. M. 2007.«Ecological and hormonal correlates of antipredator behavior in adult Belding's ground squirrels (*Spermophilus beldingi)* ». *Behavioral Ecology and Sociobiology*. vol. 62, no 1, p. 37-49.

Montiglio, P. O. 2009. «CHAPTER I : Individual variation in temporal activity patterns and the measurement of activity/exploration in an open-field test in the Eastern chipmunk (*Tamia striatus*) ». *Département des sciences biologiques.* P. 12-35. (Montréal, UQAM - Université du Québec à Montréal).

Moretz, J. A., E. P. Martins and B. D. Robison. 2007.«Behavioral syndromes and the evolution of correlated behavior in zebrafish ». *Behavioral Ecology*. vol. 18, no 3, p. 556-562.

Mostl, E. and R.Palme. 2002.«Hormones as indicators of stress ». *Domestic Animal Endocrinology*. vol. 23, no 1-2, p. 67-74.

Némoz-Bertholet, F. and F. Aujard. 2003.«Physical activity and balance performance as a function of age in a prosimian primate (*Microcebus murinus*) ». *Experimental Gerontology*. vol. 38, no 4, p. 407-414.

Ottoni, E. B. 2000.«EthoLog 2.2: A tool for the transcription and timing of behavior observation sessions ». *Behavior Research Methods, Instruments & Computers*. vol. 32, no 3, p. 446-449.

Perrin, C., D. Allainé and M. Le Berre. 1993.«Socio-spatial organization and activity distribution of *Marmota marmota:* preliminary results ». *Ethology*. vol. 93, no 1, p. 21-30.

Pinheiro, J. C. and D. M. Bates.2001.«*Mixed effects models in S and S-Plus*». (New York, Springer Verlag).

Quinn, J. L., S. C. Patrick, S. Bouwhuis, T. A. Wilkin and B. C. Sheldon. 2009.«Heterogeneous selection on a heritable temperament trait in a variable environment ». *Journal of Animal Ecology*. vol. 78, no 6, p. 1203-1215.

R. (2008) R: A language and environment for statistical computing. (Vienna, Austria). http://www.r-project.org.

Ranghetti, L. 2009. «Eco-etologia della marmotta alpina (*Marmota marmota*): distribuzione spaziale e temporale delle attività ». (Master thesis, Università degli Studi di Pavia, Italy).

Réale, D. and M. Festa-Bianchet. 2003.«Predator-induced natural selection on temperament in bighorn ewes ». *Animal Behaviour*. vol. 65, no 3, p. 463-470.

Réale, D., S. M. Reader, D. Sol, P. T. McDougall and N. J. Dingemanse. 2007.«Integrating animal temperament within ecology and evolution ». *Biological Reviews*. vol. 82, no 2, p. 291-318.

Sgoifo, A., T. Costoli, P. Meerlo, B. Buwalda, M. A. Pico'-Alfonso, S. De Boer, E. Musso and J. Koolhaas. 2005. «Individual differences in cardiovascular response to social challenge». *Neuroscience and biobehavioral reviews*. vol.29, no1 SPEC. ISS., p. 59-66.

Sih, A., A. Bell and J. C. Johnson. 2004.«Behavioral syndromes: an ecological and evolutionary overview ». *TRENDS in Ecology and Evolution*. vol. 19, no 7, p.372-378.

Sih, A., L. B. Kats and E. F. Maurer. 2003.«Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system ». *Animal Behaviour*. vol. 65, no 1, p. 29-44.

Sundström, L. F., E. Petersson, J. Höjesjö, J. I. Johnsson and T. Järvi. 2004.«Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): Implications for dominance ». *Behavioral Ecology*. vol. 15, no 2, p. 192-198.

Van Oers, K., P. J. Drent, P. De Goede and A. Noordwijk. 2004.«Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities ». *Proceedings of the royal B society*. vol. 271, p. 65-73.

Verbeek, M. E. M., P. T. Drent and P. R. Wiepkema. 1994.«Consistent individual differences in early exploratory behaviour of male great tits ». *Animal Behaviour*. vol. 48, no 5, p. 1113-1121.

Wilson, A. D. M. and J.-G. J. Godin. 2009a.«Boldness and intermittent locomotion in the bluegill sunfish, *Lepomis macrochirus* ». *Behavioral Ecology*. vol. 21, no 1, p. 57-62.

Wilson, A. D. M. and J. G. J. Godin. 2009b.«Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus* ». *Behavioral Ecology*. vol. 20, no 2, p. 231-237.

Wilson, A. D. M. and R. L. McLaughlin. 2007.«Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations ». *Animal Behaviour*. vol. 74, no 4, p. 689-698.

Wilson, D. S. 1998.«Adaptive individual differences within single populations ». *Philosophical Transactions of the Royal Society B: Biological Sciences*. vol. 353, no 1366, p. 199-205.

Zelenka, G. 1965.«Observations sur l'ecologie de las marmotte des alpes ». *Tierre Vie*. vol. 19, p. 238-256.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev and G. M. Smith.2009.«*Mixed Effects Models and Extensions in Ecology with R*».(New York).

FINAL CONCLUSION

This thesis had two main objectives:
1) to evaluate individual behavioural consistency in the open-field test and in the behavioural reactions towards handlers, and to correlate this variation with measures of physiological parameters characterising different personalities;
2) to integrate the study of personality in the context of vigilance behaviour; we related differences in personality among individuals with their vigilance in the field during foraging activity.

Our study shows that individual Alpine marmots differed consistently in their behavioural and physiological responses; we provided measures of physiological parameters (heart and breathing rate, and body temperature) and activity in the open field and of their repeatability. We found that heart rate was a consistent index of individual response to the stress triggered by capture and handling. Breathing rate was not significantly repeatable and body temperature was lowly repeatable. In other studies physiological measures have been used as indicators of stress with a comparable repeatability (Carere and van Oers, 2004; Fucikova, *et al.* 2009). We thus show that marmot's coping style of personality can be appropriately characterised by using heart rate during handling and activity in an open-field. A limitation of our study, though, is that we did not have the basal measure of physiological parameters; this could limit our estimation of an individual's coping style. The difference between the basal level and the measure after a fixed period of restraint has been already consider as a index of individual stressability (Carere and van Oers, 2004). Furthermore, other authors have used more detailed measures of heart rate such as heart rate variability (Koolhaas, *et al.* 1999). With our results we thus have to assume that one measure of heart rate during restraint is positively correlated with its increase from the basal level. This, however, does not seem to limit our ability to detect inter-individual variation in heart rate since differences in heart rate among individuals was positively related with differences in activity in the open-field as predicted by studies on coping styles. In the field conditions experienced during this study, given the distance between the traps and the observation area it was not possible to obtain a measure of heart rate as soon as the animal was captured. Other works encompassed this problem by implanting subcutaneous transmitter or by radiotelemetric heart rate recordings (Eisermann, 1992; Nephew and Romero, 2003; Wascher, *et al.* 2009). This method allowed researchers to measure the basal level of heart rate and eventually to evaluate the increase after a challenge or novelties. However, we opted for a lower precision of data in order to avoid surgical operations in the field.

Another good indicator of coping styles was the individual production of glucocorticoids during a restraint test (Koolhaas, *et al.* 1999; Carere, *et al.* 2003; Mateo, 2006). To this aim, in most of captures (pups excluded) we have collected two blood samples for each individual (see Chapt. I, METHOD). Preliminary results on a small size of blood samples of the summer 2007 suggests that the increase in cortisol between the two samples was negatively related to heart rate during handling, as predicted by previous authors (Koolhaas, *et al.* 1999). Although data have been collected for the other years of the study the analyses have not been done for all the samples yet, and could not be presented in this thesis.

Individual Alpine marmots also differed consistently in their behavioural reaction to novelty in the open field test. With this test we wanted to measure behavioural responses of Alpine marmots in a new environment. At one extreme some individuals were moving constantly-or they were trying to escape from the arena by jumping and digging and trying to break down the walls; at the other extreme others reacted by freezing and remained immobile all or most of the time. Activity level was consistent over successive trials and was positively correlated with heart rate. Future analysis of the data on the Mirror Image Stimulation (that we performed straight after the open field without interruption, see Chapt. I, METHOD) could provides a measure of sociability.

In this study we found an effect of habituation on individual level of activity: marmots reduce their activity in the arena with the number of trials. These results are similar to those obtained in studies of personality in chipmunks and red squirrels (Boon, Réale and Boutin, 2007; Martin and Réale, 2008). It would be interesting to see if there is any variability in the habituation and see if, for example, individuals tend to habituate faster than others. This habituation also raises a problem by limiting the number of tests that can be done on a marmot; after three tests almost all the marmots stop moving reducing the estimation of repeatability. Curiously, doing two trials separated by a year has the same effect, suggesting that marmot remember the test over a relatively long period of time.

The strong positive correlation between an individual's heart rate and activity is in accord with previous studies (Benus, *et al.* 1991; Korte, *et al.* 1998; Koolhaas, *et al.*

1999; Montiglio 2009). Based on this result, and because heart rate was easy to measure, was lowly invasive, did not necessitate complex equipment and was not affected by habituation, it may be one measure of personality to consider for future work on Alpine marmots.

We linked data on personality with data on vigilance behaviour. Heart rate was positively related to vigilance rate in the field. We explained this result by assuming that proactive individuals tend to take more risk. In fact several studies found a positive correlation between proactivity and risk-taking (Verbeek, Drent and Wiepkema, 1994; Brick and Jakobsson, 2002; van Oers, *et al.* 2004; Lopéz, *et al.* 2005; Wilson and McLaughlin, 2007; Wilson and Godin, 2009). Thus the higher vigilance would reflect an adjustment to the degree of risk. This means that for a given level of risk (a given distance from the burrow) proactive individuals may show lower levels of vigilance than reactive ones, but that they would tend to spend more time under more risky situations than reactive ones (for example they may spend more time farther away from a burrow of nearer their territory boundaries). Future studies should therefore include a measure of the risk for each observations. For Alpine marmots measures of risk could be provided by measuring the distance from the main burrow or from the centre of the territory or by environmental characteristics in case of heterogeneous habitat; it could be also interesting to include the number of conspecifics close to the focal individual. It would finally be interesting also to integrate an index of vegetation quality with the risk of predation and vigilance rate.

Our resulta show that dominant individuals have higher levels of vigilance and that vigilance decrease throughout the summer. Dominant individuals may monitor more frequently the territory to be aware of what conspecifics are doing. We also found a constant decrease of vigilance rate throughout the season, from May to September. These results seem to indicate a major role of agonistic intraspecific interactions on vigilance rate in marmots. In fact aggressive and agonistic interactions occurred at a higher rate in May and June (Arnold, 1990a; Ranghetti, 2009). Since dominance status could be achieved at different ages it would be interesting to link data on personality with the probability to reach a dominant status; also it would interesting to verify if individual heart rate varies with the dominance position (Eisermann, 1992).

Other potential factors that could affect the behaviour of vigilance during the season could be monitored: touristic impact, energetic requirements, vegetative period and predation pressure.

In conclusion, marmots exhibit individual behavioural differences in the way they cope with stressful and challenging situations. These differences may have multiple consequences on how individuals in the population deal with predators and competitors, take decisions about where to forage, or whether dispersing or staying . This work is thus a further step in the study of behavioural ecology and it suggests new interesting studies of wild animal behaviour.

APPENDIX A

THE GRAN PARADISO NATIONAL PARK

Gran Paradiso National Park was established in 1922 and is the first national park created in Italy. The park is located in the Graian Alps in North-West Italy and covers about 70.000 hectares. The territory of the Park has an average height of 2.000 m with altitudes from 800 meters to 4.061 meters on top of the Gran Paradiso, the highest Italian peak. The park includes five valleys: Cogne, Rhêmes and Valsavarenche within the region Valle d'Aosta, and the Orco and Soana valleys within the region Piemonte.
To the west, the park borders the Vanoise National Park in France and together these two parks represent the largest protected area in Western Europe.
In 1856, part of the current territory of the park was declared to be Royal Hunting Reserve by King Vittorio Emanuele III. The King simply intended to reserve this area for himself to hunt Alpine ibex (*Capra ibex*), but luckily this decision preserved this species from extinction. At that time a group of specialized foresters was created and paths and mule tracks were built that are still today part of the structure of the protected area; the surveillance service is still operative and constantly monitors the Park area and its environment. In 1922, King Vittorio Emanuele III gave the Italian government the 2.100 hectares of the hunting reserve in order to create a national park, the Gran Paradiso National Park.

Local fauna and flora

The local fauna consists of a native population of Alpine ibex, high densities of chamois (*Rupicapra rupicapra)* and roe deer *(Capreolus capreolus*). The protected area has a high density of Alpine marmots (*Marmota marmota*) and some medium to large sized carnivores such as red foxes (*Vulpes vulpes*), stoat *(Mustela erminea)* and wolf *(Canis lupus).*

The Park contains more than 100 bird species. Raptors include the golden eagle (*Aquila chrysaetos*), the bearded vulture (*Gypaetus barbatu*), the eurasian eagle owl *(Bubo bubo)* and the peregrine falcon *(Falco peregrinus*). Passerines include the alpine chough *(Pyrrhocorax graculus*) and chough (*Pyrrhocorax pyrrohocorax*), the northern wheatear (*Oenanthe oenanthe*) and the snow finch (*Montifrigilla nivalis*).

The two main types of wood in the park are coniferous and deciduous wood: European larch (*Larix decidua),* pine *(Pinus silvestris)*, Norway spruce *(Picea abies)*, Arolla Pine (*Pinus cembra*), European Silver Fir (*Abies alba*) and European beech (*Fagus sylvatica*). Above the tree line the landscape changes into alpine meadow, with rhododendron (*Rhododéndron ferrugineum*) and juniper (*Juniperus communis*). The alpine meadow is rich in variable fescue (*Festuca varia),* Alpine meadow grass *(Poa alpina),* buttercup *(Ranunculus montanus)* and bluebell (*Campanula barbata)*. Clovers (*Trifolium pratense*) and dandelions (*Taraxacum officinale*) grow on slopes that are less steep.

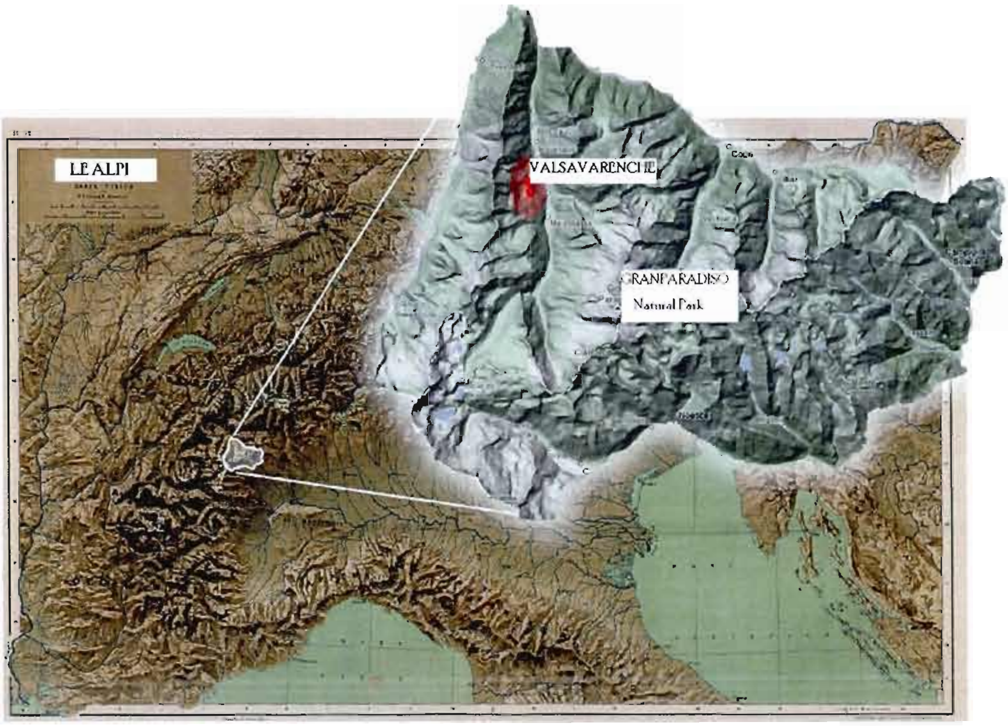

FIGURE B.1: The territory of the entire Gran Paradiso Natural Park and its location in the Alps.

LITERATURE CITED

Allainé, D., F. Brondex, L. Graziani, J. Coulon and I. Till-Bottraud. 2000.«Male-biased sex ratio in litters of Alpine marmots supports the helper repayment hypothesis ». *Behavioral Ecology*. vol. 11, no 5, p. 507-514.

Allainé, D. 2000. «Sociality, mating system and reproductive skew in marmots: Evidence and hypotheses ». *Behavioural Processes*. vol.51, p.21-34.

Allainé D. 2004. «Sex ratio variation in the cooperatively breeding alpine marmot *Marmota marmota*» . *Behavioral Ecology*. vol. 15, no. 6, p. 997-1002.

Archer, J. 1973.«Tests for emotionality in rats and mice: a review ». *Animal Behaviour*. vol. 21, no 2, p. 205-235.

Arenz, C. L. and D. W. Leger. 2000.«Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need ». *Animal Behaviour*. vol. 59, no 3, p. 535-541.

Armitage, K. B. 1962.«Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*) ». *Animal Behaviour*. vol. 10, no. 3-4, p. 319-331.

---. 1979.«Food selectivity by yellow-bellied marmots ». *Journal of Mammalogy*. vol. 60, no. 3, p. 628-629.

---. 1991.«Social and Population Dynamics of Yellow-Bellied Marmots: results from long-term research ». *Annual Review of Ecology and Systematic*. vol. 22, p. 379-407.

Armitage, K. B. and D. H. Van Vuren. 2003.«Individual differences and reproductive success in yellow-bellied marmots ». *Ethology Ecology and Evolution*. vol. 15, no. 3, p. 207-233.

Arnold, W. 1988.«Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*) ». *Journal of Comparative Physiology - B Biochemical, Systemic, and Environmental Physiology*. vol. 158, no 2, p. 151-156.

---. 1990a.«The Evolution of Marmot Sociality: I. Why Disperse Late? ». *Behavioral Ecology and Sociobiology*. vol. 27, no 4, p. 229-237.

---. 1990b.«The Evolution of Marmot Sociality: II. Costs and Benefits of Joint Hibernation ». *Behavioral Ecology and Sociobiology*. vol. 27, no 4, p. 239-246.

Arnold, W. and J. Dittami. 1997.«Reproductive suppression in male alpine marmots ». *Animal Behaviour*. vol. 53, p. 53-66.

Bachman, G. C. 1993.«The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels ». *Animal Behaviour*. vol. 46, p. 233-244.

Barash, D. P. 1973.«Habitat utilization in three species of mountain mammals ». *Journal of Mammalogy*. vol. 54, p. 247-250.

Bassano, B., E. Macchi, P. Durio, M. Tarantola and A. Vita. 1991. « Caratteristiche ecologiche degli insediamenti di marmotta alpina (Marmota marmota) ». *Proceedings of the 1st International Symposium on Alpine Marmot Marmota marmota and on genus Marmota.* (Saint Vincent, Aosta-Italy, October 28-30).

Beauchamp, G. 2008.«What is the magnitude of the group-size effect on vigilance? ». *Behavioral Ecology*. vol. 19, no. 6, p. 1361-1368.

Beauchamp, G. and B. Livoreil. 1997.«The effect of group size on vigilance and feeding rate in spice finches (*Lonchura punctulata*) ». *Canadian Journal of Zoology*. vol. 75, no. 9, p. 1526-1531.

Bednekoff, P. A. and D. T. Blumstein. 2009. «Peripheral obstructions influence marmot vigilance: Integrating observational and experimental results ». *Behavioral Ecology*. vol. 20, no. 5, p. 1111-1117.

Bednekoff, P. A. and S. L. Lima. 1998. «Randomness, chaos and confusion in the study of antipredator vigilance ». *TRENDS in Ecology and Evolution*. vol. 13, no. 7, p. 284-287.

---. 2002. «Why are scanning patterns so variable? An overlooked question in the study of anti-predator vigilance ». *Journal of Avian Biology*. vol. 33, no. 2, p. 143-149.

---. 2005.«Testing for peripheral vigilance: Do birds value what they see when not overtly vigilant? ». *Animal Behaviour*. vol. 69, no. 5, p. 1165-1171.

Bell, A. M. 2005.«Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*) ». *Journal of Evolutionary Biology*. vol. 18, no. 2, p. 464-473.

Benus, R. F., B. Bohus, J. M. Koolhaas and G. A. Van Oortmerssen. 1991. «Heritable variation for aggression as a reflection of individual coping strategies ». *Experientia*. vol. 47, no. 10, p. 1008-1019.

Blumstein, D. T. 1998. «Quantifying predation risk for refuging animals: A case study with golden marmots ». *Ethology*. vol. 104, no. 6, p. 501-516.

Boissy, A. 1995. «Fear and fearfulness in animals ». *Quarterly Review of Biology*. vol. 70, no 2, p. 165-191.

Boon, A. K., D. Réale and S. Boutin. 2007. «The interaction between personality, offspring fitness and food abundance in North American red squirrels ». *Ecology letters*. vol. 10, no. 11, p. 1094-1104.

Brick, O. and S. Jakobsson. 2002. «Individual variation in risk taking: The effect of a predatory threat on fighting behavior in *Nannacara anomala* ». *Behavioral Ecology*. vol. 13, no 4, p. 439-442.

Brown, J. S. and B. P. Kotler. 2004. «Hazardous duty pay and the foraging cost of predation ». *Ecology letters*. vol. 7, no. 10, p. 999-1014.

Brown, J. S., B. P. Kotler and T. J. Valone. 1994. «Foraging under predation: a comparison of energetic and predation costs in rodent communities of the Negev and Sonoran deserts ». *Australian Journal of Zoology*. vol. 42, no. 4, p. 435-448.

Buchanan-Smith, H.M. 1999. « Exploration of unfamiliar areas and detection of potentially threatening objects in single and mixed-species groups of tamarins». *International Journal of Comparative Psychology* vol.12, p. 2-20.

Budaev, S. V. 1997. «"Personality" in the Guppy (*Poecilia reticulata*): a correlational study of exploratory behavior and social tendency ». *Journal of Comparative Psychology*. vol. 111, p. 399-411.

Cameron, E. Z. and J. T. du Toit. 2005. «Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*». *Animal Behaviour*, vol.69, no.6, p. 1337-1344.

Carere, C., T. G. G. Groothuis, E. Mostl, S. Daan and J. M. Koolhaas. 2003. «Fecal corticosteroids in a territorial bird selected for different personalities: Daily rhythm and the response to social stress». *Hormones and Behavior*. vol.43, no.5, p. 540-548.

Carere, C., P. J. Drent, L. Privitera, J. M. Koolhaas and T. G. G. Groothuis. 2005.«Personalities in great tits, *Parus major*: Stability and consistency ». *Animal Behaviour*. vol. 70, no. 4, p. 795-805.

Charnov, E. L. 1976. «Optimal foraging: attack strategy of a mantid ». *American Naturalist*. vol. 110, p. 141-151.

Civantos, E. 2000. «Home-range ecology, aggressive behaviour, and survival in juvenile lizards, *Psammodromus algirus* ». *Canadian Journal of Zoology*. vol. 78, no. 9, p. 1681-1685.

Cohas, A., N. G. Yoccoz and D. Allaine. 2007. «Extra-pair paternity in alpine marmots, *Marmota marmota*: Genetic quality and genetic diversity effects ». *Behavioral Ecology and Sociobiology*. vol. 61, no. 7, p. 1081-1092.

Coleman, K. and D. S. Wilson. 1998. «Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific ». *Animal Behaviour*. vol. 56, no. 4, p. 927-936.

Cote, J. and J. Clobert. 2007. «Social personalities influence natal dispersal in a lizard». *Proceedings of the Royal Society B: Biological Sciences*. vol. 274 no. 1608, p. 383-390.

Cote, J., A. Dreiss and J. Clobert. 2008 .«Social personality trait and fitness». *Proceedings of the Royal Society B: Biological Sciences*. vol. 275, no. 1653, p. 2851-2858

Dall, S. R. X., A. I. Houston and J. M. McNamara. 2004. «The behavioural ecology of personality: Consistent individual differences from an adaptive perspective ». *Ecology Letters*. vol. 7, no 8, p. 734-739.

Damsgard, B. and L. M. Dill. 1998.«Risk-taking behavior in weight-compensating coho salmon, *Oncorhynchus kisutch* ». *Behavioral Ecology*. vol. 9, no. 1, p. 26-32.

Darwin, C.1859. «*On the Origin of Species by Means of Natural Selection*».(London).

Devereux, C. L., E. Fernández-Juricic, J. R. Krebs and M. J. Whittingham. 2008. «Habitat affects escape behaviour and alarm calling in Common Starlings *Sturnus vulgaris* ». *Ibis*. vol. 150, no. SUPPL.1, p. 191-198.

Dingemanse, N. J., C. Both, A. J. Van Noordwijk, A. L. Rutten and P. J. Drent. 2003. «Natal dispersal and personalities in great tits (*Parus major*) ». *Proceedings of the Royal Society B: Biological Sciences*. vol. 270, no 1516, p. 741-747.

Dingemanse, N. J., C. Both, P.J. Drent, K. Van Oers, A.van Noordwijk. 2002. «Repeatability and heritability of exploratory behaviour in great tits from the wild». *Animal Behaviour*. vol. 64, no. 6, p. 929-938.

Dingemanse, N. J. and P. De Goede. 2004. «The relation between dominance and exploratory behavior is context-dependent in wild great tits ». *Behavioral Ecology*. vol. 15, no. 6, p. 1023-1030.

Dingemanse, N. J. and D. Réale. 2005. «Natural selection and animal personality ». *Behaviour*. vol. 142, no. 9, p. 1159-1184.

Dingemanse, N. J., J. Wright, A. J. N. Kazem, D. K. Thomas, R. Hickling and N. Dawnay. 2007. «Behavioural syndromes differ predictably between 12 populations of three-spined stickleback ». *Journal of Animal Ecology*. vol. 76, no. 6, p. 1128-1138.

Drent, P. J., K. Van Oers and A. J. Van Noordwijk. 2003.«Realized heritability of personalities in the great tit (*Parus major*) ». *Proceedings of the Royal Society of London - Biological Sciences*. vol. 270, no. 1510, p. 45-51.

Ehlinger, T.J. and D. S. Wilson. 1988. «Complex foraging polymorphism in bluegill sunfish ». *Ecology*. vol. 85, no. 6, p. 1878-1882.

Eisermann, K. 1992. «Long-term heart rate responses to social stress in wild European rabbits: Predominant effect of rank position». *Physiology and Behavior*. vol.52, no.1, p. 33-36.

Erhard, H. W., M. Mendl and S. B. Christiansen. 1999. «Individual differences in tonic immobility may reflect behavioural strategies ». *Applied Animal Behaviour Science*. vol. 64, no. 1, p. 31-46.

Ferrari, C., G. Bogliani and A. von Hardenberg. 2009. «Alpine marmots (*Marmota marmota*) adjust vigilance behaviour according to environmental characteristics of their surrounding ». *Ethology, Ecology & Evolution*. vol. 21, no 3-4 *in press*.

Fox, R. A., L. D. Ladage, T. C. Roth Ii and V. V. Pravosudov. 2009. «Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*». *Animal Behaviour*, vol. 77, no. 6, p.1441-1448.

Frid, A. 1997.«Vigilance by female Dall's sheep: interactions between predation risk factors ». *Animal Behaviour*. vol. 53, no.4, p. 799-808.

Fucikova, E., P. J. Drent, N. Smits and K. Van Oers. 2009. «Handling stress as a measurement of personality in great tit nestlings (*Parus major*) ». *Ethology*, vol. 115, no. 4, p. 366-374.

Ginnett, T.F. and M.W. Demment. 1997. « Sex differences in giraffe foraging behavior at two spatial scales ». *Oecologia*. vol. 110, no 2, p. 291-300.

Groothuis, T. G. G. and C. Carere. 2005. «Avian personalities: Characterization and epigenesis». *Neuroscience and biobehavioral reviews*. vol. 29, no. 1 SPEC. ISS, p. 137-150.

Gosling, S. D. and O. P. John. 1999. «Personality dimensions in nonhuman animals: A cross-species review ». *Current Directions in Psychological Science*. vol. 8, no. 3, p. 69-75.

Gosling, S. D. 2001. « From mice to men: What can we learn about personality from animal research? ». *Psychological Bulletin*. vol. 127, no. 1, p 45-86.

Gould, T. D., D. T. Dao and C. E. Kovacsics. 2009.«The open field test ». *Neuromethods*. vol. 42, p. 1-20.

Hacklander, K., E. Mostl and W. Arnold. 2003. «Reproductive suppression in female Alpine marmots, *Marmota marmota* ». *Animal Behaviour*. vol. 65, no. 6, p. 1133-1140.

Hamilton, W.D. 1971. « Geometry for the selfish herd ». *Journal of Theoretical Biology*. vol.31, no.2, p.295-311

Höjesjö, J., J. I. Johnsson and M. Axelsson. 1999.«Behavioural and heart rate responses to food limitation and predation risk: an experimental study on rainbow trout ». *Journal of Fish Biology*. vol. 55, no. 5, p. 1009-1019.

Holmes, W. G. 1979. «Social behaviour and foraging strategies of hoary marmots (*Marmota caligata*) in Alaska ». PhD thesis, University of Eashington, Seattle.

---. 1984. «Predation risk and foraging behaviour of the hoary marmot in Alaska ». *Behavioral Ecology and Sociobiology*. vol. 15, p. 293-301.

Jones, B. R. 1982. «Experimental novelty and tonic immobility in chickens (*Gallus domesticus*) ». *Behavioral Processes*. vol. 9, no. 2-3, p. 255-260.

Koenig, A. 1998. «Visual scanning by common marmosets (*Callithrix jacchus*): Functional aspects and the special role of adult males ». *Primates*. vol.39, no. 1, p. 85-90.

Koolhaas, J. M., S. M. Korte, De Boer S.F., Van Der Vegt B.J., Van Reenen C.G., Hopster H., De Jong I.C., Ruis M.A.W. and B. H.J. 1999. «Coping styles in animal: current status in behavior and stress-physiology ». *Neuroscience and biobehavioral reviews*. vol. 23, no. 7, p. 925-935.

Krause, J. and J. G. J. Godin. 1996. «Influence of prey foraging posture on flight behavior and predation risk: Predators take advantage of unwary prey ». *Behavioral Ecology*. vol. 7, no. 3, p. 264-271.

Krebs, J. R. and A. Kacelnik. 1991. *Behavioural ecology : an evolutionary approach.* 3rd edition.(Oxford). Blackwell Scientific Publication.

Krebs, J. R. and N. B. Davies.1993. «*An Introduction to Behavioural Ecology*». (Oxford). Blackwell Scientific Publication).

Lima, S. L. and L. M. Dill. 1990.«Behavioral decisions made under the risk of predation: a review and prospectus ». *Canadian Journal of Zoology*. vol. 68, no. 4, p. 619-640.

Longland, W. S. and M. V. Price. 1991. «Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? ». *Ecology*. vol. 72, no. 6, p. 2261-2273.

Lung, M. A. and M. J. Childress. 2007. «The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park ». vol. 18, no. 1, p. 12-20.

Makowska, I. J. and D. L. Kramer. 2007. «Vigilance during food handling in grey squirrels, *Sciurus carolinensis* ». *Animal Behaviour*. vol. 74, no. 1, p. 153-158.

Martin, J. G. A. and D. Réale. 2008. «Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus* ». *Animal Behaviour*. vol. 75, no. 1, p. 309-318.

Mateo, M., J. 1996. «The development of alarm-call response behaviour in free-living juvenile Belding's ground squirrels «. *Animal Behaviour*. vol. 52, no. 3, p. 489-505.

---. 2006. «Developmental and geographic variation in stress hormones in wild Belding's ground squirrels (*Spermophilus beldingi)* «. *Hormones and Behavior*. vol.50, p. 718-725.

Nephew, B. C. and L. M. Romero. 2003. « Behavioral, physiological, and endocrine responses of starlings to acute increases in density». *Hormones and Behavior*. vol.44, no.3, p. 222-232.

Pays, O. and P.J. Jarman. 2008. «Does sex affect both individual and collective vigilance in social mammalian herbivores: the case of the eastern grey kangaroo?». *Behavioral Ecology and Sociobiology*. vol. 62, no. 5, p.757-767.

Perrin, C., D. Allainé and M. Le Berre. 1993. «Socio-spatial organization and activity distribution of *Marmota marmota:* preliminary results ». *Ethology*. vol. 93, no.1, p. 21-30.

Poysa, H. 1994. «Group foraging, distance to cover and vigilance in the teal, *Anas crecca* ». *Animal Behaviour*. vol. 48, no. 4, p. 921-928.

Prins, H.H.T. and G.R. Iason. « Dangerous lions and nonchalant buffalo». *Behaviour*. vol. 108, no. 3-4, p. 262-296.

Ranghetti, L. 2009. «Eco-etologia della marmotta alpina (*Marmota marmota*): distribuzione spaziale e temporale delle attività ». (Master tesi, Università degli Studi di Pavia, Italy).

Réale, D. and M. Festa-Bianchet. 2003. «Predator-induced natural selection on temperament in bighorn ewes ». *Animal Behaviour*. vol. 65, no.3, p. 463-470.

Réale, D., S. M. Reader, D. Sol, P. T. McDougall and N. J. Dingemanse. 2007. «Integrating animal temperament within ecology and evolution ». *Biological Reviews*. vol. 82, no. 2, p. 291-318.

Ruxton, G. D., T.M. Sherratt and M.P Speed. 2004. «*Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry* ». (Oxford University Press,U.K.)

Sih, A., A. Bell and J. C. Johnson. 2004. «Behavioral syndromes: an ecological and evolutionary overview ». *TRENDS in Ecology and Evolution*. vol. 19, no. 7, p. 372-378.

Sih, A., A. M. Bell, J. C. Johnson and R. E. Ziemba. 2004.«Behavioral syndromes: an integrative overview ». *The Quarterly review of Biology*. vol. 79, no. 3, p. 241-277.

Sih, A., L. B. Kats and E. F. Maurer. 2003. «Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system ». *Animal Behaviour*. vol. 65, no. 1, p. 29-44.

Stamps, J. A. 2007. «Growth-mortality tradeoffs and 'personality traits' in animals ». *Ecology Letters*. vol. 10, no.5, p. 355-363.

Trouilloud, W., A. Delisle and D. L. Kramer. 2004. «Head raising during foraging and pausing during intermittent locomotion as components of antipredator vigilance in chipmucks ». *Animal Behaviour*. vol. 67, no. 4, p. 789-797.

Van Oers, K., P. J. Drent, P. De Goede and A. Van Noordwijk. 2004. «Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities ». *Proceedings of the royal B society*. vol. 271, no. 1534, p. 65-73.

Verbeek, M. E. M., A. Boon and P. J. Drent. 1996. «Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits ». *Behaviour*. vol. 133, no. 11-12, p. 945-963.

Wascher, C. A. F., I. B. R. Scheiber, B. M. Weib and K. Kotrschal. 2009. « Heart rate responses to agonistic encounters in greylag geese, *Anser anser*». *Animal Behaviour*. vol.77, no.4, p. 955-961.

Wilson, D. S., A. B. Clark, K. Coleman and T. Dearstyne. 1994. «Shyness and boldness in humans and other animals». *TRENDS in Ecology and Evolution*. vol. 9, no. 11, p. 442-446.

Wilson, A.J., U. Gelin, M.-C. Perron and D. Réale. 2009. «Indirect genetic effects and the evolution of aggression in a vertebrate system ». *Proceedings of the Royal Society B: Biological Sciences*. vol. 276, no. 1656, p.533-541.

Wilson, A. D. M. and J. G. J. Godin. 2009. «Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus* ». *Behavioral Ecology*. vol. 20, no. 2, p. 231-237.

Wilson, D. S. 1998. «Adaptive individual differences within single populations ». *Philosophical Transactions of the Royal Society B: Biological Sciences*. vol. 353, no. 1366, p. 199-205.

Wolf, M., G. S. Van Doorn, O. Leimar and F. J. Weissing. 2007. «Life-history trade-offs favour the evolution of animal personalities ». *Nature*. vol. 447, no 7144, p. 581-584.

Wood, W. A. 1973.«Habitat selection and energetics of the Olympic marmot ». Master Thesis, Western Washington University.

Wright, S. and T. Dobzhansky. 1946. «Genetics of Natural Populations. Xii. Experimental Reproduction of Some of the Changes Caused by Natural Selection in Certain Populations of *Drosophila pseudoobscura* ». *Genetics*. vol. 31, no.2, p. 125:156.