THE SOCIOENDOCRINOLOGY OF AGGRESSION-MEDIATED STRESS IN TIMBER WOLVES (*Canis lupus*)

by

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This thesis is dedicated to the memory of Will Moger, my thesis committee member and friend from 1994 to December 2001. Will was a great teacher, an understanding and supportive committee member and a caring, generous friend.

William H. Moger (1945-2001)

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Abstract

The goal of this study was to evaluate the impact of sociogenic stress (more specifically, aggression-mediated stress) in a large pack of captive timber wolves (*Canis lupus*). Urine contaminated snow was collected for three consecutive winters (from early December to the end of March) encompassing the mating seasons (January to mid-March). Audio-video recording of behaviour, with a focus on agonistic behaviour, was performed during the same time period. Urine samples were assayed for Creatinine (Cr), Cortisol (C) and Testosterone (T). The frequency and intensity of intra- and inter-sexual dyadic agonistic interactions were scored for both initiators and recipients. The data were examined for sex differences, for annual differences, and for individual differences in relation to rank and status in the pack. C:Cr ratios were higher in beta and omega animals as were the T:Cr ratios in some of the same animals. The associations between hormonal levels, aggressive behaviours, and weather parameters were shown to vary from one breeding season to the next. There was an increase in pack C:Cr levels over the three years of this study. Weather was an unlikely factor in the rise of cortisol across seasons. Historically, models of social stress as a regulator of group size have been based on studies conducted with rodents and have predicted higher glucocorticoid levels and lower androgen levels among low-ranking animals. Consistent with recent models of more social species in general, and of cooperative breeders specifically, the patterns here suggest an alternative trend. The data also suggest that behavioural-physiological mechanisms of reproductive suppression in subordinates by dominant individuals may not be as crucial as are purely behavioural strategies. The data are discussed in the context of recent socioendocrinological theories of social stress and reproductive suppression in the literature on Primates and Carnivores.

List of Abbreviations

5-HT	Serotonin or 5-hydroxytryptamine
5-HTP	5-hydroxytryptophan
ACTH	Adrenocorticotropic hormone
ADH	Antidiuretic hormone or vasopressin
ANS	Autonomic nervous system
c.v.	Coefficient of variation
C:Cr	Cortisol:creatinine (ratio)
CCWR	Canadian Centre for Wolf Research
CNS	Central nervous system
CORT	Cortisol
cpm	Counts per minute
CRH	Corticotropin releasing hormone
CT	Calcitonin
DA	Dopamine
DBH	Dopamine-b-hydroxylase
DHEA	Dehydroepiandrosterone
DHT	Dihydrotestosterone
EP	Epinephrine (or adrenaline)
FSH	Follicle stimulating hormone
GAS	General Adaptation Syndrome
GH	Growth hormone
GnRH	Gonadotropin releasing hormone
HPA	Hypothalamic-pituitary-adrenal
II	Intensities for initiators
IR	Intensities for recipients
IRS's	Individual Response Stereotypies
LH	Luteinizing Hormone
LHRH	Luteinizing hormone-releasing hormone
NaOH	Sodium hydroxide

NE	Norepinephrine (or noradrenaline)
NO	Nitric oxyde
NSB	Non-specific binding
OFI	Observed frequencies for initiations
OFR	Observed frequencies for receptions
PNMT	Phenylethanolamine-N-methyltransferase
PRL	Prolactin
RIA	Radioimmunoassay
s.d.	Standard deviation
sem	Standard error to the mean
SSRI	Selective serotonin re-uptake inhibitor
S-VHF	Super VHF
T	Testosterone
T:C	Testosterone:Creatinine / Cortisol:Creatinine
T:Cr	Testoterone:creatinine (ratio)
T3	Triiodothyronine
T4	Thyroxine (or tetraiodothyronine)
TC	Total count
TH	Tyrosine hydroxylase
VITC	Vertical Interval Time Code
VTA	Ventral tegmental area

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1. The Socioendocrinology of Aggression-Mediated Stress in Timber Wolves (*Canis lupus*).

1.1 General Overview

The purpose of this study is to better understand the proximate mechanisms underlying the social behaviour of wolves (*Canis lupus*) during the reproductive season. More specifically, I will try to elucidate some of the control mechanisms (behavioural and physiological) associated with monogamy, cooperative breeding and aggression. Wolves, as well as a few other canid species (dholes, *Cuon alpinus* and African Wild Dogs, *Lycaon pictus*) live in primary groups, that is, packs formed around the reproductive unit. In wolves, this breeding unit is determined by the dominance hierarchy. Usually, only the alpha male (emerging from the male dominance hierarchy) and the alpha female (emerging from the female dominance hierarchy) will breed. The mechanisms underlying this phenomenon are not completely understood; it is unclear to what extent they are behavioural, physiological, or a combination of both. In this study, I examine the role of stress, and more specifically social stress, in relation to the physiological, social and reproductive dynamics of semi-wild captive wolves.

This study involves predominantly observational and correlational approaches to social behaviour and social endocrinology. It has an ethological perspective with strong psychological undertones (especially when stress and social stress are discussed). The focus is on one large pack with an analysis of the individuals' behaviour and endocrinological profiles for three full reproductive seasons. It therefore justifies an ethological (descriptive) and longitudinal approach.

This project involved three steps: 1) Raw data collection: collecting urine samples from snow and videotaping behaviour for three consecutive breeding seasons (December to March from 1993 to 1996). 2) Development and validation of the assays for creatinine, cortisol and testosterone, and assaying of all urine samples. 3) Coding and analysis of the behavioural data (primarily aggressive interactions) from over 100 hours of videotapes accumulated over the three years of the field study.

Section 1.2 reviews and discusses the literature on agonistic behaviour. Section 1.3 addresses stress and social stress. Section 1.4 narrows the concepts presented in the previous sections. It focuses on themes directly relevant to canids (monogamy, cooperative breeding, paternal and alloparental care and reproductive and social organization in wolves and related canines). The final section of the introduction, Section 1.5, describes the predictions based on the literature review.

Socioendocrinology is a young sub-discipline of behavioural endocrinology. Until recently there has been relatively little focus on canids. For this reason, it is important to present a solid and comprehensive overview of its theoretical bases. Socioendocrinology, by its multidisciplinary nature, has much to offer but also presents a challenge of synthesis. For example, the concept of aggression has been discussed for decades yet few scientists (ethologists, psychologists, sociologists, biologists) agree on a definition of the term. Johnson (1972) thought that the concept was too complex to define and Zillmann (1998) stated "The common usage of the word aggression is so broad as to render the concept vague and useless for scientific inquiry" (p. 22). Zillmann proceeded to say that when "assertion" and "initiative" are viewed as aggression by some authors, there is little hope of finding a consensus. This is probably and unfortunately true, but in such circumstances, it seems imperative to discuss the available definitions, the one or ones that were selected in this study, and the rationale for my choice.

The following sections are an attempt to integrate and consolidate the concepts and views of agonistic behaviour (Section 1.2), stress and social stress (section 1.3) and mating/social systems (Section 1.4).

1.2 Agonistic Behaviour: Aggression and Submission

The study of aggression in animals and humans has been a prolific line of research and concern since the modern beginnings of the social sciences. Highly social mammals, especially primates, became the centre of interest for many psychologists and anthropologists because they were seen as an uncomplicated model for human social behaviour and a window to understanding human violence. In this section, I will review the major theories of animal aggression relevant to the general field of animal behaviour, including ethology, animal psychology, psychobiology and behavioural endocrinology. I will first focus on the behavioural aspects of aggression and submission and then discuss the physiological perspective. The latter will focus on the endocrine system and more precisely, the androgens.

1.2.1 Behaviour

In this section I will discuss agonistic[1] behaviour (a term coined by the late J.P. Scott: Scott, 1958, 1964; Scott & Fuller, 1965; Scott & Fredericson, 1951), that is, the whole continuum of aggression and submission. The study of

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[1] *Agonistic*, as well as ***antagonism***, and other derivatives, has its origins in the Greek noun ***agôn***, which means "gathering" (especially for the Olympic games) and hence "competition" and "fight" (Picoche, 1971).

aggression (technically and terminologically an action or act)[2] rarely occurs without an examination of the actual interactions between individuals (at least two), including the response to the aggressive act. Aggression does not necessarily lead to reciprocity (i.e., responding aggressively) and it goes without saying that the reaction to an aggressive act can be quite the opposite, for example, a retreat, an escape, or an appeasing behaviour. This point was raised by Darwin in his principle of antithesis. Darwin (1872/1965; also in Mook, 1996) noticed that when animals caught in a conflict decide to respond to an aggressive act or display with an appeasing (submissive) attitude, a diametrically opposed set of acts or displays to those of the aggressor is manifested. For example, if a male dog threatens a rival, it will typically stare at the opponent, stand as high from the ground as possible with the legs stretched, erected hair on its back, erected ears, and erected tail, and it will produce low pitch, harsh vocalizations (e.g., growling; see Morton, 1977). The rival can choose to either reciprocate (adopting the same posture and behaviours) or submit. In the submissive dog, the appeasement of the attacker is achieved by adopting the antithetic postures and attitudes: avoiding eye contact, positioning the body

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[2] Ramirez (1998), would distinguish between the objective aspect of aggression, or the act, and the subjective aspect, or the feeling. The more common distinction is between

close to or on the ground, with legs flexed, ears flattened backwards, tail between the legs and making high pitch, soft vocalizations. As Scott (1958) pointed out, these appeasement behaviours are no more and no less than affiliative behaviours used by a submissive animal in the context of conflict.

Darwin recognized that we are, in fact, dealing with a continuum of agonistic displays and attitudes, and modern authors remind us of the dangers of excessively "polarizing" the possible agonistic reactions (Nelson, 2000). As mentioned earlier, agonistic behaviours are expressed along a continuum, from the brutal attack resulting in a fight, to the desperate escape or flight. As noted by Immelman and Beer (1989), the fleeing part of the agonistic continuum is often left out of the literature, mainly because many authors equate agonistic behaviour with aggressive behaviour. Darwin actually made a point of describing the middle range of the continuum, when the conflict is still in negotiation: threat and appeasement. Figure 1.1 depicts the continuum and some of the terms often used in the literature to describe each zone. The zone between threat and appeasement includes a full array of "neutral" behaviours including "doing nothing" (as a friendly and economical social signal

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aggression, the action, and aggressiveness, the internal state that may or may not lead to overt aggression (see Lorenz in Evans, 1975; Moyer, 1976).

(Moyhinan, 1998)), expressed indifference, and cowardice (Moynihan, 1998). Neutral behaviours also might result from an unawareness or misinterpretation of the threat, rather than a reaction to the threat per se. Note also that the terms "fight" and "flight" common in motivational theories of fear, stress, and aggression (e.g., Gray, 1987) are included here because of Berkowitz's (1994) distinction between the "flight" network (a brain network of escape and avoidance) and the "fight" network (a brain network of anger and aggression) in the context of hostile behaviour. Which network is activated depends on a number of genetic, learning, and situational factors[3]. Figure 1.1 also highlights the relativity of the concept of agonism or agonistic behaviour. Nelson (2000) suggests an alternative model of agonistic behaviour that identifies aggression and submission as two different aspects of an individual's behaviour. For Nelson, they are not part of the same continuum (from submissiveness to aggressiveness), but are two distinct continua, one ranging from low submissiveness to high submissiveness and the other from low aggressiveness to high aggressiveness. The implications of such a perspective are potentially important and can influence predictions about the physiology and psychology

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[3] Situational factors can be of a physical origin (such as territoriality, dietary factors, and aversive events) or of a social origin (such as isolation, crowding, exposure to strangers,

of agonistic behaviour. In this study, however, I chose to take a dialectical approach to agonistic behaviour, that is, to consider hostile interaction as a "dance" or "negotiation" between two individuals (the dyad) trying to attain an optimum equilibrium (for a similar suggestion, see McLeod, 1996 and McLeod & Fentress, 1997).

Figure 1.1. The continuum of agonistic and conflictual interactions.

It is important to note that the behaviours in the escape category of Figure 1.1 do not necessarily imply submission. For example, withdrawal and retreat could alternatively suggest careful behaviour or "indifference" from the recipient (in the case of a unilateral retreat) or between the recipient and initiator or co-interactant (in the case of a bilateral retreat). The same is true for companion terms often used in the literature (Moynihan, 1998): avoidance (interspecific) and exclusion (intraspecific). The absence of overtly aggressive or submissive behaviours is obvious in many cases of mutual avoidance and

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competition over resources, social disorganization and instability).

exclusion. In order to avoid misunderstanding, behavioural scientists have to define the terms they use very carefully and explicitly.

Accordingly, I will now define the terms that will be used throughout this text. First, agonistic behaviour will refer to a hierarchy of species-specific behavioural patterns used during a conflict between conspecific individuals and based on species-specific social rules. Furthermore, aggression is often provoked by a violation of these same social rules or conventions (Crook, 1966). A polarity exists in the continuum of agonistic behaviour and is defined by the aggressive and submissive actions and reactions of individuals, from the extreme actions of fight (attack) and flight (retreat), to the negotiation in the situation of conflict (threat and appeasement). The negotiation can end in reconciliation, in which case both parties actually engage in affiliative behaviour, or in escalation.

Aggression is an action, it is a set of behaviours used to induce fear, distress (via threats) or injury, pain, and discomfort (via attacks). This definition of aggression, animal or human, is common and agreed upon by many authors (for example Baron & Richardson, 1994; Bernstein, 1991). For some authors (e.g., Bandura, 1973), the final goal of aggression is recognized as not being primarily destructive, but as being an expression of assertiveness (see Barnett, 1981[4] for the view that assertiveness is a form of aggression). In the context of dominance hierarchies and the battle for status and rank (e.g., Sapolsky, 1982), Bandura's focus is particularly relevant. By aggression, I will not refer to the disposition (state) or predisposition (tendency or trait) of aggressiveness. Aggressiveness is the complex conative (motivational), affective or emotional as well as perceptual and cognitive dimension of aggression (cognitive as long as "intention" requires planning or decision making). It cannot easily be evaluated without a focus on individuality, temperament and, in humans, character (the last two forming the concept of personality; for a psychobiological discussion of temperament and personality, see Cloninger, 1994). Submission, like aggression, is an action, a behaviour intended to appease an attacker or a threatening individual (more precisely, an individual who is perceived as threatening). The most dramatic or explicit version of submission is the escape or flight and often subsequent avoidance behaviours.

Barnett (1981)[5], in an effort to re-conceptualise aggression and search for a more objective terminology to describe agonistic behaviours, discussed treptic behaviours in rats, that is, interactions between individuals characterized by

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[4] Assertiveness is, for Barnett, the first form of human individual aggression on a continuum including dominating behaviour, assault without battery, assault, and murder.

approach and withdrawal. Treptic behaviours are composed of apotreptic behaviours, or behaviours causing a conspecific to withdraw (including the threat behaviours discussed earlier) and epitreptic behaviours, or behaviours causing a conspecific to approach (including the appeasement behaviours mentioned earlier). According to Barnett, the advantage of this system lies in the fact that it makes no assumptions about the intentions or the states of the actor, which would require subjective measurements. Only the effects of the actor's behaviour on the recipient actually count. Barnett defines aggressive interactions as being primarily apotreptic, that is, associated with threat behaviour and causing the recipient to avoid the threatening animal. This perspective and terminology reminds us of Karen Horney's (in Hergenhahn, 1984) terminology: move toward (approach and compliance), move away (withdrawal and detachment) and move against (aggression)[6]. Unfortunately for Barnett, the terminology never caught on even though a number of behaviourists were previously using an approach-retreat perspective on social interactions to assess dominance hierarchies (Bernstein, 1976; Bernstein & Sharpe, 1966; Deag, 1977; Rowell, 1974; Seyfarth, 1980).

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[5] Barnett was influenced by Schneirla's approach-withdrawal theory or theory of biphasic processes (1959, 1965, 1966).

Over the years, many ethologists began to use synonyms or quasi-synonyms to describe different aspects of the aggressive or submissive ends of the agonistic continuum. Concerns with objectivity and the descriptive aspect of defining agonistic behaviour (e.g., precise ostensive definitions) gave rise to many different terminologies. Table 1.1 is the result of an effort to assemble these terms as much as possible. Note that if it is agreed that aggression is an overt process or action, then the term aggression should not be used, according to some authors (e.g., Wittenberger, 1981) to describe the behaviours in the second column.

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[6] It is important to remember that Horney was describing strategies (as in *life strategies* or solutions to neurotic conflicts), not tactics.

Table 1.1. Summary of the terminology used to describe the agonistic continuum.

AGGRESSION - Overt[1] - Explicit - Direct[2] - Active - Contact/physical[3]	"AGGRESSION" - Covert[1] - Implicit - Indirect[2] - Passive - Ritualised/display	SUBMISSION A "mirror image" of the two first columns' terminology is sometimes used for submissive behaviours but usually fails to be as concrete or as precise (or even appropriate) as the common descriptive terms (such as, "appeasement" and "escape").	
Fight/Attack	Threat, intimidation	Appeasement	Flight/Escape
Apotreptic behaviours		Epitreptic behaviours	
Body contact (haptic or tactile) guaranteed. Attack with physical contact (e.g., bites) sometimes preceded by a warning. Actual "intention" to harm inferred.	Ritualised aggression, often visual contact but little or no body contact except for dominance mounting (common in primates and canids). Low pitch vocalizations. Communication of the intent to harm. In dominance hierarchies, rank symbols are used.	Ritualised submission, avoidance of visual contact. Affiliative contact possible: soliciting, begging, submissive greeting. High pitch vocalizations. Infantile/juvenile behaviours common.	Running away. Retreat. Avoidance can follow.
Primarily tactile (Moynihan, 1998), visual, auditory.	Visual, auditory, olfactory (scent marking).	Visual, haptic, auditory (olfactory? Fear pheromones?)	

(1) The overt/covert dichotomy is very common and "covert" is often used in conjunction with ritualised. This is a term used by Moynihan (1998).

(2) The direct/indirect dichotomy can be traced to Schaller (1977). Used also by Ramirez (1998).

(3) Contact aggression: see discussion in the Methods and Oswald & Erwin's (1976) distinction between contact aggression, non-contact aggression, and submission in pigtail monkeys.

Note: The first row displays the "technical" terms, the second row the vernacular terms, the third row Barnett's terminology (when applied to agonistic interactions). The fourth row gives a rough description of the behaviours involved (postures, movements, vocalizations). The fifth row emphasizes the sensory modalities involved in most social mammals.

A fifth column could be placed between the second and third with the heading "neutral behaviour". As stated by Moynihan (p. 69): "The simplest pattern of a possibly friendly nature is doing nothing in a social situation. This can be a signal at times. It certainly is economical." So doing nothing, immobility and freezing are also possible responses to a threat.

Barnett's other important contribution for this discussion is his analysis of the causes and effects of apotreptic behaviour in rats, for both the attacker and the attacked. Table 1.2 summarizes causes and effects identified by Barnett. Note that physiological, environmental and observational (ethographic) variables are identified and, even more interesting for our concerns, the stress-related impact of threat is identified for both the attacker (or threatening individual) and the attacked/threatened, including enlarged adrenals in both. In sharp contrast with the other taxonomies of aggression and agonistic behaviour (see below) is the omission of the concept of resources as a cause for conflict. Barnett's proximate perspective justifies this exclusion.

Table 1.2. Causes and effects of threatening behaviour in rats (adapted from Barnett, 1981).

	Attacker/threatening individual	**Attacked/threatened individual**
Causes	• Internal states (e.g., hormonal) • External stimuli (e.g., approach by a stranger)	• Approach • Exploration
Effects	• Shorter latency of threat • Higher intensity of threat • Possibly enlarged adrenals	• Flight (escape), submission • Enlarged adrenals • Pathologies, death

Another innovative perspective, that seemed to have made its first appearance in animal behaviour via anthropologists and primatologists (e.g., Chapais, 1991) is (human) developmental psychologist Dodge's (Dodge & Coie,

1987) concern with context and the intentions of the initiator. Although intention is a manifest ethographic problem (i.e., how can we identify, or better, measure the intentions of an animal?), the context (social or environmental) can often suggest or hint at the intent. Dodge and Coie (1987) distinguish between reactive aggression (from provocation) and proactive aggression (initiated without provocation). From an ethological point of view each type can be inferred from the context. Reactive aggression is caused by frustration (sociogenic or other) and is no more and no less than a reciprocation in the context of a dyad or triad. Proactive aggression is not provoked, has a strong instrumental value (used to obtain resources, such as food or mates) and does not typically involve anger. Ethologists have been flirting with these concepts by talking about defensive versus offensive aggression, with the important distinction that defensive aggression is more specific than reactive aggression; it implies a reaction to a threat or attack. The interesting notion offered by reactive aggression is that the context need not be social; the stimulus can be almost anything perceived as a threat.

Two authors come to mind when looking for ethological theories similar to the one offered by Dodge and Coie: Hinde (1970) distinguishes between "instrumental aggression" and "hostile aggression" and Zillmann (1979) between "incentive-motivated" and "annoyance-motivated" aggressions. Despite the risk of ignoring subtleties between the three theories, Table 1.3 summarizes the Dodge-Hinde-Zillmann models. It is important to note that similar dichotomies were offered in the human literature before Dodge and Coie (e.g., Bandura, 1971; Buss, 1961; Feshbach, 1964). Each had the same purpose, to discriminate between two types of primary intent: distress and fear versus harm and power.

Table 1.3. The Dodge-Hinde-Zillmann models of aggression.

Reactive / hostile / annoyance-motivated aggression *	**Proactive / instrumental /incentive-motivated aggression** (no provocation)
Defensive reaction to a threatening, potentially threatening or perceived to be threatening stimulus. Typically: 1. Anger or frustration involved 2. Impulsive 3. In response to perceived provocation (i.e., reciprocation)	Aggression without provocation used to attain some specific goal (object, subject, etc.). Typically: 1. Non-angry 2. Planned 3. Reward-centered, instrumental
* also called "indiscriminate" aggression by Ramirez (1985) and includes: defensive reactions, maternal aggression, and irritable aggression.	

The reactive, hostile, and annoyance-motivated type of aggression can express itself in paradoxical ways, such as redirection or displacement aggression on animate or inanimate objects (Blanchard & Blanchard, 1990; Miller, 1948, inspired by Freud; Moynihan, 1998).

A discussion on aggression would not be complete without the more traditional, less proximate, and more functional approaches to aggression: functional typologies are numerous and indispensable for pure, traditional observational work[7]. They represent a classification of the ultimate factors involved in aggressive behaviour. Table 1.4 summarizes these typologies. The Ramirez typology (Ramirez, 1998) is the most recent and represents a noble attempt to merge the functional theories and the causal-consequential theories presented earlier with a desire to recognize the difference between defensive aggression (defence) and offensive aggression (offence). This last dichotomy has been trendy since the late seventies in neuroscience (Adams, 1979; Ramirez, Salas, & Portavella, 1988) and experimental ethology (Blanchard & Blanchard, 1984, 1989).

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[7] As suggested by Moynihan (1998), it is important to discriminate between aggression at the strategic level (i.e., the ultimate factors involved in the study of aggression; traditionally the focus of sociobiologists and behavioural ecologists) and aggression at the tactical level (i.e., the proximate factors involved in the study of aggression ; traditionally the focus of ethologists and comparative psychologists). With regard to tactics, the focus of the present study, Moynihan reminds us that "Strategies are important in evolution. They can only work through or by tactics" (p.7).

Table 1.4. Typologies of aggression by Archer, Moyer, Ramirez, Wilson, and Wittenberger.

Archer (1988) Functional typology: aggression as a strategic solution to a problem.	1. Protective aggression: in response to a threat of physical attack 2. Parental aggression: in response to a threat to young 3. Competitive aggression: in response to a threat to status or access to resources
Moyer (1968, 1976) Causal typology: aggression as a response to a stimulus.	1. Predatory aggression 2. Intermale aggression 3. Fear-induced aggression 4. Irritable aggression: labelled anger or rage 5. Sex-related aggression 6. Maternal/parental aggression 7. Instrumental aggression 8. [Territorial aggression: Discarded in 1976 because of the highly context dependent nature of this type]
Ramirez (1985) Rejected in favour of the 1998 version (see next row).	1. Interspecific aggression: defence against predators, interspecific competition; can be reactive. 2. Intraspecific aggression: hostile behaviours, usually not leading to injuries. Often leads to escape 3. Indiscriminate aggression: "reactive aggression" including defensive reactions, maternal and irritable aggression.
Ramirez (1998)	1. Direct aggression (physical character) a. Offence (involving conspecifics) b. Defence (reactive) c. Irritable, indiscriminate: non-specific, reactive to any provocative stimulus. 2. Indirect aggression a. Dominance displays (ritualised aggression) b. Symbolic aggression (human type)
Wilson (1975) Partially influenced by Trivers' (e.g, 1974) reciprocal altruism models.	1. Territorial aggression 2. Dominance aggression 3. Sexual aggression 4. Predatory aggression, including cannibalism 5. Antipredatory aggression (defensive) 6. Parent-offspring aggression: a. associated with weaning b. disciplinary aggression c. "moralistic" aggression

Wittenberger (1981) Historically inspired by Wilson (1975)	1. Intrasexual aggression: territorial, dominance. 2. Intersexual aggression: courtship, territorial (solitary species), dominance. 3. Parental aggression 4. Infanticide: parental aggression, male takeover (lions). 5. Peer aggression: fratricide, social dominance, aggressive play (hyenas). 6. Defensive aggression: self-defence or defence of offspring. 7. Redirected aggression: frustration. 8. Predatory aggression: predator-prey aggressions.

Although many modern discussions of aggression open by citing Lorenz, I mention his work late in the behavioural segment of this section on agonistic behaviour in part because his simple classification of aggressive behaviours is not valued by contemporary ethologists and, although I could say much on Lorenz' theory, his contribution on the topic has been tarnished by controversies, the criticism of oversimplification (e.g., the hydraulic model of motivation, applied to aggression), and the view that aggression is an instinct[8]. Overall, his book "On Aggression" (1966) is a classic. Despite theoretical disagreements with most modern ethologists, the book offers great insights into the phylogenetic analysis of the behaviour and some of the earliest descriptions and discussions of canine aggressive displays and ritualised aggression. Lorenz was not concerned with functional typologies and classifications, but was

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[8] As stated by Karli (1987) there is likely no aggressiveness or aggression instincts, only territorial, maternal, etc and protection instincts.

interested in a purely descriptive approach of intra-specific aggression. He described individual aggression (towards conspecifics of the same group), collective aggression (towards conspecifics from another group) and also mentioned interspecific aggression and predator-prey interactions and their contexts. Lorenz (1966) believed that individual aggression is increased by stress, nervousness, and irritation and was convinced that aggression evolved from sexual competition and access (i.e., to fight off competing males, to "convince" females, either by showing off or by coercive action).

The link between aggression and sex is widely studied by animal behaviourists and psychologists alike (see Zillmann, 1998 for a comprehensive review) and is of great relevance to my study, considering the ultimate goal would be (with further research) to understand reproductive suppression in wolves through behavioural and/or physiological means (i.e., via aggression, as a social stressor). Already by the middle of the past century, Kinsey et al. (Kinsey, Pomeroy, & Martin, 1948, Kinsey, Pomeroy, Martin, & Gebhard, 1953) were describing the multiple similarities between sexual and aggressive behaviours: of all the physiological measures recorded in both states, many were common to both aggressive and sexual arousal.

Ritualised aggression as a set of behaviours (actions and displays) is like dominance hierarchies as a social organization and structure: it is a means to avoid chaos within groups. Moynihan (1998) even suggests that ritualisation may grant "emotional relief" (Moynihan, 1998, p. 30) during stressful times. This idea is similar to data suggesting that stereotyped behaviours (Mason, 1991, 1993; Rushen, Lawrence, & Terlouw, 1993) actually reduce stress hormones levels (cortisol) in some mammals. Ritualised aggression, being by definition, ritualised, may then serve two purposes: to carry a message and induce relaxation and reduction in stress.

Moynihan's (1998) discussion of ritualised aggression is the most comprehensive and innovative of which I am aware. Moynihan was interested in the intensity of ritualised aggression. This is an interesting concept, as we know the importance of the intensity of the stressors (in addition to their frequency, duration and sequencing). If we consider aggression to be a stressor, then the intensity of aggressive encounters, despite the difficulty of evaluating them, is highly pertinent to a discussion on social stress. In agonistic encounters between canines, there is no doubt that contact aggression (e.g., a bite) is more "intense" than a display (e.g., a raised tail). The difficulty lies in the "gradation" or scaling of ritualised aggressions. Often subtle, ritualised displays are complex enough to be heavily nuanced in their expression (see Gadbois & Fentress, 1997 a & b; Fentress & Gadbois, 2001; Gadbois & Fentress, in prep.): the behavioural flow in time and space can be highly complex, especially when behaviours are analysed beyond simple frequencies and latencies. The durations of actions, their sequencing and their spatio-temporal properties (amplitude of movements, durations of rhythmic events, etc.) can be modulated like any graded signal. Moynihan offers a simple and relatively objective classification of ritualised behaviours in social contexts in four groups (see Table 1.5 for a summary): (1) Simple unritualised approach-withdrawal movements (Moynihan's terms are actually "advance and retreat movements") and intention movements, (2) Ritualised attacks and escape movements, (3) Hostile displays without physical contact and finally (4) Hostile displays with physical contact. Moynihan also mentions a fifth group: the "intense" or out of control fight (i.e., leading to injury).

Table 1.5. Moynihan's scaling of ritualised aggression displays and contact aggression.

Categories	Category 1: Unritualised approach / withdrawal movements and intention movements	Category 2: Ritualised attack and escape movements	Category 3: Displays and behaviours without physical contact	Category 4: Displays and behaviours with physical contact	Category 5: Behaviours with injurious physical contact
Description	The signal sent by this category of displays and behaviours is: "I intend to attack/escape". Vocalizations common.	Similar to previous category but highly stereotyped and expressive in time and space (e.g., high frequency, long duration, high amplitude). Vocalizations common.	Often diversions; non-hostile behaviours: grooming, feeding, drinking, etc.	Similar to previous category but incorporates derivations of allogrooming, allosex (also called pseudosex, e.g., pseudo-copulation like dominance mounting in canids and primates).	This category is obviously the most radical form of conflict resolution and is not "ritualised" per se. Animals get to this level when all other categories of ritualised behaviour have failed.
Sensory modalities involved	Visual (postures & movements), auditory (vocalizations), olfactory?	Visual (postures & movements), auditory (vocalizations), olfactory?	Visual (postures & movements), auditory (vocalizations), olfactory?	Visual (postures & movements), auditory (vocalizations), tactile (haptic), olfactory?	This is "contact" aggression, so the primary modality would be tactile, but all are involved.

Moynihan sees a progression in this scaling, an increase in intensity (from left to right) as though paralleling a range of emotions from irritation to rage

(Averill, 1982; Ramirez, 1998) or a range of behaviours or consequences from assertiveness to murder (Barnett, 1981). This conflict intensity is apparent in the "relative or comparative, not (or not only) the actual, strengths of the tendencies involved" (Moynihan, 1998, p. 106). Unfortunately, Moynihan, who in fact studied a wide range of taxa (cephalopods, birds, primates) offers no comment on how this scale applies across species. Typical of the problems encountered in studying agonistic behaviours, Moynihan reminds us that the primary intent of the behaviours and displays described above is not always certain. It could be dominance assertion, tension regulation, reconciliation or alliance formation. Speaking of intent may well be too ambitious and anthropomorphic: it is possible that some of these behaviours are quasi-reflexes, although following strict rules. For this reason, a detailed study of the interactions between individuals is necessary; actions and reactions of both the initiators and recipients of agonistic behaviours need to be documented before any attempt is made to infer intention.

I am in favour of a proximate perspective on the study and analysis of agonistic behaviours. By proximate, I suggest the traditional ethological concern with direct observation of social behaviours and the underlying physiology and biochemistry. As Bernstein (1998) eloquently and pragmatically reasons: "Rather than focusing on cause or function, we would need to demonstrate that the presence of an agonistic element in a behavioural sequence increased the probability of an injury occurring during that sequence. This prediction would be testable." (p. 636). Such a direct, proximate cause-effect relationship, on the one hand, is not without reminding us of Barnett's preoccupation with the effects of threats or attacks on the recipients; on the other hand, it would seem to discredit the usefulness and validity of most of the current typologies of agonistic behaviour and aggression. Allow me to conclude the behavioural sub-section with Bernstein's own conclusion: "The alternative, recognizing as many distinct types of agonistic behaviour as we can recognize functions or motivations, is not a true alternative. When we describe 'types' of agonistic or aggressive behaviour, we are implicitly recognizing the unity of agonistic behaviour, aggressive behaviour, or both and must still identify the basis of that unity. Without an explicit definition we can anticipate endless controversy concerning 'predatory aggression', 'punishment', 'defence', etc." (Bernstein, 1998, p. 636). After the hostilities are over, all that may count is the outcome (i.e., who "won", who "lost") for both the actors and the observers.

1.2.2 Physiology

The physiology of aggression and submission is complex. It incorporates many different emotional and motivational systems, involves at least two physiological systems, neuronal and endocrine, and if the reactions of the recipient animal are considered, stress, fear, helplessness and other psychological states or emotions need to be included. The focus of this section will be primarily on aggression, that is, the behaviour and physiology of an initiator. Submission and the various behavioural and physiological reactions of a recipient will be covered in Section 1.3 on stress and social stress.

Although many brain structures are involved in the genesis and control of aggressive behaviour (e.g., frontal lobe, temporal lobe, hippocampus, thalamus and midbrain structures such as the central gray, the ventral tegmental area, the periaqueductal gray), the limbic system, and especially the hypothalamus and the amygdala, have been the most studied and are thought to be central to the modulation of aggression (Niehoff, 1999; Panksepp, 1982). A wealth of research has been published in neuroscience on the neuroanatomy of fear- or aversion-induced aggression (e.g., Gray, 1987; LeDoux, 1996 for reviews), and irritability- or frustration-induced aggression (e.g., the classic studies of Dollard, Doob, Miller, Mower, & Sears, 1939 and Miller, 1941). There is a trend in the literature towards developing behavioural taxonomies of aggression or, more globally, of agonistic behaviour, that will parallel physiological systems. The hypothalamus, for instance, a specialist in offence and defence (i.e., in initiating and responding to threats or attacks) has two main structures, each specialized in its own type of attack. The ventromedial nucleus is activated during defensive attack and, in animals like the cat, is responsible for growling, hissing and attacking with the claws, whereas the lateral hypothalamic area is activated during direct attacks (e.g., biting) involving no defensive component (Flynn, 1967). Also, low ranking rhesus monkeys (*Macaca mulatta*) become behaviourally dominant if their hypothalamus is electrically stimulated (Robinson, Alexander, & Browne, 1969). The amygdala, the central processor of emotionally charged stimuli (LeDoux, 1996) appears to be essential for the production of an aggressive reaction when the stimulus is perceived as potentially threatening (Potegal, 1994). My focus will now turn towards the biochemistry of aggression.

1.2.2.1 Neurotransmitters

Neurotransmitters play a key role in the biochemistry of aggression. Historically, serotonin (5-HT), dopamine (DA) and norepinephrine (NE) have been identified as the most likely neurotransmitters to modulate aggressive behaviours but more recently, nitric oxide (NO) has also been identified as having a significant role (Nelson, Demas, Huang, Fishman, Dawson, Dawson, & Snyder, 1995). Table 1.6a summarizes the association between each of these neurotransmitters and aggression. Note that the third column includes information on stress and depression. Both are relevant to my discussion on stress and social stress in Section 1.3.

Table 1.6a. Main neurotransmitters involved in aggressive behaviour and their corresponding neural structures.

NEUROTRANSMITTER	STRUCTURE(S) INVOLVED	COMMENTS
Serotonin (5-HT)	Serotonergic system: • Raphé nuclei (caudal, rostral)	• if levels too **low**, then high aggression • low levels also associated with depression • socially isolated mice have low 5-HT levels and become aggressive
Dopamine (DA)	Dopaminergic system: • Substantia nigra • Ventral tegmental area (VTA)	• if levels too **high**, then high aggression • low levels also associated with depression • stress sensitizes the dopaminergic system
Norepinephrine (NE) (noradrenaline)[9]	Noradrenergic system: • Locus ceruleus • Lateral tegmental NE cell system	• if levels too **high** (usually) or too low, then high aggression • low levels also associated with depression • fighting elevates NE levels (Modigh, 1973) • stress sensitizes the noradrenergic system
Nitric oxide (NO)		• aggression in males (mammals) • low levels = high aggression

Note: Information for this table was collated from a number of sources: Archer (1988); Brain and Haug (1992); Conner (1972); Karli (1987); Moyer (1968, 1976); Niehoff, 1999; Rosenzweig, Leiman, and Breedlove (1999); Vincent (1994); Zillmann (1979, 1998).

1.2.2.2 Hormones

Since the literature on neurotransmission and aggression is vast and not the immediate focus of this study I would like to concentrate next on the

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[9] Epinephrine (adrenaline): has a similar effect as NE but mainly at the endocrine (adrenal medulla) level.

endocrinology or neuroendocrinology of aggression. Table 1.6b summarizes the hormones and endocrine glands that have been identified as playing a role in aggressive behaviour.

Table 1.6b. Hormones and glands involved in the modulation and control of aggressive behaviour.

HORMONAL CLASSES	STRUCTURE(S)/HORMONES	COMMENTS
Testosterone and other androgens[10]	**Androgenic system:** • Testes: testosterone, DHT • Adrenal cortex: DHEA and androstenedione	• high levels associated with aggression, aggressiveness, assertiveness
Estrogens and progestogens	• Estradiol (high aggression) • Progesterone (low aggression)	• prominent role in female aggression • estrogens important in birds • anti-estrogens have anti-aggression effects in rats and mice • injections of progesterone reduce irritability (also a treatment of premenstrual syndrome)
Peptide hormones	• endogenous opioids (endorphins) • oxytocin • vasopressin • prolactin • LH	• not as important for modulating aggressive behaviour as much as affiliative and maternal behaviour • endogenous opioids: social grooming and social contact • vasopressin and oxytocin affect DA and 5-HT
Thyroid hormones	• T3, T4, CT	• important in fish
Glucocorticoids	• cortisol • corticosterone	• at least in mammals, in relation to stress, anxiety, fear, and frustration
Melatonin	• Pineal gland	• Responsible for aggressive behaviour independently of modulatory effects on reproductive steroids (*)?

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[10] Testosterone has its effects on behaviour (i.e., aggression), via aromatisation, that is, its conversion to estrogens in the hypothalamus. Schlinger & Callard (1990) argue that the rate of aromatisation explains differences in aggression. In their research with quails, they demonstrated that aromatase activity in the brain correlates with aggressiveness.

Note: The information contained in this table has been extracted from many sources including Becker, Breedlove, and Crews (1992), Becker, Breedlove, Crews, McCarthy (2002), Brown (1994), Nelson (2000) and Svare (1983, 1990).
* Syrian hamsters: Jasnow, Huhman, Bartness, & Demas (2002).

Two classes of hormones will be highlighted for the purpose of this study: androgens and glucocorticoids. The latter will be discussed in much more detail in a subsection of the chapter on stress, Section 1.3.1.6, and not in the context of aggression per se and the former will be considered here exclusively. Both androgens and glucocorticoids are steroid hormones (derived from cholesterol) and produced by the adrenal glands (glucocorticoids and androgens) or gonads (androgens). Both are fairly easy to measure (via radioimmunoassay) in blood, saliva, urine, and faeces.

The role of glucocorticoids in aggressive behaviour, and in behaviour in general, is full of contradictions. As we will see in Section 1.3, there is a substantial body of literature showing that high glucocorticoid levels are associated with submission (including low aggression) and low sexual activity. There are data suggesting, however, that high levels of glucocorticoids (in humans and a number of other species) could play a role in promoting sexual interest and increasing aggression (Zillmann, 1998). The neurophysiology of serotonin and depression hints at that possibility as well: it is known that anxiety is correlated with higher sexual activity in humans and lack of anxiety is correlated with low sexual drive (Niehoff, 1999; Zillmann, 1998). This is supported by the observation that SSRI antidepressants that increase the availability of serotonin at the post-synaptic level or dietary supplementation of 5-HTP (from *Griffonia simplicifolia*)[11] that increases the production of 5-HT (serotonin) usually decrease sexual motivation in humans. In the same vein, if corticosterone (the main glucocorticoid in rodents and birds) is eliminated from the circulation in mice (via adrenalectomy), aggressive behaviours are dramatically reduced (Brain, Nowell, & Wouters, 1972; Harding & Leshner, 1972). A similar connection between glucocorticoids and aggression has been found in primates. Rhesus monkeys (*Macaca mulatta*) with high aggressiveness have high levels of cortisol (the main glucocorticoid in primates and carnivores) metabolites[12] in their urine (Levine, Gordon, Peterson, & Rose, 1970). Even more relevant to our concern with stress and dominance, is Leshner and Candland's (1972) data suggesting that squirrel monkeys (*Saimiri sciureus*) with high urinary cortisol levels attain higher rank in dominance hierarchies than individuals with low urinary cortisol levels. Zillmann (1998) points out that, in these species, high dominance ranking and sexual privileges seem to be highly

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[11] See van Praag (1981, 1984).

correlated with high cortisol levels. He is quick to note that high adrenal activity in general increases both sexual and aggressive behaviours. As mentioned earlier in this section this cannot be generalized to all mammals and baboons, close cousins of *Saimiri sciureus* and *Macaca mulatta*, do not follow that pattern (Sapolsky, 1998).

Of all hormones, androgens have been most strongly associated with aggressive behaviour and aggressiveness. Testosterone (T) and, to a lesser extent, dihydrotestosterone (DHT), have been correlated with aggression and dominance in many mammals. Three main lines of evidence reveal that interdependence. Firstly, sex differences: in almost all species of mammals (with the exception of spotted hyenas, *Crocuta crocuta* and hamsters, genera *Mesocricetus* and *Cricetus*) males are more aggressive then females and have much higher levels of circulating androgens (mainly testosterone) than females. Secondly, seasonal changes: there is, in many social mammals, an increase of aggression during the reproductive season, especially in males. This rise in aggressive and sexual activity parallels the seasonal rise in androgen levels. Thirdly, pubertal changes: androgens peak at puberty in mammals, mainly in males, and

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[12] More precisely, 17-hydroxycorticosteroid, easily measured in urine and often measured to assess adrenal function and diagnose hypoadrenalism or hyperadrenalism in humans and

aggressive acts are known to be on the increase (and sometimes peaking) at puberty. Although the correlational evidence presented above is quite compelling, it is not the full story and exceptions are known to exist (see Nelson, 2000, for a full review).

The next section (Section 1.3) reviews stress, social stress and the role of glucocorticoids. In that section reproductive hormones and reproductive behaviour are discussed in the context of their interdependence with stress (but androgens in wolves will not be discussed until Section 1.4).

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dogs.

1.3 Stress and Social Stress

1.3.1 Overview

This section will deal primarily with the behavioural and physiological dimensions of stress and social stress. The focus will be on mammals, especially carnivores and primates. In the first part of this discussion, I will review the behavioural and physiological definitions of stress. Next, I will discuss the hormones triggered by psychogenic and, more specifically, sociogenic stress. To complete this section, I will describe the general effects of social stress on animal reproductive physiology and behaviour.

1.3.2 Proximate factors: Physiology and behaviour

Hans Selye (1936, 1956, 1993) borrowed the term "stress" from the engineering literature and used it to describe a state of behavioural and physiological unbalance, unease or strain. When applied to the human body and mind, a unified definition of stress is difficult to find. This section addresses some of the conceptual problems behind the definition of stress and discusses stress at the behavioural and physiological level. Questions regarding the functions, adaptive value and possible benefits of stress will be discussed in Section 1.3.2, "Ultimate factors: social stress and population regulation".

1.3.2.1 Definitions and dimensions of stress

The "embryo" of the stress concept can be traced to the French physician-experimentalist Claude Bernard (1813-1878), who described the notion of "Milieu Interne" or internal milieu, and the interaction of that milieu with stimuli from the outside (i.e., the environment). Cannon (1871-1945) developed the concept of homeostasis, referring to the stability of the internal milieu of an organism. He also coined the phrase "fight or flight" to describe the precarious equilibrium of an organism's response to stressful event. Cannon emphasized the universality of the stress response, essentially recognizing only one stress response for any arousing event. For example, he believed that stress manifests itself in very similar ways in both the attacker and the attacked in hostile social interactions. Cannon based most of his conceptualisation of stress on his knowledge of the catecholaminergic system, in particular, the secretion of adrenaline (the main catecholamine involved in the short term stress response; see below) by the medulla of the adrenal gland. Cannon's theory is based on the concept of homeostasis, balance, or equilibrium. As such, it assumes a single optimum. This view is considered to be inadequate in the modern definition of stress, which relies instead on the concept of "allostasis" (McEwen, 1998). If homeostasis is about balance, allostasis is more akin to adaptation. This concept recognizes multiple optima depending on the situation or context, or many possible optimal operating ranges. Allostasis is a process which allows the maintenance or gain of stability (homeostasis) through change.

Hans Selye (1907-1982) is often considered to be the father of the physiology of stress (as mentioned above, he introduced the term stress to the fields of physiology and medicine). Selye (1993) developed the General Adaptation Syndrome model (GAS) in order to explain the effect of the other major class of stress hormones: the glucocorticoids. He also distinguished between eustress or positive stress, usually associated with high performance typical of the adaptation or resistance phase of the GAS and distress or negative stress, usually associated with low or null performance typical of the alarm and exhaustion stages of the GAS (Selye, 1976). This theory dealt mainly with the role of chronic stressors[13] (those which were introduced for long periods of time or very frequently) in the inhibition of anabolic processes. Selye's contribution lays the foundation for the immune system breakdown perspective of stress-induced disease. We will come back to some of these authors and their ideas later (see Section 1.3.2, "Social stress and population regulation"). Selye's

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[13] Selye initially called stressors "nocuous agents" (Selye, 1936).

definition is typically a "response" definition of stress (Beck, 2000); the focus is on the pattern of responses or physical symptoms. In other words, the presence of stress is inferred from the response. This definition ignores the antecedent, trigger, or stress-inducing situation (e.g., danger, noise). A response definition is considered to be more useful to scientific investigation than a "stimulus" definition, which is based on a presumably stressful trigger. The main limitation of the latter is that it is based on the stressed individuals' subjective perception or interpretation of the trigger. This is problematic since a given stimulus may be stressful to one individual, but not to another (Beck, 2000).

John Mason (1975) brought a strong psychological (cognitive) perspective to the definition of stress. Above all, he suggested a strongly multi-dimensional, interactive (Beck, 2000) definition of stress. For Mason, psychological variables can trigger or modulate the response to stressors. He was among the first to argue that two identical stressors can be perceived differently (the perceptual-cognitive aspect) by different individuals and/or in different situations. Unlike some pure stimulus definitions, which define stress only by the presence of a stressful event, Mason's theory recognizes and allows for this kind of variability.

In order to study stress empirically, one also should be aware of three additional dimensions of stress. The first dimension defines stress in terms of the stimulus-response association and pattern. This dimension considers stressful events as either physical or psychogenic; either from the physical environment (e.g., noise, heat, smells, etc.), or from a psychological source (this includes social and emotional stress). This is a critical distinction because modern research often measures one without consideration of the other. A common example would be studying social stress in wild animals without consideration of the potentially stressful weather patterns.

The second dimension distinguishes between internal and external environments or intrinsic versus extrinsic stressors. Once more, many modern studies fail to consider the health, immune integrity or metabolic state of the organisms under investigation, while examining the influence of external factors such as weather. A compromised immune system or metabolism will not respond in the same way to extreme cold weather. The third dimension is a temporal dimension. Stress or stressors can be brief and acute or persistent and chronic. Additional temporal characteristics (e.g., duration, latency, frequency, etc.) of stress and stressors are equally fundamental when the response to stressors is studied.

In summary, stress is not a unitary or one-dimensional concept, contrary to what early authors (e.g., Cannon) believed. This is true both at the physiological and behavioural level. Stress is also a very subjective concept: for a given stressor (with a certain duration, intensity, and frequency), two individuals are likely to have different experiences and react differently to the stressful event. Stress, as an experience, can be seen as having three main components: (1) the feeling or subjective experience, (2) the physiological arousal and its consequences (e.g., shaking, sweating), (3) the actions, or response to the stressful stimulus or situation.

In the next three sub-sections, I will discuss three different aspects of stress: the stressor (stressful stimulus/situation), the responses (behavioural and physiological), and the processing system (or individual).

1.3.2.2 Stressor(s)

The first component, the stressor (or stress stimulus) is simply the collection of situational or contextual factors causing the experienced stress. For species with a high cognitive capacity (such as prospective processing in primates), it should first be determined whether the stressor is current (i.e., experienced "here and now") or anticipated. Then, the following basic temporal characteristics can be extracted from the occurrences of stressful events: the duration of the stressor(s), the frequency of the stressor(s), and the latency between stressors or occurrences of the stressor. These temporal characteristics can be extracted from basic laboratory or field observations, or they can be controlled in a laboratory setting.

To better understand the nature of the stressor, basic situational characteristics can also be identified. Firstly, the intensity of the stressor(s), broadly defined (from the magnitude of an electric shock to the violence of an attack) should be considered. Secondly, the predictability of the stressor(s), which is related to the anticipation mentioned above, can also modulate the impact of the stressor(s). Uncertainty in itself could be defined as an intrinsic stressor and therefore play a major role in the stress level of an individual. Note that predictability is not always a positive factor: knowing too much, too little, too late or too early about a coming stressful event can have a negative impact (Sapolsky, 1998). Also, predictive information on very common or very rare events is simply not useful. It is also important to point out that knowing about a coming stressor does not provide immunization from stress. This fact is unfortunately overlooked by a number of biologists who study social stress (Creel, 2001; Wingfield & Ramenofsky, 1997). Thirdly, controllability (sense of control), before and after coping mechanisms are initiated, is a crucial determinant of the stress response as it influences the subjective experience of stress.

Temporal factors (duration, frequency, intensity) and situational factors (intensity, predictability, controllability) are the most commonly identified variables in the literature. When a study has a social undertone, basic psychosocial and coping characteristics also need to be considered (e.g., Sapolsky, 1998, 2000). Below, five psychosocial characteristics of the stressors are described.

Outlets for frustration, including displacement aggression, have been identified as a very important coping mechanism, notably in primates (Sapolsky, 1998). As far as I know, no data exist on displacement aggression and outlets for frustration in canids.

At the cognitive level, *situational perception*, that is, the cognitive assessment of the situation, is important. This includes the processing of predictive information. This type of processing is known to be common in primates (e.g., Cheney, Seyfarth, & Smuts, 1986; Cheney & Seyfarth, 1990a, 1990b, 1990c) and is likely used, at least at some level, in canids. Again, this concept has not been studied systematically in canids.

Social perception, linked to the concept of social intelligence, is related to the "predictability" of a stressor in the sense that it pertains to the correct assessment of the threat and an accurate evaluation of the outcomes of a social interaction. As will be discussed later, it seems that some wolves may have problems evaluating outcomes and/or threats accurately.

Social affiliation (or support) is another important factor in social species: having friends and allies for play and grooming positively impacts stress levels in primates (Keverne, 1992; Keverne, Martensz, & Tuite, 1989). For instance, social isolation is stressful as the large body of literature on "separation anxiety" in primates demonstrates (e.g., Berman, Rasmussen, & Suomi, 1994; Harlow, 1958; Harlow & Zimmerman, 1959; Suomi, 1984, 1991). It is important to note here that being in a hostile, strange or crowded environment can be very stressful as well (see Section 1.3.3 on the ultimate factors). Other coping strategies using social affiliations include a species-specific array of reconciliatory behaviours (see Aureli & de Waal, 2000 for a comprehensive review with primates; this is another neglected area of research in canids). The formation of strategic affiliations (coalitions or alliances) is an issue discussed in chapter 1.2 on agonistic behaviour and again, is not as well understood in canids as in primates.

The final factor is very important and basically adds the "social" to the controllability factor discussed above: *social control.* Tightly linked to the concept of learned helplessness and depression, social control seems to be at the basis of chronic social stress (Sapolsky, 1998). As proposed by Sapolsky, the perception of control is as important as the actual amount of control over social interactions. Despite the fact that an animal may involve itself in violent (in principle, stressful) interactions, if it initiates the aggression and the outcome is under its control, it may not perceive the situation as stressful. A frequently losing subordinate animal who never initiates the fights may, in contrast, suffer from high levels of stress. This last comment stresses the importance of actual versus perceived control.

Rothbaum, Weisz, and Snyder (1982) differentiated between primary and secondary control. In primary control, an individual tries to control the situation or stressful events (an "active" disposition) as opposed to secondary control when the individual merely tries to adjust to the situation or stressful events (a "passive" disposition). Secondary control includes failure (acceptance of failure), since it can become a predictable outcome. Control should be seen as an adaptive response that lies on a continuum between these two extremes.

1.3.2.3 Response(s)

The second component, the stress responses (behavioural and physiological) is highly interdependent with the processing system factors described below. We can distinguish between the short term responses, that is, immediate autonomic responses and the long term responses (including disease, coping, etc.). Individual variables (personality and demographics) apply here as well. Responses can be defined and measured very much like stressors: their duration, intensity, latencies and frequency can be monitored (depending on the methods used and systems targeted) but again, personality and individuality are strong modulators of the responses. For example, Lacey and Lacey (1970) used autonomic responses to evaluate emotions and arousal. They found that psychophysiological measures do not discriminate well between emotions (including types of arousal or stress such as "positive" and "negative" stress), but that they do discriminate very well between individuals. Lacey and Lacey called these differential patterns or Individual Response Stereotypies or IRS's.

For example, for a given stimulus, some individuals respond with heart rate changes, others with gastric contractions, and others with blood pressure fluctuations. Even more interesting, these patterns are very consistent throughout development.

1.3.2.4 Individual(s)

The third component is the processing system or processing organism. This component recognizes that the individual is not a passive receptor of stimuli and events, and that it actually cognitively assesses the subjective feeling of stress and the stressful situation. As in the context of agonistic interactions, an animal is also an information processor and decision maker with its own cognitive abilities and limitations. Perceptions of threat and perceptions of control (over the situation) are the first cognitive steps that can be identified. Following this initial processing of the stimulus/event, the animal may have to assess or evaluate the situation, as well as the options, in more detail. The animal becomes a decision maker and a potential intelligent user of coping resources. It is important to note that the efficiency of these perceptual-cognitive factors depends on the somatic integrity of the animal's nervous, endocrine and immune systems. The concept of individuality is essential to any discussion of the organism as a processing system. This refers to individual differences and their expression in the "processing" of the stress response (i.e., perception of threat) and the responses, behavioural or physiological.

The study of personality in stress research is now gaining attention from the scientific community. For example, Sapolsky's classic book on stress ("Why Zebras Don't get Ulcers"; Sapolsky, 1998) introduces, in the second edition (5 years after the first), a full chapter on personality. Both components of personality, temperament (dispositional, hereditary factors) and character (from learning, experience, environment)[14], are necessary to understand an individual's processing style and efficiency (more on this later). Demographic data are also relevant in the understanding of the stress response. The sex, age and social status of the animal can influence its sensitivity to the perception of threat. For example, in the context of social status in baboons, the stress hormone cortisol has a prolonged increase in subordinates and testosterone levels recover faster in dominant animals (Sapolsky, 1991a, 1991b, 1992, 1998).

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[14] Breaking down personality into "temperament" and "character" is a common practice in psychology as well as other behavioural sciences, for example: Cloninger, 1994 & Sapolsky, 1998.

At the core of the literature on human stress, is the question of individuality, introduced earlier with Lacey and Lacey's (1970) concept of Individual Response Stereotypies (Section 1.3.2.3). The literature on the psychobiology of personality and, more specifically, temperament has a lot to offer here. I will now provide a general overview of the concepts as they are relevant to animal behaviour.

The concept of animal personality or more precisely, animal temperament, is certainly a useful framework to explain individual differences. Pavlov (1955) had a typology of the dogs nervous system based on their activity-reactivity to stimuli and their conditionability, that is, how easy or difficult they were to classically condition. He distinguished between two main types of nervous systems or temperaments in dogs: weak (the "melancholic" dogs) and strong. The latter was divided in two subtypes: unbalanced (the "choleric" dogs) and balanced. Within the balanced type, Pavlov identified two further sub-types: mobile (the "sanguine" type) and slow (the "phlegmatic" type). Interestingly, about 100 years ago this physiologist identified four types of dogs based on the "strength" of their immune system, using a terminology put forward by the Ancient Greeks (Galen, Hippocrates). Even today, these terms are used or at least referred to by a number of personality theorists with a biological bent.

Pavlov's "temperament theory" has been revised and extended by a few authors (Gray, 1964, 1972 a & b; Nebylitsyn, 1972; Strelau, 1972, 1983 a & b; 1987) and some, such as Gray, gave it an "Eysenckian" flavour, using extroversion and introversion concepts as one dimension. Gray's and Strelau's theories are applied to humans and can be classified as "biological theories of human personality" or, in a more precise and less ambitious label, "neuroendocrine models of temperaments"[15].

The literature on animal temperament (or personality) is in its infancy. In the fifties, a few authors risked the suggestion that animals, like humans, have personalities. For example, Diamond (1957), in his book "Personality and Temperament" reserves a full chapter for cats and dogs and uses Pavlovian terminology as a base for his discussion. Later, many saw the pressing need to discuss individual differences in highly social carnivores and primates and began to use terms such as temperament and personality, often under the guise of the study of emotions (e.g., Plutchik, 1980). The canine literature followed Diamond's initiative (e.g., Scott & Fuller, 1965) and more specifically, wolf

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[15] Many other authors could be mentioned here. Eysenck, Gray, Kagan, Plutchik and Zuckerman are five obvious figures in the psychobiology of temperament applied to humans or sub-human primates. Because of Pavlov's influence, numerous Russian and Polish authors

specialists started using the term: Fentress (1967), Mech (1970), Woolpy and Ginsburg (1967). More recently, the domestic cat received similar attention (Feaver, Mendl, & Bateson, 1986; Mendl & Harcourt, 1988), as did other highly social carnivores such as spotted hyenas, *Crocuta crocuta* (Gosling, 1998). Sapolsky (1991a & b, 1998, 2000) uses the term regularly (with baboons) and as suggested in this text, there seems to be no doubt that there is variation in temperament in social primates and carnivores.

Sociobiologists would agree that the degree of heterogeneity of individual differences (personalities) in a species is associated with the degree of sociality. Section 1.4.5 will discuss some dimensions of this issue with canids. As a partial preview, Fox (1975) divided social wild canids into three categories, based on the species' social arrangements. Type I includes the Red Fox (*Vulpes vulpes*) and most fox-like canids. Type I animals have "transient families" where pairs are formed for sexual activity (courtship and mating) and parental care (usually including some paternal care). Type II includes mid-size canids such as the four jackal species and coyotes (*Canis latrans*). This type is characterised by temporary families, based on a permanent pair and in some cases a social grouping (pack-

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could be mentioned, for example, Nebylitsyn, Sechenov and Teplov (see Strelau's references for review).

like structure). Type III includes the wolf (*Canis lupus*), the African or Cape Hunting dog (*Lycaon pictus*), and the Dhole (*Cuon alpinus*). This last type represents the ultimate social sophistication among carnivores, typified by the extended-family pack structure. Fox (1975) links these different social structures to individual differences in terms of temperamental diversity. Wolves are defined as polymorphic, that is, having high heterogeneity of temperament. Foxes are defined as monomorphic because of the homogeneity of their temperaments. Coyotes are oligomorphic, or somewhere in between the wolves' heterogeneity and the foxes' homogeneity.

This typology seems very relevant to a discussion of stress and social stress. A similar classification could be applied to other highly social mammals in stress studies which tried to account for the variability of the stress-responses, the social perception of threat, and the differentiability in hormonal fluctuations between individuals of the same social status or rank.

1.3.3 Stress hormones: Glucocorticoids and catecholamines

The hormones I am going to refer to in this sub-section are often labelled "stress hormones" (mainly adrenal hormones) because they characteristically are released in response to stressful situations (although not necessarily at the same rate, amount, or following the same physiological processes). Because these hormones are produced under stress, they are often used in psychoendocrinology and behavioural endocrinology research to assess stress (McKinnon, Baum, & Morokoff, 1988; Wagner, 1988). Hormones and hormone metabolites can be extracted from plasma, urine, saliva or faeces (Brown, 1994; c.f., Kirschbaum & Hellhammer, 1994 for a review of salivary cortisol).

The two main categories of stress hormones usually recognized are the steroid hormones and the catecholamines. An important difference between these two types is the pathway of neuroendocrine activation. The hypothalamic-pituitary-adrenal (HPA) axis is the path taken by the steroid hormones and the autonomic nervous system (ANS) is the path taken by the catecholamines.

It should be noted at this point that the endocrine response to stress is not limited to the catecholamines or the adrenal steroids. Prolactin (PRL), growth hormone (GH; also called somatotropin or somatotropic hormone), β-endorphins and vasopressin (also called antidiuretic hormone or ADH) are also responsive to intense, novel, unexpected or frightening stimuli. All of the above and the pancreatic hormone glucagon are released in greater amounts following a stressor. According to Meltzer and Lowy (1986), after adrenal steroids and catecholamines, GH levels are the most likely to increase in humans during stressful events, followed by prolactin levels.

All stress hormones affect the adrenal response in one way or another (biochemically or even structurally); the difference resides mainly in the processes involved, the biochemical structure of the hormone and the specific area of the adrenal gland involved in the process. The following details have been gathered primarily from Becker, Breedlove, and Crews (1992), Becker, Breedlove, Crews, and McCarthy (2002), Brown (1994), Levine, Coe and Wiener (1989), Clarke (1978), Greenspan and Strewler (1997), Nelson (2000), and Sapolsky (1992, 1998).

Steroid hormones can be divided, at the behavioural level, into two main classes: the sex or gonadal steroids and the stress or adrenal steroids[16]. This categorisation in itself strongly suggests a link between stress and sexual behaviour. This has already been suggested and discussed in Section 1.2.2.2 and has been extensively covered by Zillmann's (1998) appropriately entitled book "Connections between sexuality and aggression".

The adrenal cortex secretes three types of steroid hormones: adrenal steroids or corticosteroids, including mineralocorticoids (from the zona glomerulosa of the adrenal gland, mainly aldosterone[17]) and glucocorticoids (from the zona fasciculata and zona reticularis). Glucocorticoids will be the focus here, particularly cortisol (also called hydrocortisone) as it is the main stress hormone in primates (including humans) and carnivores. Corticosterone is its counterpart in rodents. All mammals produce both, but the dominance of one over the other seems to be species-specific.

The other steroids, the sex or gonadal steroids have already been reviewed in 1.2.2.2. These include androgens (mainly testosterone, dihydrotestosterone, androstenedione), estrogens (estrone, estradiol, estriol) and progestins (progesterone and pregnenolone).

All steroid hormones are synthesized from cholesterol in the adrenal cortex and gonads and ACTH (adrenocorticotropic hormone) stimulates steroidogenesis in the adrenal gland. ACTH is a polypeptide produced by the anterior pituitary (adenohypophysis) and it is considered a tropic hormone (i.e.,

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[16] This dichotomy is somewhat of a simplification as adrenal glands produce sex steroids as well: androstenedione and dehydroepiandrosterone or DHEA.

it stimulates the secretion of hormones by other endocrine glands). In this case, ACTH controls the production and release of hormones of the adrenal cortex. Following the processing of a stressor by the hypothalamus, ACTH causes the release of corticosteroid hormones from the adrenal cortex. This sequence of events allows the organism to react, but mainly to recover from, a stressful event since both glucocorticoids (cortisol and corticosterone) are involved in glucose metabolism. In fact, if the sequence is examined in more detail, the timing and amount of each hormone (CRH, ACTH, cortisol or corticosterone) can be indicative of which state the organism is in, that is, either at the beginning of a stress response, in the middle of a high stress period or in recovery. If CRH and ACTH are high, and cortisol is low, it can be concluded that the organism is just starting to respond to the stressor. If CRF, ACTH and cortisol are simultaneously high, it can be concluded that the organism is highly stressed. If cortisol is high but CRF and ACTH are low, it can be concluded that the organism is in a recovery period. This last state (high cortisol in recovery) could suggest that cortisol is more indicative of recovery than stress

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[17] Aldosterone production is primarily controlled by the renin-angiotensin system; this hormone will not be mentioned again.

per se (unless it simply indicates that the organism is slow to respond to the termination of the stressor).

With prolonged stress, these hormonal responses can eventually suppress the immune response to possible pathogens. Very intense or prolonged stress can severely suppress the immune system and cause the individual to develop disease (Stein & Miller, 1993). Chronic corticosteroid secretions can induce shrinking of the thymus, atrophy of the lymph nodes, and inhibition of the inflammatory reaction (Selye, 1993).

ACTH is also highly sensitive to circadian rhythms (because it is under hypothalamic control and processing): this has to be taken into consideration when measures of ACTH-dependent hormones are taken. Concern about the timing of measures also applies to gonadal steroids because circannual rhythms impact on the reproductive physiology of all mammals.

The full sequence, from the exposure to the stressful stimulus to the stress response itself, consists of a number of steps: Upon the presentation of a stressor to an organism, an activation of nerve cells in the hypothalamus or of nerve endings in the median eminence takes place and CRH (corticotrophin or corticotrop[h]ic releasing hormone) is secreted to act on the pituitary. The CRH being released from the hypothalamus (within seconds following the presentation of the stressor) will induce the secretion of ACTH (adrenocorticotrophic hormone) from the anterior pituitary gland (roughly 15 seconds later; Sapolsky, 1992). In some cases, vasopressin and oxytocin (two neurohypophyseal or posterior pituitary hormones) will be produced by the hypothalamus concurrently with CRH but unlike CRH, their secretion is much more stimulus-specific and is not mandatory. A few minutes after ACTH reaches the adrenal cortex, a secretion of glucocorticoids (cortisol and corticosterone) is triggered. What follows is a process called gluconeogenesis which will supply a source of energy for an adaptive reaction to the stressor. During that process, stress hormones and glucagon stimulate the liver to convert fatty acids and amino acids into glucose.

If there is a surplus of ACTH, a feedback loop returns to the hypothalamus-pituitary axis and stops the production of ACTH. This feedback process can act directly on the anterior pituitary gland but is more likely to act on the median eminence of the central nervous system (CNS; Clarke, 1978). Endorphins, very similar to ACTH in biochemical structure, will also be produced under very intense stress and can help to suppress the sensation of pain. This is an excellent short term effect when, for example, an animal is engaged in a fight and is badly injured.

None of these feedback mechanisms would be possible without the corresponding glucocorticoid receptors. Glucocorticoids bind to two types of receptors in the brain (Brown, 1994; Greenspan & Strewler, 1997; Nelson, 2000; Williams, 2002): Type I receptors (also called "mineralocorticoid receptors" despite their high affinity for cortisol and corticosterone) and type II receptors (also called "glucocorticoid receptors" with low affinity for cortisol and corticosterone but high affinity for exogenous glucocorticoids). Type I receptors are found in high density in the limbic system, mainly in the hippocampus, amygdala, and septum, and in a number of other brain areas in lower densities, including the anterior pituitary. Type I receptors tend to be occupied when glucocorticoid levels are at baseline, that is, relatively low. Type II receptors are found mainly in the hypothalamus and the anterior pituitary. Type II receptors are occupied only when glucocorticoid levels are high after stress and they play a major negative feedback role in the endocrine system during stress.

A discussion of the endocrinology of stress would not be complete without mentioning the catecholamines. The adrenal medulla secretes two hormones that are also secreted in the brain as neurotransmitters via the sympathetic branch of the autonomic nervous system. With dopamine, they are classified as catecholamines and include adrenaline (or epinephrine) and noradrenaline (or norepinephrine). Both are synthesized from tyrosine (an amino acid) in the adrenal medulla. Catecholamines are biogenic amines or monoamines like the indoleamines (such as the neurotransmitter serotonin, already mentioned in Section 1.2.2.1 and the hormone melatonin).

Both epinephrine and norepinephrine are used by adrenergic synapses in the brain as neurotransmitters. Epinephrine is also synthesized and stored in large granules by chromaffin cells of the adrenal medulla (granules that store and release peptides such as enkephalins; Scheller & Hall, 1992), to be eventually released as a hormone in the bloodstream. Norepinephrine is considered to be a sympathetic neurotransmitter because it is synthesized and stored in sympathetic nerve terminals and is released upon stimulation of the sympathetic nerves (Levitan & Kaczmarek, 1991).

The difference between catecholamines and glucocorticoids is that neural activity caused by a stressor can directly provoke the adrenal gland, via a swift stimulation of the sympathetic branch of the autonomic nervous system, and thus a faster response to the noxious stimulus. Therefore, the release of adrenaline takes less time than the complex chain of event that leads to the release of glucocorticoids (a few seconds at the most; by the time CRH is secreted in the anterior pituitary, the adrenal medulla is already activated). This means that glucocorticoids are more involved in the second phase of reactions to the stressor; they act as homeostatic/allostatic agents and contribute mainly to the recovery process.

Catecholamines are discussed here because their biosynthesis is greatly influenced by glucocorticoids: in fact, tyrosine hydroxylase (TH), the base of catecholamine production, is affected by the glucocorticoid production from the adrenal cortex. Dopamine-β-hydroxylase (DBH), another important enzyme in the synthesis of catecholamines from tyrosine is also influenced by glucocorticoids. Finally, Phenylethanolamine-N-methyltransferase (PNMT), an enzyme that converts noradrenaline to adrenaline is also regulated by glucocorticoid secretion (Cooper, Bloom, & Roth, 1991; Gray, 1987; Levitan & Kaczmarek, 1991).

Because the catecholamines involve the activation of the sympathetic branch of the autonomous nervous system, it is only logical that the parasympathetic system will be inhibited by stress. This inhibition will affect the reproductive behaviour and physiology of the organism. The next section will discuss this process in more detail.

1.3.4 Reproductive inhibition and suppression

The effects of stress on the brain and behaviour have been widely investigated and discussed in the literature over the past 20 years (Bronson, 1989; Gray, 1987; Henry, 1977; Henry, 1986; McEwen & Mendelson, 1993; Selye, 1976, 1993; Stein & Miller, 1993 to name only a few reviews). Anatomical structures known to be crucial in the processing of cognitive stimuli and information appear to be very sensitive to stress and could be significantly damaged under chronic or long term stress. The hippocampus is an example of one of these structures (Sapolsky, Krey, & McEwen, 1985 and Sapolsky 1986 a & b, 1990 a & b). Serious damage to the hippocampus would likely impair important cognitive functions such as memory and learning.

Stress seems to be a means of reproductive inhibition in many species and may be an important part of population control in gregarious and social mammals (Bronson, 1987, 1989; Christian, 1980; Desportes, 1979; Sapolsky, 1987). The literature on population control and population regulation is abundant and it will be only briefly reviewed here. It is through this link that behavioural neuroendocrinology merges strongly with behavioural ecology and population biology/ecology.

Other hormones not discussed previously but relevant to this discussion include mainly the gonadotropic hormones (from the pars distalis of the pituitary gland). Below, a short description of the function of each of these hormones in the reproductive (and parental) behaviour of most mammals will highlight their importance in the reproductive success of an individual or species.

Firstly, LH (luteinizing hormone) stimulates ovulation and progesterone secretion in females and stimulates androgen secretion in males. Secondly, FSH (follicle stimulating hormone) stimulates growth of the primary follicle and estrogen secretion in females; it also regulates sperm production in the testes of males. Thirdly, PRL (prolactin) inhibits sexual behaviour and facilitates parental behaviour in part by modulating catecholamine levels. Finally, we have to add the gonadal or sex steroids produced by the gonads, the gonadotropin releasing hormone (GnRH) and insulin, a pancreatic hormone and "counterpart" of glucagon.

Many factors have to be taken into consideration when looking at the phenomenon of reproductive inhibition or suppression[18]. We have to distinguish between behavioural, social and environmental factors as well as the complex interplay among each of these factors. On the physiological-behavioural dimension, as I already discussed, individual differences are to be taken into consideration: personality and temperament (see above, Section 1.3.2.4), activity-reactivity differences (e.g., Gray, 1987) or social status and dominance (Drews, 1993; Sapolsky, 1987, 1991 a & b, 1992).

An increase in population density or a reduction in food resource are known to inhibit reproductive behaviour or at least reproductive success (Bronson, 1987; Christian, 1980; McClintock, 1987). These two variables are the main environmental factors investigated in population biology/ecology. The influence of climatic variations and weather fluctuations incites behavioural ecologists to turn towards the study of biorhythms, biometeorology, environmental physiology and physiological ecology.

At a purely behavioural level, sociobiologists and socioecologists (Crook, 1989) are the main initiators of the investigation of social regulation of populations. With this approach, new expressions are born such as social contraception, social castration; the role of social stress in sexual or reproductive inhibition appears to be increasingly obvious (Dunbar, 1988). The following authors contributed to this literature by their research on primates: Abbott (1984, 1989), Keverne (1992), and Sapolsky (1982, 1987, 1992). Similar observations are suspected in many social carnivores such as wolves (Derix, Van Hoof, DeVries, & Wensing, 1993; Packard & Mech, 1980; Packard, Mech, & Seal, 1983; Packard, Seal, Mech, & Plotka, 1985; Packard, 1989; Peterson, Woolington, & Bailey, 1984; Zimen, 1975, 1976, 1982), silver-backed jackals (Moelhman, 1983), and dwarf mongoose (Rood, 1980). Section 1.4.6 discusses some of these studies in more detail, with a focus on reproductive suppression in canids specifically.

Dominance hierarchies are seen as a major factor in psychogenic or sociogenic stress. Social subordination seems to have the potential to inhibit ovulation in female primates and social canids. Some evidence discussed in the

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[18] The term inhibition is used here in reference to a partial suppression of reproductive ability. Suppression refers to a total block of reproductive ability.

next section points towards the idea that social subordination can induce psychological castration in male social canids by significantly reducing testosterone production. In females, the means of inhibition are numerous. Because of CRH and β-endorphin activity during stress, GnRH production is inhibited, creating a decrease in LH and FSH production, due to the inhibitory action of raising levels of glucocorticoids and prolactin. This chain of events will inhibit the production of estrogens and progesterone (and even activate the secretion of androgens in females of some species). Low levels of progesterone and high levels of prolactin will prevent the egg from implanting into an appropriate uterine wall (if the egg is even viable at this point). Abbott (1989) found that high levels of plasma cortisol or prolactin were not responsible for the ovarian failure of the female marmoset monkey. Ovulation suppression was apparently due to low GnRH secretions from the hypothalamus. This is a cautionary note: cortisol cannot be blamed for all cases of reproductive inhibition or suppression in primates or carnivores.

Similar processes to the one described above are hypothesized as responsible for the male decrease in sperm production and testosterone production. A more mechanical disruption of male sexual behaviour is caused by the activity of catecholamines and their inhibition of the parasympathetic processes, which is translated into the absence of erection. This an important consequence of persistent and intense stress such as could be experienced by a low-ranking male in a dominance hierarchy. If erection ever takes place, premature ejaculation is likely to occur (Sapolsky, 1994, 1998).

The data concerning social stress induced by dominance hierarchies is still inconclusive and incomplete. As noted by Sapolsky (1992), dominant primate males sometimes show more signs of stress than subdominants, although, as a general rule, the highest ranking animals have the most efficient stress responses. Other signs of stress in subordinate animals include the size of their adrenals (a stressed animal would have enlarged adrenals) and their activity-reactivity levels (i.e., their rate of physiological response to threatening stimuli).

According to Sapolsky, important factors in the interplay between social stress and dominance hierarchies include the stability of the dominance hierarchy, styles of dominance (heavily based on the "personality" of the leader or leaders; also discussed by de Waal, 1989) and social-cognitive factors (discussed in Section 1.3.2). I use the term "social-cognitive" (not used by Sapolsky) to refer to Seyfarth and Cheney's (Cheney, Seyfarth, & Smuts, 1986; Cheney & Seyfarth, 1990a, b & c) phenomenal work on the cognitive aspects of primate social behaviour. As mentioned in earlier sections, social perception including the perception of threat from others is a crucial factor in the survival of subordinate animals combined with the ability of predicting stressful events. Although many primatologists are referring, implicitly or explicitly, to a primate social cognition (e.g., Bernard Chapais, R. I. M. Dunbar, H. F. Harlow, Sandy Harcourt, Robert Hinde, Hans Kummer, David Premack, to name only a few), the same trend has not been observed among canid specialists to discuss the social life of canids.

1.4 Reproductive Suppression and Social Stress in Canids in Relation to Social and Mating Systems

1.4.1 Overview

This section examines issues that are at the centre of my research on social stress and aggression in wolves. Now that both aggression and stress have been reviewed, these concepts will be applied to the species under scrutiny and discussed in the context of reproductive suppression. In this section, the stress of conflictual social interactions (aggression) will be discussed as a potential factor modulating reproductive suppression in canids and wolves in particular. Since the only other canid species studied in this framework to date is the African Wild Dog (*Lycaon pictus* [19]), a comparative analysis of the wolf and lycaon will be presented.

Prior to looking at these two species specifically, I will review the social and reproductive life of canids in general. This broader view will provide an important context for understanding how stress influences the social dynamic (including dominance, agonistic and affiliative interactions), how the social

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[19] The name lycaon, from the genus, will be used from now on to avoid confusion with the Indian wild dog or dhole and other "wild dog" appellations often used for large canids.

dynamic influences stress levels, and how these proximate mechanisms define the mating and social systems of canids.

I will first introduce the major mating system in canids (monogamy) and discuss the related matters of cooperative breeding, paternal care and alloparental care. I will argue that the latter two clusters of behaviours are important although often overlooked parameters in the reproductive and social life of canids, as well as major barometers of sociality in mammals. As mentioned above, a species by species review of social and reproductive organisation in canids will be presented followed by a comparative analysis of the relevant life history of wolves and lycaons.

1.4.2 Monogamy

Relatively few species of mammals, about 3% to 5% (e.g., beavers, a few species of *Peromyscus* mice and *Microtus* voles) are known for their monogamous tendencies [for a broad review of monogamy in mammals see Carter & Roberts (1997), Clutton-Brock (1989), Dewsbury (1988), Kleiman (1977), Packard (1989), and Solomon & Getz (1997)]. It is well known in the scientific literature (Asa, 1997; Asa & Valdespino, 1998; Bekoff, Daniels, & Gittleman, 1984; Clutton-Brock, 1989; Kleiman 1967, 1977; Kleiman & Eisenberg, 1973; Kleiman & Malcolm, 1981; Malcolm, 1985) that canids are exceptional among carnivores as the whole family has a strong bias towards monogamy. It should be noted however that uncertainties remain for some South American species (Table 1 of Appendix A will detail that information) and that there are numerous debates about the extent of the monogamous relationships.

Some other families of carnivores also have strong monogamous tendencies (the sub-family Herpestinae in Viverrids, some Mustelids), but do not necessarily adopt the family unit found in most canids (i.e., immediate or extended family groups). This is a critical distinction as it is preferable to compare species that share similar social and reproductive characteristics. It is reasonable to expect that the mechanisms underlying monogamy in these other carnivores (Viverrids & Mustelids) may not be comparable to the ones identified in canids.

The family structure (social system) found in canids is based on their mating system (monogamy), the role of the parents (parental care, especially paternal care) and the role of the other members of the social unit in the context of reproduction (alloparental care). As we will see later, the canid literature often mentions reproductive suppression of subordinate individuals as a defining characteristic of the family (as a social unit... and as a taxon)[20]. Monogamy should be an easily defined term with a high consensus among the researchers who study mating systems. The reality does not reflect this, as definitions vary considerably. Achieving a consensus is particularly important since most definitions of polygamy (polygyny or polyandry), polygynandry[21], and promiscuity[22] rely on the definition of monogamy as a point of reference.

One criterion that most mammalogists use to define a monogamous species is the presence or absence of sexual dimorphism (Kleiman, 1977). In monogamous mammals, the sexes are more likely to have equal body size, maturation rate and reproductive variance. That is, there is relatively little or no sexual dimorphism in monogamous mammals, whereas the opposite is true of polyandrous and polygynous species. Although this criterion is a fairly reliable one, sexual dimorphism does not impact directly on the social structure and social dynamics of a species. The focus here will be on other criteria of monogamy which do.

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[20] Reproductive suppression combined with monogamy, paternal care and alloparental care is also found in primates, almost exclusively in the South American Callitrichidae family composed of marmosets and tamarins.

[21] The strict definition does not include the promiscuous system and describes polygynous males with polyandrous females in a *non-random* choice of partners.

Among the most commonly applied criteria is the number of sexual partners in time, a criterion often labelled "exclusivity of mating" (e.g., Dewsbury, 1988) or copulatory exclusivity. Although most would agree that having more than one sexual partner at a time is not permissible within the usual definition of monogamy, many accept predilection and fondness without the requirement of unbreakable commitment as a measure of monogamy. Carter (e.g., Carter & Roberts, 1997) makes a strong case that monogamy is only a *preference* for a partner, and that both males and females of many “monogamous” species can be quite opportunistic. This looser definition leaves room for gallivanting (i.e., a certain number of indiscretions or infidelities), as is observed among the "monogamous" female voles studied by Carter. The other extreme is superfaithfulness often observed in birds. For example, when a greylag goose loses his or her partner, he/she will show reluctance to pair again with another individual (Lorenz, 1982). In between lies the concept of serial monogamy. For example, a red fox (*Vulpes vulpes*) may change partners every breeding season, but each year is fully committed to the partner he/she is (temporarily) bonding with.

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[22] Both sexes with multiple partners with random or at least opportunistic choice.

Another popular set of criteria considers the nature of the association and interactions within the bond, such as spatial proximity (shared home range or territory, joint denning, joint travel), frequency of interactions, and duration of interactions. Once more, from the superfaithfulness of the geese to the copulatory-restricted bond of the orang-utans (*Pongo pygmaeus*), species fall along a broad continuum.

The next criterion is not included in the more general mammalian definitions of monogamy but is quite often used to define monogamy in canids. The degree of care for offspring by both parents (biparental care) and, in some cases, alloparents, is a distinguishing characteristic of monogamy in canids. As a rule, monogamous males should invest more time in their offspring than non-monogamous ones because their paternity is, in principle, almost guaranteed. Furthermore, many monogamous species are alloparental, or, as we will discuss later, cooperative breeders (i.e., the whole family unit is involved in the care of the young). There are some exceptions, as not all monogamous species are involved in paternal (e.g., orang-utan) or alloparental care and a number of polygynous species (e.g., Indian langurs) will provide paternal care.

There are a few additional criteria used by some authors (e.g., Dewsbury, 1981, 1988; Kleiman, 1977; Mendoza & Mason, 1986) that apply to species at the high end of the sociality continuum, and to species forming extended family groups, such as wolves or lycaons. Monogamous species adopting the "immediate family" system (parents, offspring of the year) or "extended family" system (parents, offspring of the year, offspring from previous years, up to a few generations in some species) will also tend to show: 1) exclusion of strangers from the family group, including serious inter-group competition and aggression (this is the case in wolves, see Mech, 1970); 2) reproductive suppression of non-breeding individuals (the helpers) or subordinates (when a dominance hierarchy exists)[23]; and finally, 3) incest avoidance (although this is not always clear in some canid species when dispersal is limited by environmental factors or with captive animals).

To summarize, with monogamous species, especially species for which monogamy also delineates a social system, and species that tend to form families (immediate or extended), six main patterns of behaviour are possible which all contribute to the definition of monogamy: exclusivity of mating, a durable and cohesive pair bond, biparental care, segregation from strangers, reproductive suppression and incest avoidance. The last two patterns are more likely to apply to highly social species (e.g., extended family groups, such as a

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[23] Ecological and climatological conditions could mediate the suppression to some extent.

pack of wolves or lycaons), and all may have noticeable exceptions or be observed between species in various degrees.

After outlining the criteria by which monogamy can be defined, we can now take a closer look at the categories within monogamy. Some of the existing taxonomies and corresponding terminology are readily applicable to canids and will provide a structure for a comparative analysis of different species. Among sociobiologists one of the most accepted categorizations of monogamy belongs to Wittenberger (1979, 1981). Using two dimensions (temporal and spatial), Wittenberger allows for a fairly flexible system. Below, Table 1.7 summarizes Wittenberger's taxonomy of monogamy with canid examples when appropriate.

Table 1.7. Wittenberger's taxonomy of monogamy.

SPATIAL CLASSIFICATION
Territorial: Territorial monogamy is dependent on the territorial and home range configuration of the pair. If a female is adjacent or within the male's territory, then pairing is likely. Ultimately, the monogamous pair shares a common territory. This type is more common in felids in cases of permanent or temporary territory overlaps.
Female-defence: The male defends access to a female instead of defending a territory. Strictly speaking this type is not found in canids, although it is included in the next type, "dominance-based" monogamy.
Dominance-based: Dominant females restrict the behaviour of subordinate females and prevent these subordinates from pairing with the dominant male. This is typical of the most social canids such as in *Canis*, *Cuon*, *Lycaon* and *Speothos* as well as some less social species ("Grade II" species, defined below).
TEMPORAL CLASSIFICATION
Serial: The sexual partner may change from season to season. Technically, all canids fall in this category as they all can potentially change partners, but it is more typical of and more frequent among some vulpines.
Permanent: Bonding is permanent, as in for life, at least in principle. In some species, the permanence can end if reproductive failures occur. This is possible in most species of canids in the "Grade III" group described below, such as wolves, lycaons and dholes.

Kleiman (1977, 1981) proposes a simple system differentiating facultative monogamy and obligate monogamy, acknowledging the flexibility and variation in the monogamy found in mammals. As Carter proposes (e.g., Carter & Roberts, 1997), the rules governing monogamy are not rigid, as both males and females will be opportunistic if other potential partners happen to show up at the right time and the right place. In Kleiman's facultative monogamy, paternal investment can be low, the pair association can be quite loose and flexible and occasional polygyny occurs. Facultative monogamy is typical of many canid species, including many vulpines or fox-like canids. In contrast, in obligate monogamy, the association between male and female is more cohesive, paternal care is common, and extrapair mating is relatively rare. Canines or dog-like canids such as wolves and lycaons are more likely to fall into this classification.

Overlapping with Kleiman's but inspired by Fox' (1975) taxonomy of social systems in canids, Poole (1985) offers a taxonomy composed of three grades: Grade I for relatively solitary species forming transient families, Grade II for species forming temporary families and Grade III for species forming permanent families (in canids, this refers to the pack structure). Note that Grades I and II correspond to Kleiman's facultative monogamy, and Grade III to obligate monogamy (see Table 1.9). Poole's grading system will be relevant to the later discussion on the reproductive and social organization of canids.[24]

1.4.3 Cooperative breeding

Cooperative breeding (also referred to as communal care and communal breeding, see Solomon & French, 1997 a & b) usually defines a system in which

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[24] Two other taxonomies that can contribute to the understanding of the mating system of canids are Wickler and Seibt's (1981), recognizing mutual, enforced and circumstantial monogamy (the latter is equivalent to Kleiman's facultative monogamy) and Brown's (1975) almost "botanical" taxonomy based on the duration of the pair bond: perennial, seasonal and serial monogamy.

individuals of a group help to raise young that are not their own progeny (although they may be related to them and, in mammals, are usually related to them). Those individuals, called helpers or alloparents, are characterised by delayed dispersal from the natal group, reproductive suppression or deferred/delayed maturation, and direct care to the offspring or pregnant or lactating mother (Solomon & French, 1997a). In groups with plural breeding (e.g., mongooses), the cooperation is among all breeders of the group, as they all care for all of the young in the group. In other words, the resources are pooled as in human communes.

In groups with singular breeding (i.e., one breeding pair per group or family, as is the case in wolves), two scenarios are observed: sub-adults from the previous breeding year assist the breeding pair in raising the young, or subordinate individuals (related or not to the breeding pair) assist in raising the young. In both scenarios, the helpers do not breed. The degree of alloparental care also varies (see Section 1.4.4).

The most puzzling and intriguing aspect of cooperative breeding is reproductive suppression of the non-breeders. In wolves, more often than not only the dominant pair will breed. There are three possible mechanisms underlying this phenomenon. Firstly, it would be logical to propose a purely reductionistic explanation: subordinate animals are physiologically unable to reproduce. Although many proximate (i.e., physiological / developmental) and ultimate (e.g., functional / evolutionary) explanations have been suggested in the past, it is still unclear which proximate mechanisms would be responsible for such physiological suppression (if any). Secondly, a purely behavioural explanation is also possible in some cases. The dominant animals can affect breeding among subordinates both pre-conception (e.g., mate-guarding in wolves: the alpha male prevents the other males from approaching the dominant female) and post-conception (e.g., infanticide). Thirdly, a behavioural-physiological explanation would take into account the interplay between physiology and behaviour. The interdependence between physiology and behavioural processes such as dominance, aggression and stress is at the theoretical centre of many recent studies on reproductive suppression in carnivores and primates (for reviews, see Sapolsky, 1998, Solomon & French, 1997 and the chapter on stress in this text). In the remaining sections of this chapter, an argument will be made that this explanation is most likely. With mammals, a fourth and rather difficult to categorize explanation has been put forward: a pheromonal explanation, emanating from studies with rodents. That is, pheromones from urine of dominant animals inhibit, suppress or delay the reproductive physiology of the non-breeders (see Section 1.3 on stress for more details). It would be almost impossible to test the pheromonal hypothesis in the field (and decipher to what extent it is behavioural versus physiological[25]).

1.4.4 Paternal care and alloparental care

Because of the strong association between paternal/alloparental care and reproductive suppression, these concepts deserve special attention and review. As has been demonstrated, parental care, especially paternal care, is an important factor in classifying a species as monogamous. Like the definition of monogamy itself, however, there are different degrees of paternal behaviour and investment. For monogamous species involved in cooperative breeding, the rate of alloparental care must also be considered. In monogamous species, since paternity is, at least in principle, more certain, the paternal investment in the progeny is worth the cost. As illustrated in Poole (1985), the parental care of males can be evaluated by examining the number of paternal activities in which the males engage. The main categories of parental behaviours apply not only to mothers and fathers but also to alloparents in an extended family group.

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[25] In fact, we would also have to determine if the scent-marking behaviour is an intentional act of dominance and aggression rather than a by-product of a physiological (endocrine)

The categories identified in the literature (Asa, 1997; Asa & Valdespino, 1998; Poole, 1985) are grooming, transporting (i.e., carrying the pups or retrieving them when alarmed), feeding (solid food or via regurgitation in canids), defending, guarding, baby-sitting, playing, and caring for the mother. Table 1.8 shows the distribution of these behaviours for 21 species of canids. The least "paternal" species are at the top of the table, the most paternal at the bottom.

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state.

Table 1.8. Comparative paternal care for 21 species of canids (adapted from Asa, 1997; Asa & Valdespino, 1998; Kleiman & Malcolm, 1981; Malcolm, 1985).

Species Note: species in italics have been documented mainly via captive studies	**Grooming**	**Carrying, Retrieving**	**Feeding**	**Defending**	**Babysitting**	**Playing**	**Guarding**	**Caring for female**
Chrysocyon brachyurus (maned wolf)				•				
Vulpes corsac (Corsac fox)				•				
Vulpes velox (swift fox)			•					
Vulpes macrotis (kit fox)			•					
Vulpes chama (Cape fox)			•					
Pseudalopex gymnocercus (Pampas fox)			•					
Dusicyon culpaeus (Culpeo, Andean fox)			•					
Nyctereutes procyonoides (raccoon dog)								•
Vulpes vulpes (red fox)			•					•
Canis rufus (red wolf)			•				•	
Alopex lagopus (arctic fox)			•			•		•
Fennecus/ Vulpes zerda (fennec)			•				•	•
Cuon alpinus (Indian wild dog; Dhole)			•	•				•
Cerdocyon thous (crab-eating fox)			•	•	•			•
Speothos venaticus (bush dog)			•	•	•	•		
Otocyon megalotis (bat-eared fox)			•		•	•	•	•
Canis mesomelas (black-backed jackal)			•	•	•	•	•	•
Canis aureus (golden jackal)			•	•	•	•	•	•
Canis latrans (coyote)			•	•	•	•	•	•
Canis lupus (wolf)			•	•	•	•	•	•
Lycaon pictus (African wild dog)	•	•	•	•	•	•	•	•

Note that the less involved fathers are common among the vulpines (fox-like canids) and the highly involved fathers are common among the canines or highly social canids (*Canis*, *Cuon*, *Lycaon* and *Speothos*). The latter genera tend to display more "direct" care to the young as opposed to indirect care (as in the case of the raccoon dog providing care to the lactating and nursing mother only). Note also that lycaon reportedly engage in grooming and carrying/retrieving, a unique paternal activity among canids.[26]

1.4.5 Reproductive and social organization: A model

The social and mating systems of canids have fascinated ethologists and animal psychologists for decades. In this section, I will present a taxonomy that synthesizes and extends existing ones and takes into consideration the following concept: as the social sophistication of canid species increases, and as the size of the family unit of those species increases, the complexity of the potential mechanisms responsible for the group-size regulation[27] also increases. Furthermore, as Fox argued (1975), the higher the social sophistication, the higher the individual variations within a group, (and therefore, the higher the variance in individual adjustments to social stimuli, stressful or not). Highly social canids (e.g., wolves) have more behavioural individual differences than

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[26] It is interesting to note at this point that the male callitrichids (the most monogamous and family-oriented of all primates) also provide all or most of the paternal categories of care listed in Table 2. See Snowdon (1990 and 1998) for reviews of the family and their social/mating system.

[27] Note that the use of the expression "group-size regulation" is not meant to refer to the group-selectionist arguments, but to any mechanisms (if any) keeping the number of

less social canids (e.g., gray fox) and therefore display a greater continuum of individual reactions (behavioural reactivity and physiological responses) to environmental (including social) events[28].

The development of a taxonomy will not only help to illustrate this pattern, but it will also serve to situate wolves among the other canid species. As such, it will be a reminder that comparing across canid species can be a challenging enterprise and should be done with caution.

I will use as a starting point, the taxonomies of mating/social systems adopted by two canid researchers (Michael Fox and Devra Kleiman), and a socioecologist, Trevor Poole. Fox' typology (1975) has an emphasis on the social organization of canids with a strong focus on its complexity and flexibility. The starting point of his taxonomy is the hunting pattern of each canid species. Later, Fox elaborates on this by establishing a link with the reproductive organisation (mating system) of the species. This is where Poole's taxonomy becomes relevant. Poole (1985) clearly gives credit to Fox for his "grades" of monogamy (that he applies to any relevant mammalian species), although Poole's focus is on the mating system defined by the type of family

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individuals in a group within a range suitable for the environmental constraints of their territory.

bond, pair bond, paternal care and alloparental care. Based on the definitions of monogamy discussed above, it is difficult to resist a comparison between those two typologies with Kleiman's simple taxonomy of facultative versus obligate monogamy. Table 1.9 summarizes the three perspectives with the obvious and extensive overlaps.

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[28] See section 1.3.2.4 and the discussion on monomorphic, oligomorphic and polymorphic species.

Table 1.9. Social/mating system taxonomy for canids: Fox, Kleiman, and Poole.

TERMINOLOGY			**MATING/PARENTAL/ALLOPARENTAL/SOCIAL SYSTEM**					**GENERA / SPECIES**
Fox (1975)	**Poole** (1985)	**Kleiman** (1977)	**Hunting pattern**	**Family bond**	**Pair bond**	**Paternal care**	**Territory / dispersion**	
Type I Monomorphic	Grade I	Facultative	Solitary hunters.	Transient family.	Temporary pair, some parental assistance from the male.	Paternal investment is low, loose association, occasional polygyny.	Male and female defend common territory but offspring leave after weaning.	"Fox-like" group: *Urocyon, Alopex, Vulpes,* etc. *Nyctereutes* (raccoon dog)
Type II Oligomorphic	Grade II		Solitary-social hunters (transitional type).	Temporary family.	Permanent pair. Sometimes presence of helpers (e.g., red fox).		Adults are permanently paired but the dispersion of the young is delayed.	*Canis* (except *C. lupus*) and *Vulpes vulpes* and *corsac*. Coyotes Jackals Red wolf Dingo Red fox Corsac fox
Type III Polymorphic	Grade III	Obligate	Social hunters (pack type).	Permanent family. Clear-cut dominance hierarchy.	Permanent pair or pack structure. Only alpha animals breed.	Cohesive, paternal care, extra-pair mating very rare.	Status (rank)-determined monogamy (multi-male/multi-female groups).	*Canis lupus* (wolf) *Lycaon pictus* (African Wild Dog) *Speothos venaticus* (bush dogs)
Type IV	-	-	* See note					*Cuon alpinus* (dholes)

* Note: Fox (1975) recognizes in a footnote (p. 445) that *Cuon alpinus* "exemplifies a further evolution of canid social behaviour, where the term "clan" is appropriate for such a large group sharing the same range but rarely hunting together" and goes on to say that "It therefore constitutes a Type IV canid social class, the clan (analogous to the baboon troop)." Type IV would also be considered polymorphic.

In canids, the difference between the Type I and Type II social or mating systems is not clear-cut. In theory, these categories are mutually exclusive, but there are many observations that would challenge that assumption. Species previously believed to be completely solitary (e.g., Raccoon dog, *Nyctereutes, procyonoides*) seem to fit at least Type I, if not also Type II (Sheldon, 1992). It is now widely accepted that the red fox (*Vulpes vulpes*) often displays Type II social behaviours (Macdonald, 1979 1987). The male is not necessarily present after birth, but the "helper" sub-system has been identified among the females: daughters of the mother stay for an extra year to help raise the new young (this type of alloparental behaviour is called "aunting"). There have been some observations that aunting also occurs with *Vulpes corsac* and *Alopex lagopus.* Because of the possible fuzzy boundary between the Type I and Type II canids (a distinction that may be more context-dependent than species-dependent), it is therefore possible that Kleiman's (1977) taxonomy is more parsimonious and better adapted to the apparent social flexibility (and sophistication) of some "Type I" species.

At the same time, there are two groups of species that do not seem to fit any of the categories mentioned above. Firstly, male *Dusicyon microtis* (or formerly *Atelocynus microtis*; small-eared dog) and *Vulpes chama* (Cape fox) seem to be quite solitary or at least sometimes adopt a very solitary existence without much interest in the female or the progeny, suggesting the need for a classification that gives an entry to species with more solitary trends than the Type 1 group ("Level 0"[29]). Secondly, domestic dogs, pariah dogs, the New Guinea wild dog and the dingo (all technically *Canis familiaris* or *Canis lupus familiaris*) seem to be quite polygamous (polygyny) and form very loose associations with a mate (if any). Their "pack" structure is quite flexible and somewhat lax compared to that of *Canis lupus*. It seems that *Canis (lupus) familiaris* deserves another distinct class ("Level 5") to recognize that flexibility. Table 1.10 summarizes the typology suggested by these observations and introduces the typology and organisation used in Appendix A.

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[29] To differentiate my taxonomy from Fox and Poole's, I will use the term "Level" instead of "Type" or "Grade". The term "Level" was chosen to translate the idea of a continuum or gradation in the social sophistication of canids.

Table 1.10. A revised taxonomy of the levels of social and reproductive organizations in wild and domestic canids.

LEVELS	**EQUIVALENCE TO FOX / POOLE / KLEIMAN**	**BASIC SOCIAL SYSTEM**	**SPECIES/GENERA**
0	-	Solitary.	*Dusicyon (Atelocynus) microtis* (small-eared dog), "fox-like" group, e.g., *Vulpes chama.*
1	Type I / Grade 1 / Facultative	Transient family.	"fox-like" group, e.g., *Urocyon cinereoargenteus.*
2	Type II / Grade 2 / Facultative	Temporary family.	Coyotes, Jackals, "fox-like" group, e.g., *Vulpes vulpes*
3	Type III / Grade 3 / Obligate	Permanent family. Clear-cut dominance hierarchy.	Wolves, Lycaons, Bush Dogs.
4	Type IV / Grade 3 / Obligate	Clan of packs.	Dhole.
5	-	Loose associations, polygyny, context-dependent.	Domestic dog, dingo, pariah dogs (or pariah breeds, e.g., New Guinea Singing Dog, African Basenji).

In Table 1a and 1b of Appendix A, I present my own "level-based" model expanding on the Fox-Poole-Kleiman model of social and reproductive organization. Table 1a explains the Levels used in this model; the correspondence to the established models can be found in Table 1.10. Given the earlier discussion on the fuzzy boundary between Levels 1 and 2, an intermediate Level (Level 1.5) was also added to reflect a possible continuum of sociality and to allow for future integration of the mid-levels when more data are available.

Table 1b in Appendix A is a comprehensive species by species account of the Canidae family[30]. For each species, the mating system is indicated, the social system or structure is briefly described, as is the paternal and alloparental care and the available information on the presence or absence of reproductive suppression in subordinates. In addition, species specific characteristics associated with the mating or social system is presented, for example, sophistication of the communication systems. In some cases, qualifying information (e.g., research conducted only in captivity, lack of data or supporting evidence for anecdotal data) and taxonomic comments are included.

The reader should notice trends in Table 1b of Appendix A that reflect the interplay between the social and reproductive systems. Basically, it depicts the gradient of sophistication between canid species on all aspects of their mating,

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[30] The information included in both tables comes from many sources, including reviews and monographs by Ables (1975), Asa (1997), Asa & Valdespino (1998), Banfield (1977), Bekoff (1977), Bekoff & Wells (1980, 1982, 1986), Chesemore (1975), Cohen (1978), Corbett & Newsome (1975), Corbett (1988), Davidar (1975), Egoscue (1979), Estes (1991), Fritzell & Haroldson (1982), Geffen (1994), Geffen & Macdonald (1992), Gier (1975), Hall (1981), Henry 1986), Hersteinsson & Macdonald (1982), Johnsingh (1982), Kleiman (1967), Kleiman & Eisenberg (1973), Kleiman & Malcolm (1983), Kullberg & Angerbjörn (1992), Larivière & Pasitschniak-Arts (1996), Macdonald (1979, 1980, 1983, 1987), Malcolm (1985), McGrew (1979), Mech (1970, 1974), Mech & Nelson (1989), Messier & Barrette (1982), Moehlman (1986, 1989), Moehlman & Hofer (1997), Novaro (1997), Nowak (1991), Parker (1995), Sheldon (1992), Riley & McBride (1975), Sillero-Zubiri & Gottelli (1994), Sillero-Zubiri, Gottelli, Macdonald (1996), Trapp & Hallberg (1975), White & Harris (1994). Internet monographs from the IUCN/SSC Canid Specialist Group were also consulted (available at

social, parental, alloparental and reproductive complexity. For example, as you move closer to the bottom of the table (with the possible exception of the very last level), reproductive suppression of subordinates is more likely to be observed. The table suggests a continuum of social flexibility, which is highly correlated with the complexity of the family systems. Complexity is not necessarily logically associated with flexibility: it could be argued that wolves and lycaons, for example, are threatened species because of their complex social system and their lack of adaptive flexibility (i.e., inability to change their social system). The level of flexibility alluded to here, however, relates more to the idea that species at the bottom of the table have, in principle, the option to form either a pack (extended family), or simply, a breeding pair (this is common in wolves, for instance, depending on the latitude or the size of prey available). Flexibility is also apparent with the mating system: both lycaons and wolves have been observed to occasionally stray from the standard monogamy towards a more polygamous system. Figure 1.2 shows the systemic flexibility (i.e., flexibility of the mating, social, parental, alloparental and reproductive systems) of canids in the form of a continuum.

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http://www.canids.org/). Other references are given within the table when a notable pattern is mentioned.

Figure 1.2. Systemic flexibility continuum for canids.

Solitary

Limited (temporary) pair bond + limited paternal care

Pair bond + paternal care

Immediate family + paternal care + limited alloparental care + limited cooperative breeding

Extended family + alloparental care + cooperative breeding + reproductive suppression

Extended family + alloparental care + cooperative breeding + reproductive suppression + superseding clan structure

Loose and flexible system

1.4.6 Reproductive and social systems in Wolves and Lycaons

The taxonomy and data presented to this point clearly suggest that wolves and lycaons are similar, in terms of their potential for reproductive suppression. Comparisons between the two species are tempting because the only systematically studied species for reproductive suppression in an extended family group (i.e., with cooperative breeding) were done on lycaons and wolves. There are, however, significant differences between the two that prevent direct comparisons or generalizations across species.

The general information on these two species comes from Derix (1994), Estes (1991), Nowak (1991) and Sheldon (1992) as well as a number of other references listed below. Sheldon (1992) describes the lycaon as the "most highly social of the canids" (p. 97) and later asserts "This is the most highly social species in the Canidae" (p. 103). It is unclear what criteria are behind these statements. It is possible that the advanced paternal behaviour in the lycaon motivates this position but later, when discussing the dhole (*Cuon alpinus*) Sheldon states "Dholes are highly social animals, comparable in the degree of their sociality to African wild dogs (*Lycaon pictus*) and wolves (*Canis lupus*)" (p. 82). You may remember that I grouped dholes (*Cuon alpinus*), bush dogs

(*Speothos venaticus*; based on captive studies), lycaon, and wolves (*Canis lupus*) in the same category of highly social canids (see Tables 1.10, 1a, and 1b of Appendix A) Since Fox seems to recognize the "clan" system used by the dhole as a higher level of social sophistication, Sheldon's statement may be a little too strong (and notice that she does not mention bush dogs when discussing dholes, lycaons or wolves, but later writes in the bush dog section "Bush dogs appear to be among the most highly social members of the Canidae family", p. 147). This only shows that consistency and agreement between and among a number of canid specialists may be difficult to attain. At least we can agree that wolves, lycaons, bush dogs and dholes seem to represent the ultimate wild canids as far as social complexity and flexibility goes. Because of the size of their family units, if reproductive suppression for group-size regulation (see footnote 27) is needed, it will be among these four species.

Lycaons are an endangered African species and it is estimated that only 7000 individuals remain on the continent. Human civilization is, as with the wolf in North America and Europe, their main ecological problem. Table 1.11 summarizes the important differences and similarities between wolves and lycaons. Fuller (1995) contrasts these two species with an ecological perspective and Mech (1975) with a focus on the hunting behaviour. Both authors stress the similarities between the two species: that they are both carnivores at the top of the food chain, that they are both highly social, pack-living canids, and that they both exhibit sophisticated parental care and monogamous tendencies. The rest of the comparison is more dubious: the ecology of the two species is difficult to compare given the nature of the habitat (equatorial for lycaon, mainly circumpolar for the wolf) and the nature and variety of the prey sought by both species. This means that comparisons of pack sizes, litter sizes and home range sizes may not be very telling and merely reflect habitat differences. The way these factors impact on the social dynamics though, cannot be overlooked. Apparent details can actually be very significant (e.g., scent marking behaviour, discussed below and Section 1.2 on agonistic behaviour).

Table 1.11. Comparisons between lycaons and wolves.

	Lycaons	**Wolves**
Size	Shoulder: 60-78 cm Head + body length: 76-112 cm Tail: 30-41 cm	Shoulder: 65 to 80 cm (up to 90) Head + body length: 100-164 Tail: 30-56 cm
Weight	17-36 kg; males = females	18-80 kg; males > females (males 40; females 30)
Sexual dimorphism	None	None
Mammae	12-16 (unique among canids); Increasing the need for alloparental care?	8-10
Circadian activity	Crepuscular, nocturnal activity higher in hot weather, but overall one of the most diurnal large carnivore in Africa.	Crepuscular; diurnal activity higher in cold weather, nocturnal activity higher in highly populated regions (e.g., Italy).
Odour	Very strong, musky smell; Suggestive of more pheromonal communication?	Light smell
Scent marking	Not a predominant behaviour.	Very predominant behaviour; Suggestive of pheromonal suppression?
Regurgitation	Yes	Yes
Pack size	2-40, usual 10-11 (mean = 9.8) Males: 4.1 (0-10) Females: 2.1 (0-7)	2-36, usual 5-8, packs of 12 in Northern hemisphere are common. Male:female fairly equal.
Mating/breeding	Dominant female Dominant male Occasional subordinate males Rarely a second female breeder	Dominant female Dominant male Uncertainty about subordinate males Rarely subordinate female breeders
Gestation	60-80 days (69-73); Suggestive of the need for longer paternal care to the female.	62-63 days
Parturition time	All months except September.	April to June.
Litter size	2-21 (7-10); See the comment on the number of mammae.	1-11 (6)
Helpers:	Usually males.	Males and females.

	Lycaons	**Wolves**
Paternal behaviour	All of the paternal patterns documented in mammals: Grooming, carrying, retrieving, feeding, defending, babysitting, playing, guarding, caring for female. (See Table 1.8)	All of the paternal patterns documented in mammals with the exception of: Grooming and carrying. See also Table 1.8 for comparison with other canids.
Dens	In use 3 months per year.	In use 3-5 weeks per year.
Dispersal	Females. Two or more same-sex siblings leave the pack together.	Males and females. Solitary dispersal.
Sexual maturity	Female: 18-22 months.	(10)22-46 months.

Wolves are mainly found in the Northern portion of the Northern hemisphere and most of the populations are found in northernmost countries of that hemisphere, that is, Canada (30 000 individuals) and Russia (Siberia, 50 000 individuals). In Europe, the main cluster is in the Balkans although some populations are found in Portugal, Spain, Italy, Czech Republic, Slovakia, Poland, Sweden, Norway, Finland, and Denmark's territory, Greenland. In North America, no natural wolf populations are found South of the Saint-Laurent River with the exception of the Northern portions of Minnesota, Michigan, Montana and Wisconsin.

Research in the past 50 years established that significant variations are found in their social and parental behaviour that seem highly correlated with latitude (i.e., Arctic wolf versus Middle East wolf) and, as a corollary, ecological constraints and habitats. The reader should be aware that differences and similarities that I will highlight from now on are based on the quite homogeneous lycaon and an average of the more heterogeneous wolf.

The lycaons use dens for about three months of the year for parturition and until the young gain mobility. They hunt in packs, usually on medium sized ungulates and smaller animals (which are usually not shared with other pack members). Packs of lycaons seem to be more tolerant of intruding packs on their territory than wolves (Estes, 1991). It is possible that this tolerance is intrinsic to the species (maybe as with the dhole, *Cuon alpinus*) as Sheldon (1992) cites authors who reported packs of 100 or more individuals a century ago (Rosevear, 1974 and Shortridge, 1934, both cited in Sheldon, 1992).

Wolves and lycaons both live in "primary groups" (groups or packs formed around the reproductive unit) and practice "singular breeding" (i.e., there is one breeding pair per social unit, in this case, the pack structure). A recent trend (Mech, 1999) is to consider wolf packs as a "family" unit. This usage is common among biological anthropologists and primatologists (e.g., Sade, 1991) for primates such as the Callitrichidae (marmosets and tamarins). Following primatologists' and Mech's (1999) terminology, the previous sections differentiated between "immediate family" structure, when parents and young of the year form the group, and "extended family" structure, when uncles and aunts are present, as well as older generations (such as grand parents, great uncles and great aunts)[31]. This terminological detail is also meant by Mech (1999) to give less weight to the dominance hierarchy construct as the building block of the pack. This is not to say that a dominance hierarchy is not present, but it may not be as fundamental as was previously thought. Mech (1999) very much insists that the inspiration behind the dominance hierarchy concept applied in wolves came from captive studies and that the study of wild packs suggests a more cohesive, less dominance-based structure and dynamic than was previously suggested. As Mech (1999) argues, captive packs include individuals "forced" to form a social unit for a prolonged period of time (with no chances of emigration and dispersal for any members). If Mech (1999) is correct in his assertion that wild wolves are less "hierarchised" and "dominance-driven", then it is possible that they are more similar to wild lycaons (i.e., as early reports on lycaons' social dynamic suggested, low on intra-pack conflicts). What we are lacking is a set of good sociometric studies of wild packs to confirm that idea, although Mech's paper is the first step towards this goal.

In contrast to wolves, lycaons can breed at any time of the year and will give birth to young any month except September. They also have exceptionally

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[31] The extended family structure is more common in captive wolf packs and large wild packs.

large litters (see Table 1.11), packs see highly skewed involvement of males as helpers (more "uncling" than aunting), and the female lycaons disperse (i.e., leave the natal pack) as opposed to a clear trend towards dispersing males in other canids (Frame & Frame, 1976; Malcolm & Marten, 1982; McNutt, 1996). Packs of lycaons are therefore constituted mainly of related males, and they often contain only one or two females (Frame & Frame, 1977; Frame, Malcolm, Frame, & van Lawick, 1979). Estes (1991) notes that ratios of 2:1 or even 8:1 in favour of males are not uncommon. Even more interesting, the skewed sex ratios are also found in newly born litters (Estes, 1991; Malcolm & Marten, 1982).

Lycaons seem to have distinct dominance hierarchies for each sex, and female aggression may be higher overall in the pack than male aggression (Estes, 1991; van Lawick-Goodall & van Lawick-Goodall, 1971; Reich, 1977), but the literature on this topic is not always consistent (Estes & Goddard, 1967; Kühme, 1965; Sheldon, 1992). Most agonistic behaviours observed in lycaon are very similar to what is observed in dholes, wolves and other *Canis* species. Lycaon seem to be a species governed by submissive behaviour, leading to the idea that actual aggressive behaviours in that species (i.e., direct, overt aggression) are quite infrequent (van Lawick-Goodall & van Lawick-Goodall, 1971). As mentioned above, with ideologies changing in the field of animal behaviour, researchers (such as Mech) are beginning to view the social dynamics with a different perspective and to adopt new vocabularies. Interestingly though, whereas the view of wolves has changed from "dominance-driven" to "pacifically family oriented", lycaons have taken the opposite historical route: Creel, Creel, and Montfort (1996) and Creel, Creel, Mills, and Montfort (1997) continue to use the dominance hierarchy ideology when describing the social dynamics of lycaons. This is a crucial conceptual issue and as long as canid researchers continue to disagree on such basic terms (e.g., dominance, aggression) the interpretation and comparison of data will be rendered difficult.

More implicit forms of communication, including, potentially, communication of aggressive or submissive intents, should also be mentioned. I already raised the possibility earlier in this section of pheromonal communications. It is interesting to note that lycaon have a very strong body odour and display little urine marking (Estes, 1991) in contrast to the almost odourless and active urine marking wolves. This difference could be an important factor when considering the expression of dominance and submission between wolves and lycaon. The implicit expression of dominance via urine marking in wolves could be a signal or "weapon" not available to lycaons, or at least not as preponderant. Scent marking as a form of ritualised aggression in wolves should be investigated as a mechanism of reproductive suppression, although it is known that anosmic wolves can reproduce (Packard, 1980). Reviews of the urine-marking literature in wolves can be found in Asa, Mech, Seal, & Plotka (1990), Ryon & Brown (1990), Macdonald (1985), and Packard (1989), but to date, the specific link to the mating system has not been made.

Other noteworthy differences include the presence of fewer females in lycaon packs (1 or 2) than in wolf packs (close to 50%), larger litter sizes and larger packs in lycaon compared to wolves (see Table 1.11). These demographic differences could have an impact on the group dynamics, albeit a subtle one.

There is some evidence of reproductive suppression in lycaon with both captive subordinate females (van Heerden & Kuhn, 1985) and wild subordinate females (Frame, Malcolm, Frame, & van Lawick, 1979). There are also observations of multi-litters in a group (three reports of a second mother in a pack: Kühme, 1965; van Lawick-Goodall & van Lawick-Goodall, 1971; Frame, Malcolm, Frame, & van Lawick 1979). Many authors have discussed the possibility of reproductive suppression in wolf packs (Fentress & Ryon, 1982; Harrington, Paquet, Ryon, & Fentress, 1982; Mech, 1970; Packard & Mech, 1980; Rabb, Woolpy, & Ginsburg, 1967; van Ballenberghe, Erickson, & Byman, 1975; Woolpy, 1968; Zimen, 1975, 1976) but the first systematic studies of captive wolves were from Seal, Plotka, Packard, and Mech (1979), Packard, Mech, and Seal (1983) and Packard, Seal, Mech, and Plotka (1985). These studies suggested that alpha animals (the "parents") used aggression to prevent the subordinate animals from mating (although siblings were more aggressive overall than alpha or omega individuals) and no evidence of gonadal suppression was found. That is, ovulation was observed in subordinate females and testicular functions were intact in subordinate males. Seal, Plotka, Mech, and Packard (1987) also failed to find rank-based differences in cortisol levels or reproductive hormones and functions (in both males and females). Normal seasonal patterns were found for all reproductive hormones but no seasonal variations were observed for cortisol, suggesting that stress levels in packs do not vary seasonally. This is surprising considering the fact that the level of fighting increases prior to and during the breeding season (so are the levels of androgens). A lack of rank-determined differences in baseline estrogens, progestogens and LH were reported in female wolves by Seal, Plotka, Packard, and Mech (1979). Asa et al. (1986, 1987, 1990, 1998) and Asa (1997) also found lack of endocrine evidence for reproductive suppression in wolves.

As would be predicted from the general literature on testosterone and aggression, Packard, Seal, Mech, and Plotka (1985) found that male wolves who scent mark a great deal (scent marking is known to be correlated with dominance in wolves: Asa, Mech, Seal, & Plotka, 1990; Ryon & Brown, 1990) and initiate aggressive acts have high levels of testosterone response to LHRH[32] (i.e., baseline values, prior to LHRH injections, minus peak values, following LHRH injections). The same males initiated the most sexual behaviours and were recipients of the most sexual behaviours from females. It is important to note that the authors chose to focus on "explicit" aggression and sexual behaviours (what they label "behaviours of highest intensity") and to ignore threats or courtship (or more implicit aggressive or sexual behaviour). This study also employed immobilisation procedures, so these results should be interpreted with that methodological detail in mind, because an acute stressor can lead to an increase in stress hormones, which in turn, can inhibit reproductive hormones. Despite immobilization, reproductive hormones were not inhibited, suggesting that the wolves in this study were very resistant to the possible suppressing effects of stressful events.

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[32] LHRH or luteinizing hormone-releasing hormone is a releasing hormone from the hypothalamus that stimulates the release of FSH (involved in sperm production in males) and

There is little doubt that some endocrine mechanisms are involved in the mediation of reproduction but the evidence is weak and the extent of the involvement is not yet clear. The issue may not have to do with a choice between strictly behaviourally-mediated suppression (only aggressive behaviour and mate-guarding prevent mating by subordinates), behaviour-physiologic-mediated suppression (where the actual aggression is a stressor with significant endocrine impact) or purely physiologic suppression. Since most of the data with captive packs do not suggest suppression in subordinates (see Packard et al, 1983, 1985), we may be only able to find evidence for "inhibition" (i.e., dampening, not a complete suppressive effect). Therefore I recognize some mediation or modulation from behaviour on the endocrine physiology and biochemistry, but this is not sufficient in itself. Mate-guarding, pheromones and incest taboo mechanisms (see Asa, 1997, for a discussion) may be in inter-play with sociogenic stress.

In order to understand the role of sociogenic stress[33] we need to understand the subtle interplay between social dynamics and stress levels in wolves. A focus on both positive (affiliative) and negative (agonistic)

LH (involved in testosterone production in males) from the anterior pituitary.

interactions is essential as is an examination into the proximate (endocrine) causes and consequences of stress and aggression.

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[33] See section 1.3 on stress or the following general reviews: Creel (2001), DeVries (2002), Keller & Reeve (1994), Marchlewska-Koj (1997) and Wolff (1997) for different theoretical positions on sociogenic stress in mammals.

1.5 The Study: Scope and Predictions

In this study I investigated the interplay between stress and social behaviour from a socioendocrinological perspective. Levels of urinary cortisol will be measured as an index of stress. Levels of urinary testosterone will be measured as an index of agonism. Both cortisol levels and testosterone levels will be correlated with agonistic behaviour and discussed in the context of other social and environmental factors.

Specific predictions include: 1) Subordinate animals will be more stressed (i.e., will have higher cortisol levels) than dominant animals; I will also attempt to identify the distribution of stress levels among the subordinates by comparing cortisol levels (C:Cr ratios, see Section 2, Methods for details). 2) Dominant males will have higher levels of testosterone than subordinate males; it was suggested in this section that dominant animals tend to have higher testosterone levels, which may help them secure their alpha position and reproduce with the alpha female. 3) Weather fluctuations should not account for much of the variance found in cortisol levels.

When unusual fluctuations or trends are found in an individual's hormonal levels, behavioural (agonistic) and weather events from the previous 24 hours will be examined to see if they account for the variability. Basic comparisons in hormonal levels will be examined as well, including individual differences, sex differences, and changes among the three seasons of the study.

2. Methods

2.1 Animals

All of the animals involved in this study were either from the Canadian Centre for Wolf Research (CCWR) or the neighbouring Shubenanacadie Provincial Wildlife Park Zoo. Both are situated in rural Nova Scotia (45°05'N, 63°22'W), approximately 100 km north of Halifax. Animals were cared for in accordance with the guidelines and principles of the Canadian Council on Animal Care. This study complies with the American Psychological Association's ethical standards for the treatment and care of animal subjects. Animals were fed, on average daily (rarely twice a day, sometimes a day was skipped, especially following consumption of carcasses). Water was available ad lib from automatic watering systems.

The main pack (Pack 1):

The wolves (*Canis lupus*) from this pack were descendants of individuals captured in the Mackenzie River area (Canada). The main pack was housed in a 3.2 hectare (8 acre) fenced area, which was part of a 4.05 hectare (10 acre) complex. The complex also included four .2 hectare (half acre) pens for hand-raised wolves (Packs 2 and 3 below) and coyotes (*Canis latrans*). The wolves of this pack had minimum interactions with humans and all the living individuals from 1993 to 1996 had been raised by the pack. Human incursions within the enclosure were kept to a minimum (e.g., daily feeding, emergency veterinarian interventions, fence maintenance). During the three years or seasons of data collection for this study (1993-1994, 1994-1995, 1995-1996), the CCWR was managed by Dalhousie University under the direction of Dr. John Fentress.

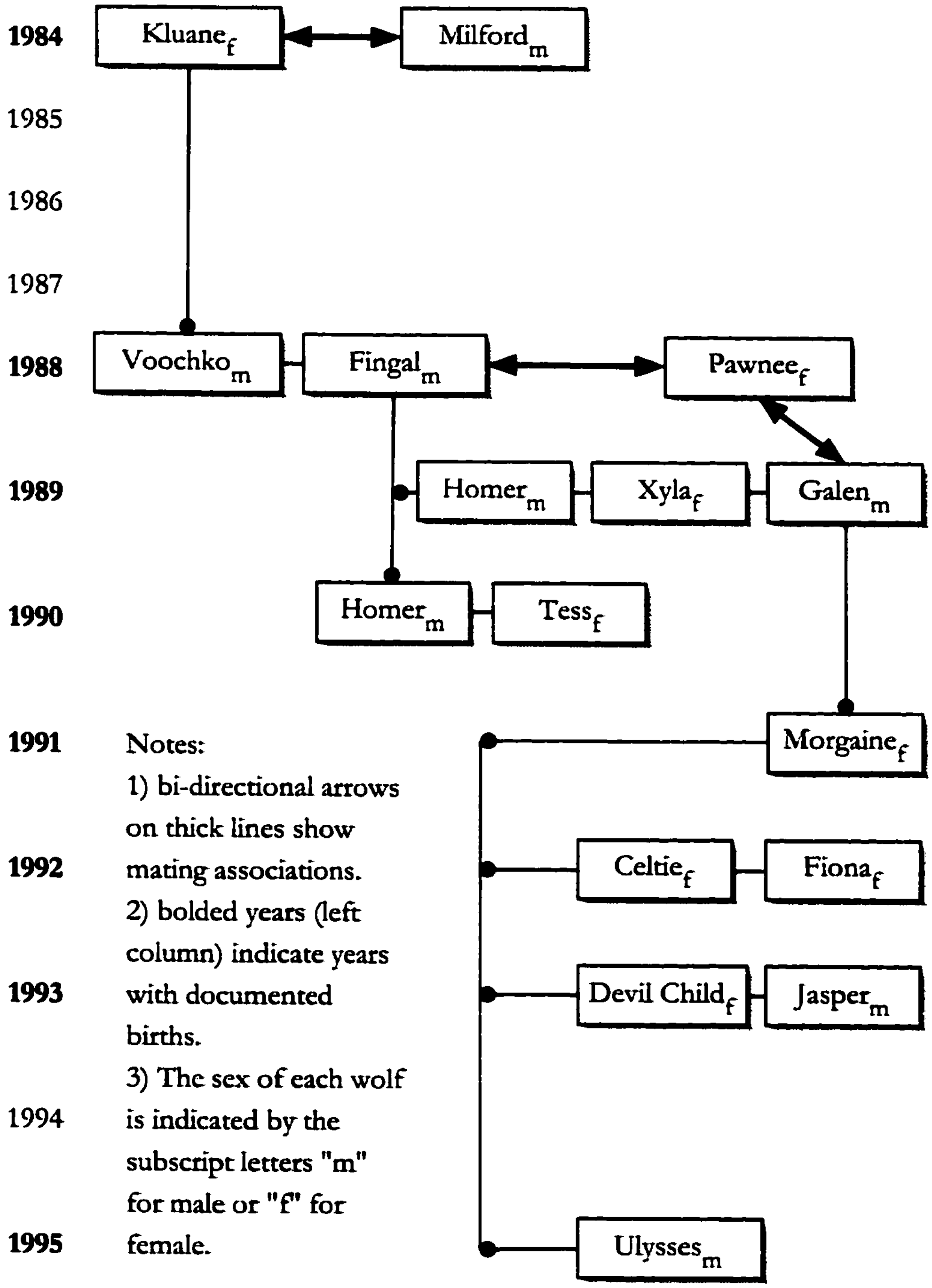
The main pack was comprised of a total of 15 animals over the three year span of the study; there were two births (1993 and 1995) and two deaths (1994). The maximum number of individuals found in the pack at any one time during this study was 14. Table 2.1 summarizes the demographics of the main pack for each of the three seasons. Appendix B presents a narrative account of the personalities of the major figures living in the main pack during the study. The genealogy of the main pack was estimated from behavioural observations which were consistent with incomplete microsatellite faecal DNA analyses of the pack (Barr, 1999). Figure 2.1 presents this genealogy, beginning in 1984. Figure 2.2 presents the percentage and absolute number of whelping females year by year, from 1974 to 1996 (McLeod, Ryon, & Fentress, 1997).

Table 2.1. Demographics of the main pack of wolves from 1993 to 1996, sorted by sex (females first), and by name.

Name	**Sex**	**Y.O.B.** *	**Status**		
			Season 1 1993-1994	**Season 2** 1994-1995	**Season 3** 1995-1996
Celtie	Female	1992	Beta flux	Beta flux	Beta
Devil child	Female	1993	Pup	Mid-ranking	Mid-ranking
Fiona	Female	1992	Mid-ranking	Mid-ranking	Mid-ranking
Morgaine	Female	1991	Beta	Beta	Mid-ranking
Pawnee	Female	1984	Alpha	Alpha	Alpha
Tess	Female	1990	Mid-ranking	Mid-ranking	Mid-ranking
Xyla	Female	1988	Omega	Omega	Omega
Ashley	Male	1980	Omega	-	-
Galen	Male	1988	Alpha	Alpha	Alpha
Homer	Male	1988	Beta flux	Beta flux	Beta
Jasper	Male	1993	Pup	Omega	Omega
Noah	Male	1990	Mid-ranking	Mid-ranking	Mid-ranking
Ulysses	Male	1995	-	-	Pup
Voochko	Male	1984	Beta	Beta	Mid-ranking
Winston	Male	1990	Mid-ranking	-	-

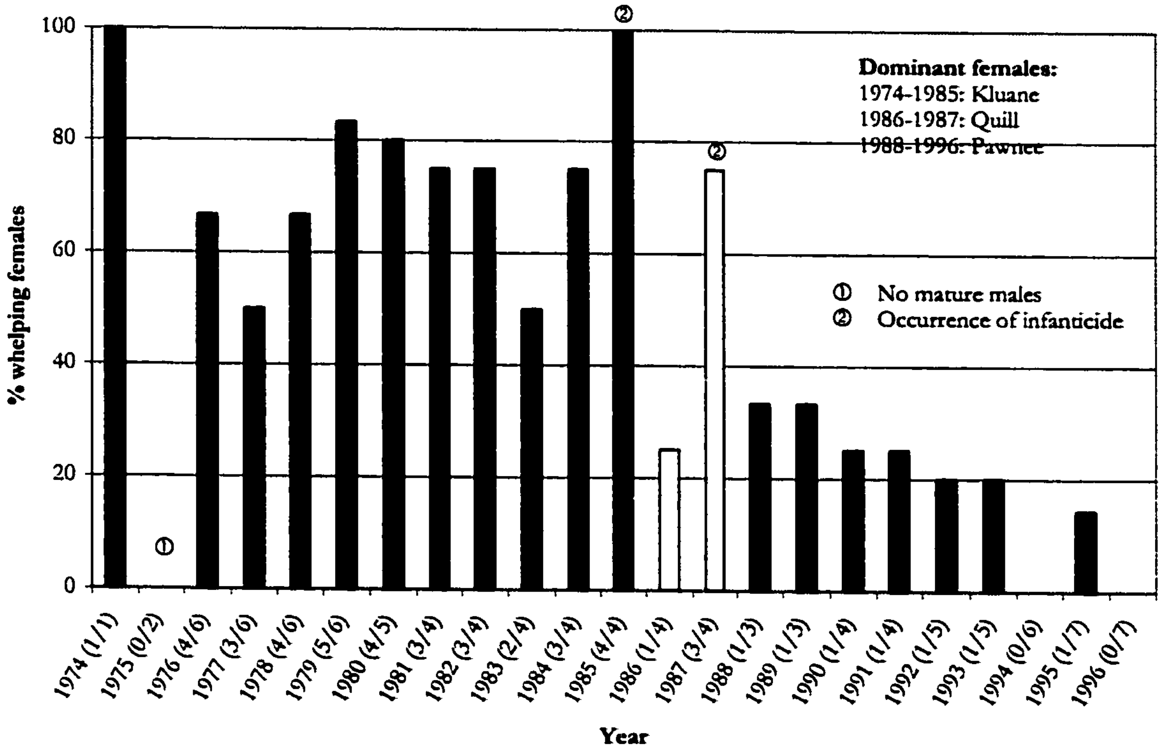
Notes: * Y.O.B.: Year of Birth; Alpha, beta and omega individuals are identified as well as the immediate contender (if existing) for the beta rank (labelled "beta flux").

Figure 2.1. Estimated genealogy of the Main Pack from the Canadian Centre for Wolf Research.



Notes:
1) bi-directional arrows on thick lines show mating associations.
2) bolded years (left column) indicate years with documented births.
3) The sex of each wolf is indicated by the subscript letters "m" for male or "f" for female.

Figure 2.2. Whelping history of the Main Pack from the Canadian Centre for Wolf Research.



Other wolves will be mentioned in this study for purposes of comparison and are from three smaller packs described below.

Pack 2 ("3-Pack"): Hand-raised wolves from the CCWR, filmed in Season 2 (1994-1995). These wolves had the same origins as the wolves from Pack 1. They were isolated from the main pack to be hand-raised in order to conduct studies requiring more direct but non-invasive contact with the animals. These four wolves were housed together in a .2 hectare (half acre) pen. The demographics of this pack are presented in Table 2.2.

Table 2.2. Demographics of Pack 2 from 1993 to 1996.

Name	**Sex**	**Y.O.B.**	**Rank**		
			Season 1 1993-1994	**Season 2** 1994-1995	**Season 3** 1995-1996
Grace	Female	1981	Alpha	Alpha	Alpha
Jane	Female	1981	Omega	Omega	Omega
Tracker	Male	1984	Omega	Alpha	Alpha
Wolfgang	Male	1987	Alpha	Deceased	Deceased

Pack 3 ("2-Pack"): Hand-raised wolves from the CCWR. As with Pack 2, Pack 3 had the same origin as the wolves from Pack 1, and were isolated from the main pack to be hand-raised. The two wolves in Pack 3 were housed together in a .2 hectare (half acre) pen. These wolves were not formally part of the study although some hormonal samples were occasionally collected. They were not filmed or systematically observed so samples available from that pack are often undifferentiated. Table 2.3 presents the demographics of this pack.

Table 2.3. Demographics of Pack 3 from 1993 to 1996.

Name	**Sex**	**Y.O.B.**	**Rank**		
			Season 1 1993-1994	**Season 2** 1994-1995	**Season 3** 1995-1996
Rory	Male	1985	Fluctuating	Fluctuating	Fluctuating
Zack	Male	1989	Fluctuating	Fluctuating	Fluctuating

Pack 4 ("Park Pack"): Wolves kept at the Shubenacadie Provincial Wildlife Park, filmed in Season 2 (1994-1995) only. The enclosure was similar (in general setting, enclosure dimensions, etc.) to the ones described for the CCWR hand-raised wolves described above except that water was manually provided (i.e., water container filled daily). Table 2.4 presents the demographics of this pack.

Table 2.4. Demographics of Pack 4 from 1993 to 1996.

Name	**Sex**	**Y.O.B.**	**Rank**		
			Season 1 1993-1994	**Season 2** 1994-1995	**Season 3** 1995-1996
Patty	Female	Unknown	Alpha	Alpha	Alpha?
Almond	Male	Unknown	Alpha	Alpha	Alpha?
Silver	Male	Unknown	Omega	Omega	Omega?

2.2 Apparatus, Equipment and Procedures

2.2.1 Behavioural analyses

2.2.1.1 Watches

An 8 mm/HI-8 video camera (Canon A-1 digital recorder - Canovision 8) was used for filming.

The taping schedule was fairly simple and flexible. In principle, when weather conditions were right (e.g., snow present on the ground or during snowfalls), the main pack was filmed every day of the working week (Monday to Friday) and sometimes weekends. The secondary packs were filmed every second day. For each pack, filming alternated daily between mornings and afternoons. For example, if Pack 1 was filmed in the morning on a Monday, it would be filmed in the evening on the Tuesday. The duration of each watch was typically one hour. Some watches, however, were terminated before the end of the hour if the animals were not in sight (this was common with Pack 1). It was common, especially during the second Season with Pack 2, to extend the watches to two hours when afternoon luminosity would allow it.

While filming, the observer or observers took note of the locations of all identifiable urination spots. Information on the samples (e.g., urination posture) was noted during the watch (see Table 2.5 for a complete list of the data collected). When the watches were completed, one or two observers would enter the compound with Ziploc® bags (sealable plastic bags), a spoon and an indelible marker. Samples were collected in the bags and data from the samples was written on the bag (including sample quality; see Table 2.5). Figure 2.3 illustrates this process from the urination to the final selection of the values used for descriptive and inferential statistics. At the beginning of each taping, the date, time, weather and snow conditions were noted, as well as any other relevant information regarding the wolves (for example, pack activity before the videotape camera was turned on, visitors present at the watch, and special food such as carcasses).

Figure 2.3. Sampling process for each urine mark from urination to statistical analyses.

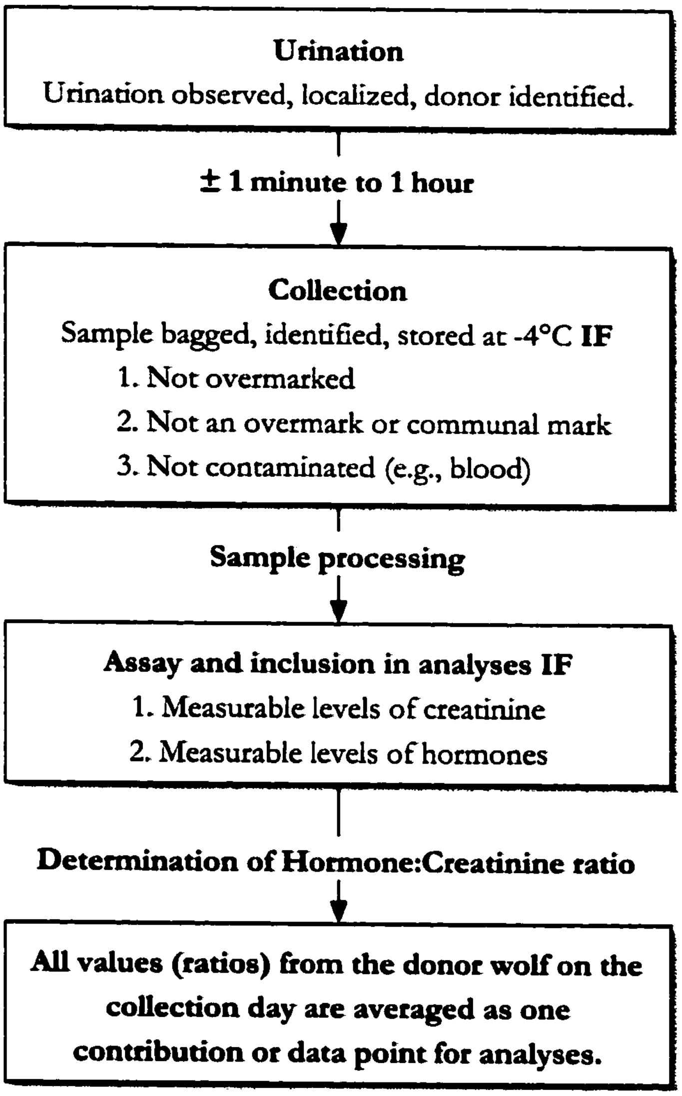


Table 2.5. Sample data collected during the watches.

Individual	The name of the animal that produced the sample.
Season	The year of the study, or more precisely, the breeding season: 1993-1994, 1994-1995 or 1995-1996.
Identification number	The number given to the sample's bag.
Date	The date of the collection.
Time	The time of the collection.
Posture	The urination postures are described and coded following the codes below: 1. HSU: high squat urination 2. HSTU: high standing urination 3. LGSTU: long standing urination 4. LGSU: long squat urination 5. LLSTU: low and long standing urination 6. LLSU: low and long squat urination 7. LSTU or LWSTU: low standing urination 8. LSU or LWSU: low squat urination 9. RLU: raised leg urination 10. RLUL: raised leg urination (left) 11. RLUR: raised leg urination (right) 12. STU: standing urination 13. SU: squat urination 14. .5 SU: half squat urination
Visual	Confirmation (yes or no) of a "visual" for the production of the sample.
Doubt	Doubt (yes or no) for the identification of the individual.
Video	Availability (yes or no) of videotaped footage of the urination.
Sample quality	Identification of possible contaminants present in or around the sample: 1. Normal (no contaminants) 2. Dirt/grass/wood 3. Bloody 4. Blood drips 5. Dog food

Licking	Some samples were licked seconds after urination. If so, this information was recorded. The "licker" or "lickers" were also identified. This information was recorded because these samples may not be considered suitable for the main analysis considering that saliva contains measurable levels of cortisol. 1. Licked after 2. Licked before 3. Licked (not specified) 4. Possibly
Overmarking	Some samples were overmarks, were overmarked or were collected in or around a communal mark. This information was recorded because these samples may not be considered suitable for the main analysis. 1. Overmarked before 2. Overmarked after 3. Overmarked (not specified) 4. Overmark (sample is an overmark of another mark) 5. Communal 6. Possibly

2.2.1.2 Social interactions

The HI-8 tapes were dubbed on S-VHF videocassettes to be viewed and scored on a S-VHF tape deck (Panasonic S-VHS AG-5710; Desktop Editor RS-232C) and high resolution monitor (Sony Trinitron Color Video Monitor model PVM-1341), allowing frame by frame scoring and/or slow motion.

The first round of video analysis was done using The Observer® Video-Pro 4.0 from Noldus Information Technologies Inc (Sterling, VA), a system for collection, analysis and management of observational data using a computer equipped with a video overlay board and a videocassette recorder. The system was equipped with a VITC (Vertical Interval Time Code) time code generator

(AEC-BOX-18; standalone LTC/VITC generator) and VITC time code reader (PC-VITC/RDR) from Adrienne Electronics Corporation (Las Vegas, NV). This allowed for the identification of the crucial or "behaviour-rich" segments of tapes, to time and score long, intense or complex interactions, and it facilitated the search for specific sequences of behaviour.

The second round of video analysis was completed using the Sociometric Module of my relational database described at the end of the Method section. This module was designed as an electronic ethogram with features similar to most event recorders. It also summarized data (descriptive statistics) using a sociometric matrix form on any search criterion (individual, age, sex, type of interaction, etc.). The module was created to store and process contextual data in conjunction with the behaviours.

Target behaviours and field data computed during the videotape analysis are described in Table 2.6.

Table 2.6. Data on social interactions collected during videotape analysis.

INFORMATION	**DESCRIPTION**
GENERAL INFORMATION REGARDING THE INTERACTION	
Date	Date of the watch (dd/mm/yyyy)
Time	Time of day of the watch (hh:mm:ss)
Tape	Tape identification (number, date)
Food	Food available during the watch (if any); discrimination between the usual dog food or the occasional carcasses (usually deer carcasses).
Exceptional situations	For example, the presence of visitors, unusual vehicles or animals, noises, equipment, etc.
Resources or context of interaction	That is, interaction in the context of specific resources (mate, food) or not.
Co-events	Human-related events taking place at the same time as the interaction or in temporal proximity with the interaction (and therefore, the possible cause of the interaction): train, automobile, planes, helicopters, voices, etc.
Type of interaction	1. Agonistic 2. Affiliative 3. Sexual
Sub-type of interaction	1. Aggressive-aggressive 2. Aggressive-submissive 3. Submissive-aggressive 4. Affiliative-aggressive 5. Affiliative-submissive 6. Sexual-aggressive 7. Sexual-submissive 8. Others
Start, end and duration of interaction	In mm:ss format.
Intensity of interaction	This is a measure evaluated on a scale of 1 (very low intensity) to 3 (high intensity).
Name and identification accuracy of initiator(s)	The identification accuracy is subjectively rated based on a scale of 1 (complete uncertainty) to 10 (absolute certainty).
SPECIFIC INFORMATION FOR THE INITIATOR AND THE RECIPIENT	
Name	The name of the initiator and recipient
Approach (for initiator) or reception (for recipient)	1. Agonistic 2. Affiliative 3. Sexual

Intensity of the approach or receptive behaviour	Same as above, evaluated on a scale of 1 (very low intensity) to 3 (high intensity).
Detailed agonistic, affiliative or sexual behaviour of the initiator and recipient	Agonistic 1. Aggressive: contact, i.e. "fight" (explicit, direct, overt) 2. Aggressive: ritualized, i.e., "display" (explicit, direct, overt) 3. Submissive active 4. Submissive passive 5. Freezing, immobility 6. Avoidance, escape, retreat, flight. 7. Other Affiliative 1. Friendly 2. Playful 3. Play-fight 4. Others Sexual 1. Courtship 2. Mating 3. Mating attempt 4. Genital investigation 5. Others
Reciprocations	The number of reciprocations recorded (if any). For each, the name of the individual, identification accuracy, receptive behaviour, intensity of the receptive behaviour and detailed type of agonistic, affiliative or sexual behaviours are recorded sequentially. Up to 5 reciprocations can be recorded. The last reciprocator is highlighted.

Because the focus of this study is social stress, the target behaviours will be from two major categories of dyadic interactions and their subcategories (defined in the Introduction). An overview of the types of behaviours under scrutiny can be found in Table 2.7.

Table 2.7. Categories of behaviours.

Agonistic behaviours	Aggressive behaviours	1. Overt, direct aggression, i.e., involving contact. Typically, fights. 2. Covert, indirect aggression, i.e., involving ritualized behaviour, e.g., growling, raised tail.
	Neutral behaviour (in a conflict situation): no specifically aggressive or submissive reactions.	
	Submissive behaviours	1. Overt, direct submission, i.e., involving escape or flight. 2. Covert, indirect submission, i.e., involving ritualized behaviour, e.g., grin, tucked tail, etc.
Non-agonistic behaviours	Affiliative (friendly) behaviours (e.g., greetings, play)	
	Sexual behaviours	

Current publications in experimental ethology and animal psychology often focus on overt, direct, or explicit interactions likely in order to avoid ambiguity in the myriad of possible implicit (ritualized) interactions and the attached interpretation problems. This methodology has some value in the context of this study considering the reasonable presumption that the most dramatic interactions are more likely to induce emotional distress/stress and other consequences (including physical consequences such as injuries). This approach is similar to Oswald and Erwin's (1976) distinction between contact aggression and non-contact aggression in pig-tailed monkeys (they also identified "submission" for the other extreme of the agonistic continuum; see also Erwin 1979, 1986). Reinhardt (1991) and Clarke and Blanchard (1994) with Rhesus Monkeys (*Macaca mulatta*), and Taylor, Brown, Lucas-Awad, and Laudenslager (1997) with Bonnet Macaques (*Macaca radiata*) made similar distinctions between contact and non-contact aggression. Despite the advantages of examining contact aggression (i.e., its overt, direct, and explicit nature, with little ambiguity regarding the intent, the intended recipient and the context) ritualized aggression was also considered here. It is believed that an aggressive stare can be as stressful as contact aggression: after all, wolves use mainly ritualized aggression and submission in their social interactions and dismissing the whole covert, indirect, implicit cluster of behaviours seems radical.

From early analyses, it was determined that about 75% of interactions were of the covert, indirect and implicit type. Considering that for our purposes initiators and recipients need to be identified, indirect agonistic interactions present a potential problem: because of the frequent absence of direct contact, the actual recipient or recipients can be very difficult to determine. For example, in a cluster of five animals (A, B, C, D & E) feeding on a deer carcass, "A" may growl or stare in the direction of "B" and "C", but the intended recipient may only be "C". This does not mean that "B" (or "D" or "E") would take "A"'s display as a serious intent to be aggressive or as a fight initiation (assuming the wolves knew to whom the signal was directed). Further, a raised tail during the approach of a food site may be a warning for the whole pack, "to whom it may concern", independently of who is actually paying attention. This point would actually bring us to Chance's (1967) notion that the "attention structure" of a group is what defines the dominance hierarchy, that is, who is watching whom and when. Chance determined that subordinates pay a lot of attention to the dominant individuals, likely in anticipation of attacks. Rowell's (1988) "movement monitoring" notion is very similar[34]. Unfortunately, this is almost impossible to measure, especially in the field conditions associated with this study. As far as I know, there has been no published data specifically examining the "attention structure" or "movement monitoring" in groups of canids. It is necessary to be careful in coding and later, interpreting the data from the covert-indirect-implicit cluster.

To use the terminology from Daanje (1950) and Moynihan (1998), I am going to code the "intent movements" as well as attacks with contact and

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[34] Rowell (1988) distinguishes between two types of social coordination in Old World monkeys: (1) Overt, specialized signals (gestures, noises) and (2) Movement monitoring requiring the animals to pay attention to who is doing what. He found that guenons

everything in between. I do this knowing that the effect of ritualized aggressive behaviour on the recipients is not known but acknowledge that a summation of such subtle messages may influence individuals, at least some individuals in some contexts. The point of this precautionary note is to recognize that the scoring of ritualized aggression and submission could add "noise" (from the erroneous identification of recipients to the difficulty in interpreting the intent) and for that reason they will be coded separately.

The identification and reaction of recipients in this context is challenging. Therefore, these agonistic behaviours (submissive or aggressive) are defined as a reaction to a specific action (initiation). Submissive behaviours are not always reactions to other actions. Submissive behaviours can be initiated to prevent aggressive behaviours from being engaged by a dominant or more aggressive animal. As noted by Benton (1982), Bernstein (1966), Rowell (1974) and Fentress, Ryon, McLeod, & Havkin (1987), subdominant behaviours can be of much higher frequency than dominant behaviours in a social group.

(*Cercopithecus* spp) were engaging mainly in overt signals and papionines (baboons, macaques & mangabeys) were mainly "monitoring".

2.2.2 Hormonal analyses

Most urine samples were collected immediately following behavioural watches and video recordings[35]. A number of samples were collected during the watches (especially for animals with low frequency of urination or samples from animals that were frequently overmarked) or at other times during the day or evening.

All samples were spooned into plastic bags (Ziploc®) within 5 to 60 minutes of urination, and were immediately labelled and frozen at -20°C on the premises of the CCWR. They were later transferred to a laboratory in the Tupper Medical Centre (Dalhousie University, Halifax Nova Scotia) for analysis. During the one hour drive from Shubenacadie to Dalhousie, the samples were kept frozen on ice in a cooler. The samples were thawed and centrifuged at 4°C for 10 minutes at 2000 x g. (1200 r.p.m. with an IEC [International Equipment Company, Needham Heights, MA; Damon/IEC division] DPR-6000 centrifuge) to remove dirt, and were refrozen at -20°C in aliquots. Aliquots were stored in 50 ml plastic tubes. Pools were prepared by using 1ml of each urine sample.

2.2.2.1 Creatinine assays

In order to correct for differing dilutions of urine in the animal's bladder and dilutions with snow, creatinine concentrations were determined for each sample of the three seasons of the study (see DelGiudice, Peterson & Seal, 1991; Mech, Seal, & DelGiudice, 1987). Creatinine is often used in a ratio for the measure of steroids in urine (most often cortisol), usually in the form or "hormone:creatinine" (Beerda, Schilder, Janssen, & Mol, 1996; Chandler & Dixon, 2002; Jones, Refsal, Lippert, Nachreiner, & Schwacha, 1990; Korhonen, Niemela, Jauhiainen, & Tupasela, 2000; Rekila, Harri, Jalkanen, & Mononen, 1999). Creatinine concentrations (expressed in micrograms per ml) were measured using Slot's modification of the Jaffé reaction with reagents from Sigma Chemical Co. (St. Louis, MO) as described in McLeod, Moger, Ryon, Gadbois and Fentress (1996). The protocol adopted is based on Sigma Chemical Co. "Sigma Diagnostics", Creatinine (procedure # 555, 1991) and it is described in detail below. Creatinine ($C_4H_7ON_3$) is a protein produced by the muscles from phosphorylcreatine ($C_4H_{10}N_3O_5P$), originating from creatine ($C_4H_9O_2N_3$) synthesized in the liver from methionine, glycine and arginine,

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[35] Appendix C presents a season by season account of the days on which watches were videotaped and urine samples were collected. "Down bars" show the days for which both

removed by the kidneys and released into the blood. Creatinine is used in this study to determine the ratios of Cortisol to Creatinine (C:Cr, in nanomoles/L and micromoles/L, respectively) and Testosterone to Creatinine (T:Cr, in nanomoles/L and micromoles/L, respectively) because creatinine levels in blood or urine are relatively stable in a given individual and the rate of excretion of creatinine is relatively constant from day to day within a given individual. Creatinine is often used as a measure of kidney function: high levels of creatinine suggest kidney problems or urinary tract obstructions.

2.2.2.1.1: Equipment and apparatus

A Beckman Spectrophotometer, DU series 600 (DU 640), Beckman Instruments Inc., Fullerton, CA, transmitting light at 500 nm, was used to determine the creatinine values. All other equipment, apparatus and instruments will be discussed within the Procedures section.

2.2.2.1.2: Procedures

The creatinine assay was performed using 100μl samples in duplicates. Polystyrene cuvets were used for the analysis. A blank with 3 ml of water (MilliQ) and a standard (from Sigma Diagnostics' Creatinine kit and protocol) with 3 ml of the Creatinine Standard (3.0 mg/dL; cat. # 925-3) were prepared

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urine samples and behavioural watches were available.

along with duplicates of the pools and samples (200μl of water with 100μl of the sample or pool). First, the alkaline picrate reagent was prepared by mixing 5 volumes of the creatinine colour reagent (cat # 555-1) with 1 volume of sodium hydroxide (NaOH; 1.0 N) solution (cat # 930-65). The alkaline picrate reagent (3 ml) was added to each of the cuvets. The cuvets were then gently shaken to mix the solution, covered with foil and kept aside for 8 to 12 minutes at room temperature. The absorbance of the standard and samples/pools was read at 500 nm compared to the blank (as a reference). Following this initial reading, 100μl of the acid reagent (cat # 555-2) was added to all cuvets and a mix by inversion (repeated twice) was immediately performed. The cuvets were allowed to stand for 5 minutes at room temperature. The final reading of absorbance was then completed at the same wavelength as for the initial reading.

Table 2.8 summarizes the steps described above (steps move sequentially from left to right for each of the three types of solutions or samples).

As noted in McLeod, Moger, Ryon, Gadbois, and Fentress (1996), no differences in creatinine levels or C:Cr levels were found between urine contaminated snow collected from different depths of the snow cover (bottom and top). Experiments were also conducted to determine if repetitive thawing or long stays out of the freezer would affect the stability of the creatinine, cortisol or testosterone readings (Gadbois, Fujita, & Moger, 1998). We found that the urine samples were surprisingly resistant to such abuse and could, for instance, be exposed to room temperature for up to 24 hours without any marked consequence on the measurements.

Table 2.8. Summary of the creatinine assay based on the Sigma Diagnostics protocol.

	H_2O	Creatinine Standard	Urine samples	Picrate solution	Time + reading	Acid reagent	Time + reading
Blank cuvet	300μl	-	-	3.0 ml	8-12 min	100μl	5 min
Standard cuvets (2)	-	300μl	-	3.0 ml	8-12 min	100μl	5 min
Samples/ pools' cuvets	200μl	-	100μl	3.0 ml	8-12 min	100μl	5 min

2.2.2.2 Cortisol assays

2.2.2.2.1 Equipment and apparatus

For Season 1 samples (Sigma protocol) the following beta counter was used: LKB Wallac Display Unit (1215 Rackbetta II Liquid Scintillation Counter), Turku, Finland. For samples from Seasons 2 and 3 (DPC protocol), the following gamma counter was used: LKB Wallac Automatic Gamma Counter (1272 Clinigamma), Turku, Finland. All other equipment, apparatus and instruments will be noted within the procedures section (e.g., polypropylene tubes, waterbath, decanting rack).

2.2.2.2.2 Procedures

Two different radioimmunoassay (RIA) protocols were used for the study. For the first year of data a protocol and antiserum from Sigma Chemical Co. was used (the description can also be found in McLeod, Moger, Ryon, Gadbois and Fentress, 1996). Volumes used for the assays ranged from 10 to 100 µl.

At 50% binding the intra-assay coefficient of variation was 9.4%, and the inter-assay coefficient of variation was 13%. The average recovery after the addition of the cortisol standard (15-250 pg) to the pooled urine samples was 108%.

For the second and third years, a DPC (Diagnostic Products Corporation, Los Angeles, CA) protocol (more specifically the Coat-A-Count Cortisol kit) was used in order to speed the process. This solid-phase radioimmunoassay uses radioactive ^{125}I cortisol and was measured by a gamma counter (described above).

The assay followed a standard RIA procedure. First, the standard curve tubes were set in duplicate in the following fashion: Two polypropylene plain tubes (i.e., non antibody coated) were used for the total count (TC) and two more were used for the non-specific binding (NSB). Next, twelve antibody coated tubes (i.e., six in duplicate; part of the DPC kit) were set for the calibrators. Some samples were assayed with an extended standard curve, that is, by adding one point to the curve in an attempt to increase the sensitivity of the assay. A new standard was thus created by dilution of the second calibrator forming the standard curve (see Table 2.8, "standard 1a" and accompanying note). Depending on the batches analyzed, pools and samples were prepared in duplicate or triplicate and at volumes of 25, 50 or 100 μl. Following the preparation of the standard curve, pools and samples, 1ml/tube of radioactive cortisol was added to each tube. All tubes were vortexed, the TC (total count) tube was set aside and the remaining tubes were incubated at 37°C for 45 minutes. The tubes were then decanted and counted with the gamma counter. The decantation procedure described by DPC was not sufficient to empty the tubes of the solution. Therefore, I modified the decanting procedure and used swabs to gently wipe the edges of the tubes when the racks containing the tubes were inverted. This procedure allowed me to remove more liquid than by decantation alone. I also pressed the racks (up-side-down) on absorbing mats after decantation, before and after the swabbing. This procedure greatly improved the readings from the gamma counter. A summary of the procedure is presented in Table 2.9.

Table 2.9. Summary of the DPC cortisol assay based on the DPC protocol.

	Tubes	Add calibrators	Add urine samples	Add ^{125}I Cortisol and vortex	Incubation (45 min; 37°C) and decantation	Time counted in gamma counter
TC	Non-coated	-	-	1.0 ml	No	1 min
NSB	Non-coated	25μl (A)	-	1.0 ml	Yes	1 min
Std 1: 0μl	Coated	25μl (A)	-	1.0 ml	Yes	1 min
Std 1a: .125μl*	Coated	25μl (B)*	-	1.0 ml	Yes	1 min
Std 2: .25μl	Coated	25μl (B)	-	1.0 ml	Yes	1 min
Std 3: 1.25μl	Coated	25μl (C)	-	1.0 ml	Yes	1 min
Std 4: 2.5μl	Coated	25μl (D)	-	1.0 ml	Yes	1 min
Std 5: 5.0μl	Coated	25μl (E)	-	1.0 ml	Yes	1 min
Std 6: 12.5μl	Coated	25μl (F)	-	1.0 ml	Yes	1 min
Pools and Samples	Coated	-	25, 50 or 100μl of samples or pools	1.0 ml	Yes	1 min
*Note that this standard was created by dilution of the "B" calibrator and was used when the curve was extended for increased sensitivity.						

The RIAPC program for radioimmunoassay calculation (Donald Rieger, © 1987) was then used to calculate the concentration of cortisol from the raw counts (in cpm) before expressed relative to the creatinine concentrations [C (nanomoles/L) : Cr (micromoles/L)].

The intra-assay coefficient of variation of C:Cr was calculated for the two pools available at the time of the validations for the DPC protocol: Pool 94 and Pool 95. Volumes of 25 and 50μl were used for each pool. Table 2.10 summarizes the intra-assay validation data for both pools and volumes. The coefficient of variation for Pool 94 and Pool 95, independently of volume, was of 9.4% (N=30, 11.93±1.12 (s.d.)) and 10.34% (N=30, 10.24±1.06 (s.d.)), respectively. The coefficients of variation for Pool 94 at the 25μl and 50μl volumes were 8.21% (N=15, 12.13±1.0 (s.d.)) and 10.52% (N=15, 11.72±1.23 (s.d.)), respectively. The coefficients of variation for Pool 95 at the 25μl and 50μl volumes were 10.68% (N=15, 10.38±1.11 (s.d.)) and 10.17% (N=15, 10.11±1.03 (s.d.)), respectively.

The inter-assay coefficient of variation of C:Cr was 10.42% when cortisol concentrations of Pool 94 and Pool 95 were measured in duplicate in 10 different assays.

Table 2.10. Summary of intra-assay validation data for C:Cr data for Pool 94 and Pool 95 at 25 and 50 μl.

Pools and volumes	c.v.	Mean	St. dev.	N
Pool 94 (both volumes)	9.40	11.93	1.12	30
Pool 94 @ 25μl	8.21	12.13	1.00	15
Pool 94 @ 50μl	10.52	11.72	1.23	15
Pool 95 (both volumes)	10.34	10.24	1.06	30
Pool 95 @ 25μl	10.68	10.38	1.11	15
Pool 95 @ 50μl	10.17	10.11	1.03	15

2.2.2.3 Testosterone assays

Although some authors (Seal, Plotka, Mech, & Packard, 1987) note that the testosterone production patterns of males cannot be estimated by the assaying of baseline serum samples, this study is based on assays of urine samples for androgen metabolites. It should be noted that developing this assay was significantly more challenging than expected and required more processing of the samples than for cortisol assays. The discussion in Section 2.2.2.1 on hormone:creatinine ratios applies in the case of testosterone as well. Studies using the T:Cr ratio (e.g.: Moss, Clutton-Brock, & Monfort, 2001; Palonek, Gottlieb, Garle, Bjorkhem, & Carlstrom, 1995) are not as common as those using the C:Cr ratio, probably because cortisol blood concentrations are much higher than most steroid hormones, thus, it can be measured in urine without hydrolysis of the sample (which is not the case with testosterone).

2.2.2.3.1 Equipment and apparatus

Both the LKB Wallac Display Unit (1215 Rackbetta II Liquid Scintillation Counter; Turku, Finland) and the LKB Wallac Automatic Gamma Counter (1272 Clinigamma; Turku, Finland) were used to assay the samples. All other equipment, apparatus and instruments will be noted in the procedures section (e.g., polypropylene tubes, waterbath, decanting rack).

2.2.2.3.2 Procedures

Testosterone concentrations were measured by radioimmunoassay (Coat-A-Count Total Testosterone, Diagnostic Products Corporation, Los Angeles, CA). Prior to radioimmunoassay, all samples were subjected to urine hydrolysis. One millilitre of each urine sample was mixed with 200 μl of hydrochloric acid (12N) in a tube, loosely capped and incubated in a boiling water bath for 15 minutes. The hydrolysed samples were stored tightly capped at –20 °C until needed for the radioimmunoassay procedure.

Immediately before radioimmunoassay, the hydrolysed samples were thawed and testosterone in the samples was extracted using diethyl ether (BDH Assurance, ACS 288-76, 1 ppm peroxide). Half a millilitre of each hydrolysed urine sample and 5 ml of diethyl ether were mixed in a glass tube, and each tube was vortexed for one minute. Next, the clear supernatant of diethyl ether fraction in each tube, within which testosterone was dissolved, was collected and transferred into another tube using glass pipettes. Another 5 ml of diethyl ether was added into the former tube with the residual sample, vortexed for one minute, and the clear supernatant was collected and pooled with the previously collected fraction. The collected samples of diethyl ether with testosterone were then placed under an air stream so that the diethyl ether evaporated while the testosterone extracted from the hydrolysed urine samples remained on the tube. Near the completion of evaporation, fresh diethyl ether was flushed on the wall of the sample tube to gather the extracts into the bottom of the tube. When evaporation was complete, 200μl of buffer (human serum-based zero calibrator from Coat-A-Count Total Testosterone kit) was added to the tube to re-suspend the extracts. The samples of re-suspended extracts were then used for radioimmunoassay immediately following the extraction procedure.

In order to correct for the differing recovery rates between samples, 25 μl of tritium-labelled testosterone (^{3}H-T; from Sigma Diagnostics Canada, Mississauga, ON) was added to each of the test tubes with hydrolysed urine samples immediately preceding the extraction procedure. By measuring how much tritium-labelled testosterone was recovered through the extraction procedure, recovery rate of testosterone for each sample was estimated, which was later used for correcting the amount of testosterone measured through radioimmunoassay. Of the 200μl of re-suspended extracts from the extraction procedure, 50 μl was set aside in a vial for counting the recovered amount of tritium-labelled testosterone for each sample. Three vials with 25μl of tritium-labelled testosterone were also prepared to measure the original amount of tritium-labelled testosterone added to the samples. Five millilitres of scintillation fluid (EcoLite Liquid Scintillation Cocktail from ICN Biomedicals, Costa Mesa, CA) was then added to each vial and placed in the beta-counter (1215 Rackbeta II Liquid Scintillation Counter, LKB Wallac Display Unit; SN 150635, part # 1215-103; Turku, Finland) for determining the counts per minute (cpm). The cpm of each sample was divided by the average cpm of the three 25μl tritium-labelled testosterone originally added giving the percentage recovery of testosterone after extraction.

Radioimmunoassay was performed following the protocol provided by Diagnostic Products Corporation. The Coat-a-Count Total Testosterone assay is a solid-phase ^{125}I radioimmunoassay that requires acid hydrolysis if used with urine samples (procedure described above). The procedure is very similar to the procedure previously described for the assay of samples for cortisol levels. An overview of the testosterone RIA procedure is described here with mention of the procedural differences. Each sample was assayed in duplicate using ^{125}I–labelled testosterone as the tracer and antibody-coated tubes. Of the 200µl of re-suspended samples, 50µl in duplicate was added into the antibody-coated tubes and 1.0 ml of ^{125}I–labelled testosterone solution was then added to each tube, vortexed, and incubated in a water bath at 37°C for 3 hours. Following the completion of the incubation, the tubes were decanted thoroughly and placed in a gamma counter (CliniGamma 1272 Automatic Gamma Counter, LKB Wallac; SN 720121, Turku, Finland) for one minute to count the amount of bound ^{125}I–labelled testosterone in each tube. A summary of the procedure is presented in Table 2.11.

Table 2.11. Summary of the DPC total testosterone assay based on the DPC protocol.

	Tubes	Add calibrators	Add urine samples	Add ^{125}I Testosterone and vortex	Incubation (3 hours; 37°C) and decantation	Time counted in gamma counter
TC	Non-coated	-	-	1.0 ml	No	1 min
NSB	Non-coated	50µl (A)	-	1.0 ml	Yes	1 min
Std 1: 0µl	Coated	50µl (A)	-	1.0 ml	Yes	1 min
Std 2: .25µl	Coated	50µl (B)	-	1.0 ml	Yes	1 min
Std 3: 1.25µl	Coated	50µl (C)	-	1.0 ml	Yes	1 min
Std 4: 2.5µl	Coated	50µl (D)	-	1.0 ml	Yes	1 min
Std 5: 5.0µl	Coated	50µl (E)	-	1.0 ml	Yes	1 min
Std 6: 12.5µl	Coated	50µl (F)	-	1.0 ml	Yes	1 min
Pools and Samples	Coated	-	50µl of samples or pools	1.0 ml	Yes	1 min

The RIAPC program for radioimmunoassay calculation (D. Rieger, © 1987) was then used to calculate the concentration of testosterone (nanomoles/L) in each sample using the cpm measured. The results were multiplied by 0.48 and by recovery rate, to obtain the testosterone concentrations of the original, non-hydrolyzed urine samples. (A factor of 0.48 was used because the urine samples were diluted 1-in-1.2 with the hydrochloric acid, then concentrated by 5-in-2 in the extraction process). Finally, the testosterone concentrations were expressed relative to the creatinine concentrations (T:Cr; nanomoles/L : micromoles/L).

The range of sensitivity of the radioimmunoassay was truncated at 0.6934 nmol/L (20 ng/dl). The intra-assay coefficient of variation of T:Cr was 10% when a set of 10 tubes from a sample was assayed in one run (N=10, average=1.00 ± 0.099 (s.d.), c.v.=10%). The inter-assay coefficient of variation of T:Cr was 24% when the testosterone concentrations of a sample were measured in duplicate in 4 different assays (N=4, average=1.2 ± 0.29 (s.d.), c.v.=24%). When a sample was diluted with the zero calibrator to make 3 different dilutions of the sample and assayed in duplicate, the testosterone concentrations (nmol/L) from the 3 diluted samples showed approximate parallelism (Table 2.12).

Table 2.12. Parallelism of a sample diluted three times.

Sample Dilution	**Observed (O)**	**Expected (E)**	**%O/E**
1.00	2.58	-	-
0.50	1.42	1.29	110%
0.25	0.79	0.64	123%

2.2.3 Weather data

Although weather observations were always made on videotape (an audio commentary was made by the observer) at the beginning of each watch, the weather data used for correlational analyses came from the databanks of

Environment Canada. The data came from the Atlantic Climate Centre (77 Westmorland Street, Suite 400 Fredericton, New Brunswick, Canada, E3B 6Z3; the Fredericton office is responsible for the coverage of New Brunswick, Prince Edward Island, Nova Scotia, Newfoundland and Labrador). Following consultation with Environment Canada, it was decided that data from the Upper Stewiacke Station (station 8206200, Colchester County; in operation since 1915; 45° 13' N, 63° 00' W; elevation: 23 metres) would be the most appropriate to reflect the Shubenacadie weather data. The Upper Stewiacke station is 44 kilometres East of Shubenacadie and has the advantage (like Shubenacadie) of being inland, away from huge masses of water (unlike Shearwater Station near Halifax and the Truro station near Cobequid Bay).

Table 2.13 lists the chosen elements and their units for the day by day monthly data as well as the barometric pressure data available hourly for each day of the 3 breeding seasons under investigation.

Table 2.13. Monthly (day by day) and daily (hour by hour) weather data provided by Environment Canada.

Elements	**Units**	**Time period**
Daily maximum temperature	0.1 °C	December 1 1993 to March 31 1994 December 1 1994 to March 31 1995 December 1 1995 to March 31 1996 One data point per day.
Daily minimum temperature	0.1 °C	
Daily mean temperature	0.1 °C	
Daily total rainfall	0.1 mm	
Daily total snowfall	0.1 cm	
Daily total precipitation	0.1 mm	
Daily snow on the ground	1 cm (full cm)	
Hourly barometric pressure (station pressure*)	.01 kPa	Same dates as above available on a 24 hour period, i.e., 24 data point per day.
* station pressure: a reminder that the barometric pressure is taken at the elevation of the station, i.e., 23 m.		

It is reasonable to believe that the daily and hourly information from Upper Stewiacke should be representative of the fluctuations observed in Shubenacadie. Inland Nova Scotia is characterized, as is most of the province, by the daily variations in temperature caused by the alternation of arctic and maritime air. Inland Nova Scotia records averages of -4 to -6°C during the month of January. Only 15% of Nova Scotia's annual precipitation takes the form of snow (this is with the exception of Cape Breton Island, where 30% is a more accurate figure). The snow cover season, defined as when 2.5 cm or more of snow are on the ground, is longest inland, with an average of 140 days.

2.3 Database and Data Management

The data were managed by a relational database that I developed for the purposes of this study. The database (created with FileMaker's FileMaker Pro Developer Edition 4.0 and updated with FileMaker Pro Developer 5.0 and 5.5) contains 7 modules: a Demographic Module with the demographic information on each wolf (sex, pack, date of birth, rank, etc.), a Sample Module describing the urine samples at the time of collection (the information summarized in Table 2.5), an Ethographic Module, which is an event recorder/ethogram of the social interactions (the information summarized in Table 2.6), a Creatinine Module containing the data from the creatinine assays, a Cortisol Module with the data from the cortisol assays, a Testosterone Module with the data from the testosterone assays and finally a Weather Module for all of the weather data provided by Environment Canada. The relational structure of this database allows the sharing of information among modules. For example, the Demographic Module feeds demographic data to the other modules identifying the names of the wolves. Both the Testosterone and Cortisol Modules link to the Creatinine Module to calculate the T:Cr and C:Cr ratios respectively. The database, in addition to the usual database functions (searches and sorts), does most of the assay calculations and computes sociometric matrices for the dyadic interactions documented in the Sociometric Module. This data management system was a central tool in the storage, management, synthesis and analysis of the data. Because of the correlational nature of the study and the massive amount of data available for analysis, the relational database was crucial for the organization and preparation of data for further statistical analysis.

3. Data Analyses and Results

Data analyses included an analysis of hormones (cortisol and testosterone), behaviour (aggression), and environmental factors (weather). Cortisol and testosterone levels were examined as a function of Season (year of study), Sex, and Wolf. Note that the cortisol data from the first year ("Season 1") of the study (1993-1994) were published by McLeod, Moger, Ryon, Gadbois, and Fentress (1996).

3.1 Hormonal Data

Urine is naturally pooled in the bladder before voiding, sometimes for long periods of time, especially in subordinate animals who do not urine-mark and therefore sometimes retain urine for long durations (see footnote 36). Although it is impossible to determine for how long an animal has been "pooling" steroid hormones in his/her bladder, or if there is consistency in their pooling amounts, it is reasonable to think that an averaging of all samples from an individual for a given day should actually provide the best estimate of his/her hormonal status[36]. Hormonal values were therefore averaged by day for each wolf, as in McLeod, Moger, Ryon, Gadbois, and Fentress (1996). This means that if a wolf produced 5 uncontaminated, non-overmarked urine marks in the snow on February 14th, the five C:Cr or T:Cr values obtained from the assays of these urine marks were averaged for that day. Only urine marks with measurable readings of Creatinine and either Cortisol or Testosterone were included in the analyses. Figure 2.3 (Section 2) illustrates this process from the urination to the final selection of the values used for descriptive and inferential statistics.

For every major data set analyzed, Grubb's tests (or the ESD method, extreme studentized deviate) were performed to identify outliers. All values included in the analyses were not considered significant outliers (at $p>0.05$).

The same sets of data were also tested for normality with the Dallal and Wilkinson approximation to Lilliefor's method, an adaptation of the Kolmogorov-Smirnov test. All sets of data passed the normality test with $p>0.10$.

3.1.1 Cortisol

McLeod, Moger, Ryon, Gadbois, and Fentress (1996) determined that there were no significant differences between samples collected in the morning

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[36] For subordinate animals, the natural pooling could include up to a few days of urine

and those collected in late afternoon and evening. Watch times could vary throughout the season. Since wolves are crepuscular animals, observations and data collection started soon after sunrise or just before sundown. For this reason, and to avoid inflating the dataset with multiple observations on the same "generous" animal to the detriment of less generous ones, C:Cr values were averaged by day for each wolf [37]. The daily values for each animal were then used for the descriptive and inferential statistics. Table 3.1 shows the number of contributions (number of daily data points) that each animal contributed for each of the three seasons of the study. The dominant male and female are also identified (α). Note that there could be a number of potential reasons for a daily contribution of "0": No sample was produced by the wolf, the sample(s) produced was/were contaminated, overmarked or contained blood[38] or there were no measurable levels of either or both Creatinine and Cortisol.

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retention, and in dominant animals, less than an hour.

[37] Remember that dominant wolves urine-mark significantly more than subordinate ones. An averaging by day is a way of controlling for the potentially important discrepancy in urination frequency between alpha and beta individuals.

[38] Because cortisol levels are higher in blood, bloody samples would automatically bias the Cortisol amount in the C:Cr ratio.

Table 3.1. Number of contributions from each wolf of the main pack per season. Note that one contribution could be the average of more than one urine sample on a given day.

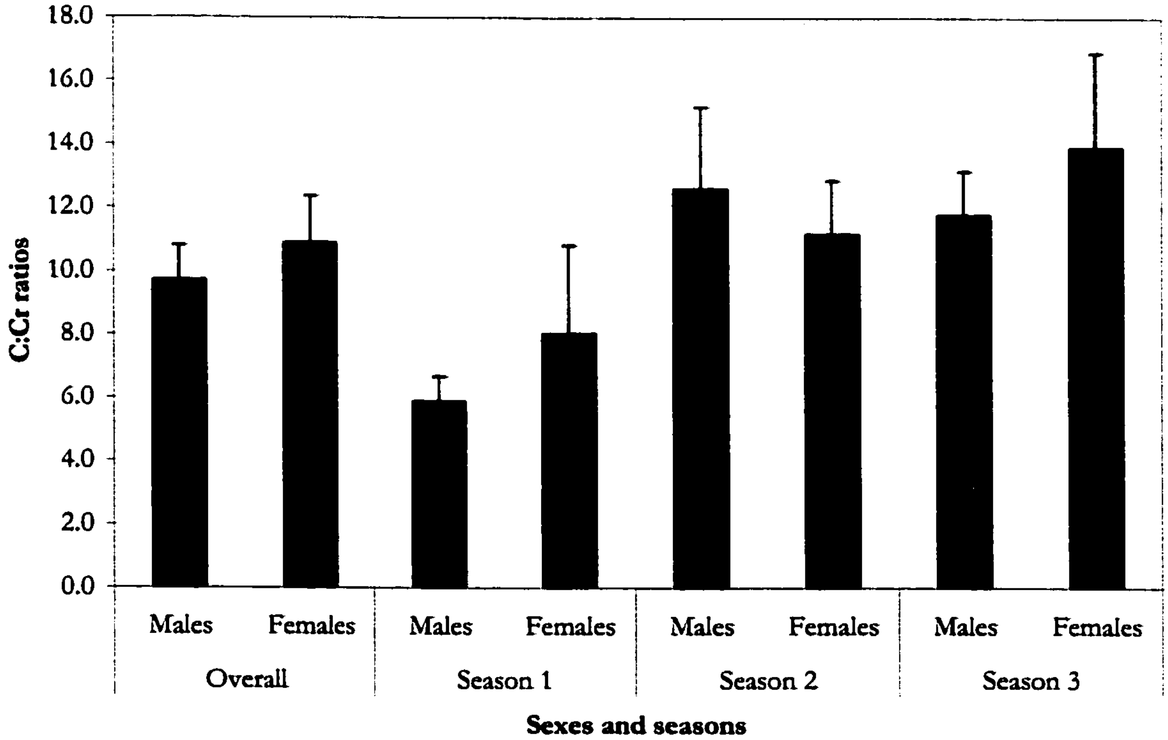
Cortisol	**Season 1**	**Season 2**	**Season 3**
MALES			
Ashley	6	Deceased	Deceased
Galen (α)	6	5	7
Homer	4	3	5
Jasper	7 (yearling)	3	2
Noah	1	6	2
Ulysses	Unborn	Unborn	3 (yearling)
Voochko	3	3	3
Winston	3	Deceased	Deceased
FEMALES			
Celtie	5	0	4
Devil Child	6 (yearling)	2	17
Fiona	7	2	4
Morgaine	6	5	2
Pawnee (α)	8	8	8
Tess	2	1	2
Xyla	4	4	7

Three steps were taken in the analysis of the data. Firstly, I wanted to confirm that there were no significant differences between males' and females' global mean C:Cr ratios for each season. The next step was to determine whether any seasonal effects were present, that is, whether the mean C:Cr ratios differed significantly between the three winters of the study. Thirdly, I examined the individual differences in C:Cr levels within each season. In addition, an overview of the other packs (see Section 2, Methods) contributing some Cortisol data for Season 1 and 2 is presented.

3.1.1.1 C:Cr ratios in males and females and between seasons

As originally reported by McLeod, Moger, Ryon, Gadbois, and Fentress (1996), no differences between male and female C:Cr ratios were found in Season 1. Figure 3.1 shows the Global (all three Seasons) and Seasonal C:Cr ratios for males and females of the main pack.

Figure 3.1. Global and Seasonal C:Cr ratios for males and females (± sem).



The data for all wolves were examined to determine the presence or absence of a gender effect and a seasonal effect in the C:Cr ratios.

Although the use of a mixed ANOVA with one between factor (Sex) and one repeated measure (Season) would seem to be the ideal approach to analyze the data in Figure 3.1, there are difficulties arising from the fact that the design is unbalanced. That is, each wolf did not contribute data to all seasons. Empty cells are present because some animals (e.g., Ulysses for Season 1 and Season 2) were not yet born, some animals (e.g., Ashley and Winston for Seasons 2 and 3) were dead, and one animal (Celtie) simply did not contribute to one Season. There are two potential remedies available to allow for the use of a repeated measures design. Both were judged unacceptable.

First, missing values could be replaced by some average value. The problem here lies in the choice of the averaged value. Would the individual's average be chosen, assuming he or she would contribute a similar value across the three years of the study? Or, should the average value for other same-sex animals within the same season be used? Neither value seems appropriate, especially given the small data set to begin with.

A second alternative would be to perform the repeated measures ANOVA with case-wise deletion of animals who do not contribute data to all three seasons. Considering that several animals in this study did not contribute many data points (in some cases, only one data point for an entire season) this solution is also unsatisfactory. An alternative would be to run separate ANOVA's for each combination of seasons (i.e., one analysis for animals contributing only to Season 1 and 2, a second analysis for those contributing to Season 2 and 3, etc.), but the partitioning of the data in this way may give more or less weight to specific sub-groups of animals, which may be problematic given the already small sample size. I chose instead to approach the problem factor by factor, with the careful use of unpaired t-tests and one-way ANOVA's, reducing the loss of subjects or the likelihood of biasing the data.

No correction for multiple tests was performed because of the small sample size and the loss of power that could occur as a result. It should be noted that these analyses are exploratory in trying to elucidate the relation between hormones and behaviour. Because data from three seasons are available, reliability can be partly assessed by examining the consistency of patterns across seasons.

The first unpaired t-test examined the differences between males and females globally, that is, collapsed across seasons. No difference was found, $t_{(174)}= 1.849, p=.0662$, although it may appear as though this result is approaching significance (females higher). If values from Xyla, who may be considered a quasi-outlier (see Figures 3.3, 3.4, 3.5) are removed from the data, however, the new analysis shows a clear lack of group difference ($t_{(159)}$= .028, p=.9780). In other words, if there were a group difference, it would be attributed to one female only rather than a pattern of differences between males and females.

The next 3 unpaired t-tests compared males and females for each of the three seasons of the study. For each season, no significant differences were found between males and females, with $t_{(66)}$ = 1.160, p=.2502 for Season 1, $t_{(40)}$ = .193, p=.8480 for Season 2 and finally, $t_{(64)}$ = 1.220, p=.2268 for Season 3.

An examination of Figure 3.1 suggests an overall increase of C:Cr levels between seasons. A one-way repeated measures ANOVA was performed on all three seasons. There was, in fact, a significant difference across Season, $F_{(2, 20)}$=12.866, p=.0003. It should be noted that, as mentioned earlier (see also Table 3.1), animals who did not contribute data to each of the three seasons were eliminated: Ashley (present only for Season 1), Ulysses (present only for Season 3), Winston (present only for Season 1), and Celtie (contributed only to Season 1 and Season 3). It should also be noted that the data presented in Figure 3.2 includes the animals omitted from the repeated measures ANOVA.

The main effect of Season was explored with Tukey-Kramer post hoc pairwise comparisons. The Tukey-Kramer is a modification of the original

Tukey HSD and allows for unequal *n*'s (Kirk, 1982). The Tukey tests are more robust than the Sheffé's when only pairwise comparisons are considered (Keppel & Zedeck, 1989; Shavelson, 1988) and they are quite conservative with small *n*'s.

The Tukey-Kramer test identified significant differences (significance level of 5%) between Season 1 (7.409; s.d.=5.911)[39] and Season 2 (11.818; s.d.=4.827) and between Season 1 and Season 3 (13.173; s.d.=5.691). Figure 3.2 shows the global increase in C:Cr levels between Season 1 and the subsequent seasons.[40]

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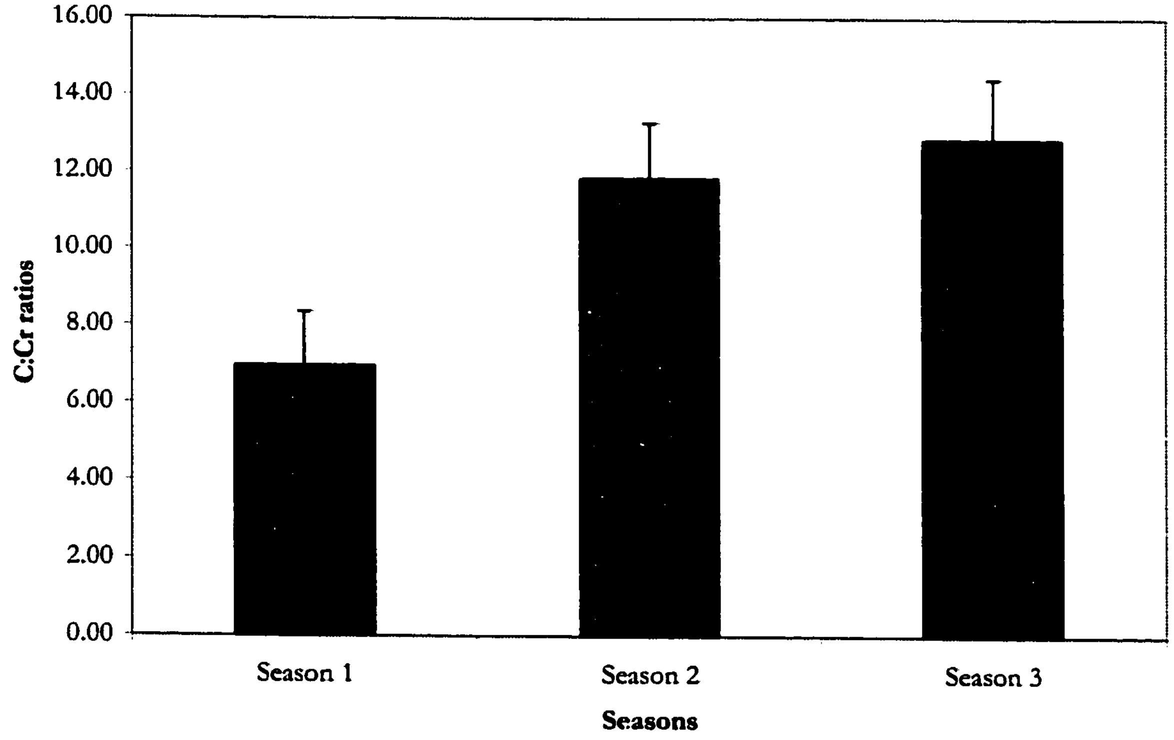
[39] Values in the parentheses are the average and standard deviation from the repeated measures ANOVA's. They do not correspond exactly to the values presented in the corresponding figure because the figure includes data not omitted from the repeated measures ANOVA.

[40] A one-way ANOVA on all samples, regardless of wolf without repeated measures (and without the corresponding loss of individuals) confirms the seasonal effect ($F_{(2,\ 173)} = 14.584$, $p<.0001$). Tukey-Kramer post-hoc tests with this design also find significant differences between Seasons 1 and 2 and Seasons 1 and 3.

Figure 3.2. Seasonal C:Cr ratio increase (± sem).



In summary, I conclude that there was no overall sex effect or season-specific sex effect. In other words, males' and females' C:Cr ratios did not differ significantly, whether collapsed across Seasons or examined within each Season. There was, however, a significant difference in C:Cr levels between Season 1 and the other two Seasons.

3.1.1.2 Individual differences

It is impossible to compute a repeated measures ANOVA (15 Wolves x 3

Seasons) with so many empty cells for so many individuals[41] (see Table 3.1). Since there is good evidence to support the idea that males and females have independent dominance hierarchies (Fentress, Ryon, McLeod, & Havkin, 1987; McLeod et al., 1996; McLeod, Ryon, & Fentress, unpublished manuscript; Zimen, 1982), individual differences were examined separately within each sex. Also, because I identified a Season effect, each Season was examined separately. Three independent one-way ANOVA's were therefore computed to examine individual differences within each Season.

Figures 3.3, 3.4 and 3.5 show the individual profiles for each of the three seasons, respectively. Note that the same seven females contributed to the data for the three years of the study. For the males, starting in Season 2, Ashley and Winston (deceased) were no longer present and a pup (Ulysses) contributed to Season 3 only.

Season 1 (Figure 3.3), as presented in McLeod et al. (1996) shows a strong homogeneity of the C:Cr values with the exception of Voochko (beta male) in males and Xyla (omega female) in females. There was, in fact, an overall difference among individual males (F(6,23)=4.267, $p< 0.0050$) and females

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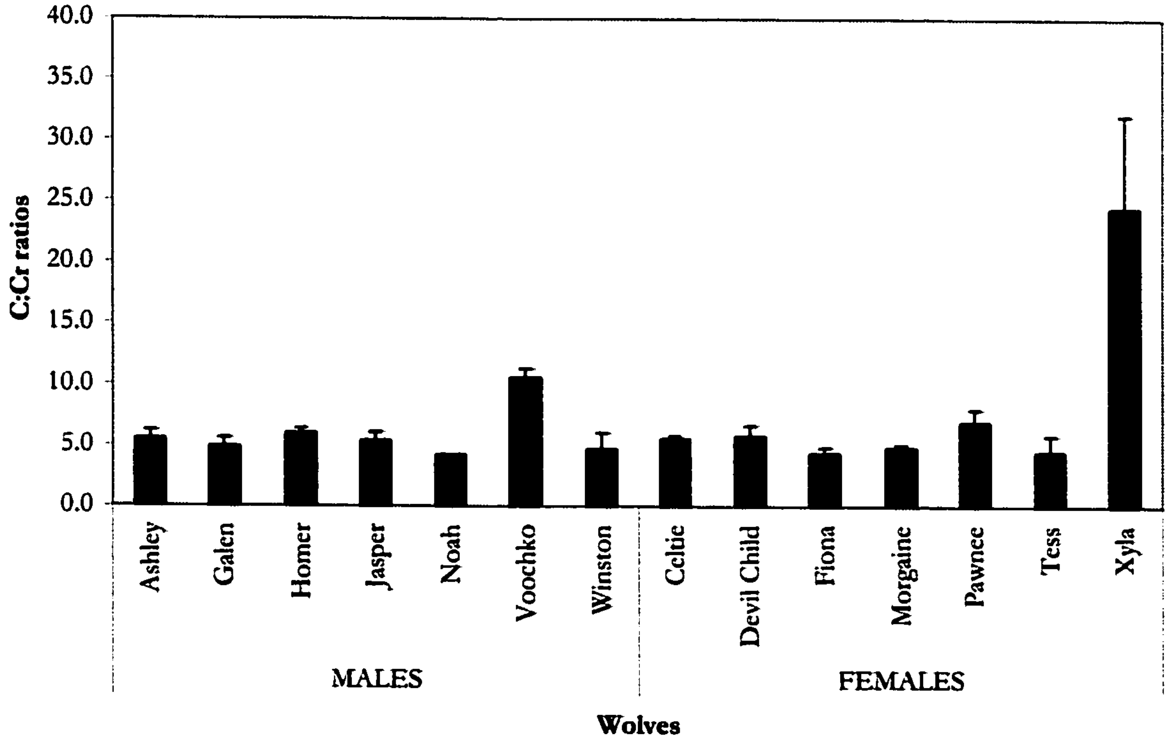
[41] Other options (deleting cases with insufficient data or filling empty cells with any measures of central tendency) were judged inadequate.

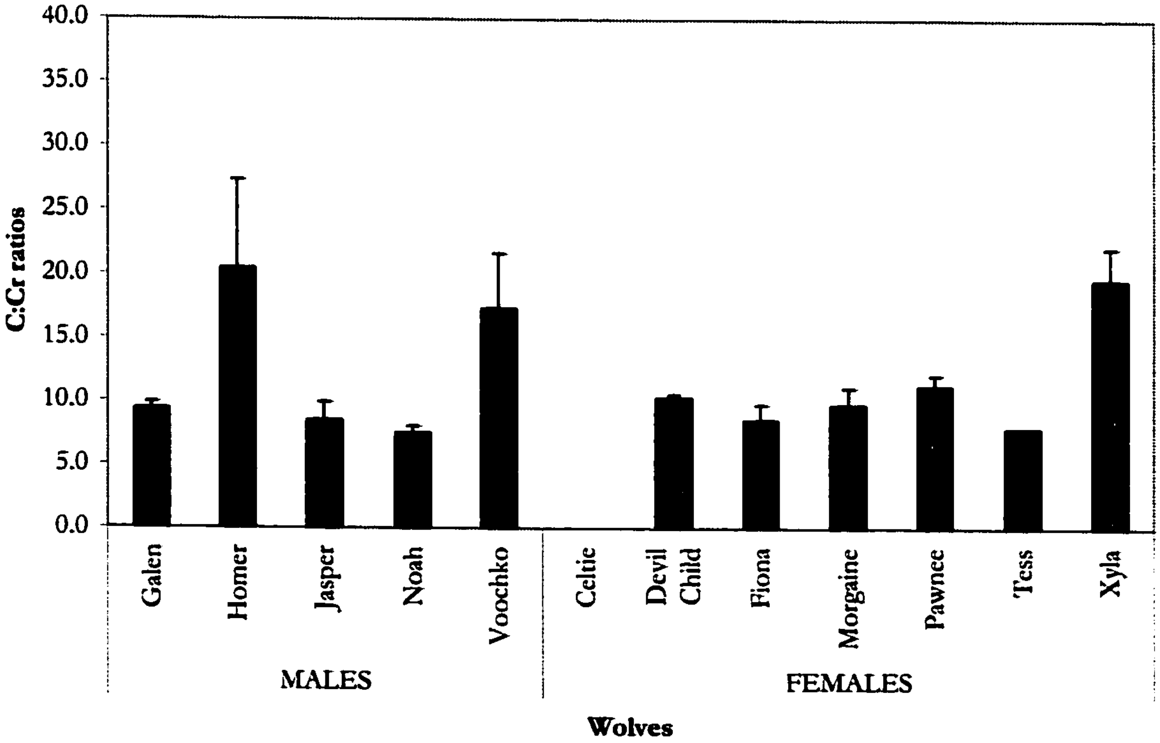
(F(6,31)=8.444, p< 0.0001). As reflected in Figure 3.3, the Tukey-Kramer tests identified Voochko as being different from all other males (except Noah, but there was only one observation for Noah) and Xyla as being different from all other females.

Figure 3.3. Mean C:Cr ratios for individual males and females for Season 1 (± sem). See Table 3.1 for sample size. Adapted from McLeod, Moger, Ryon, Gadbois, and Fentress (1996).



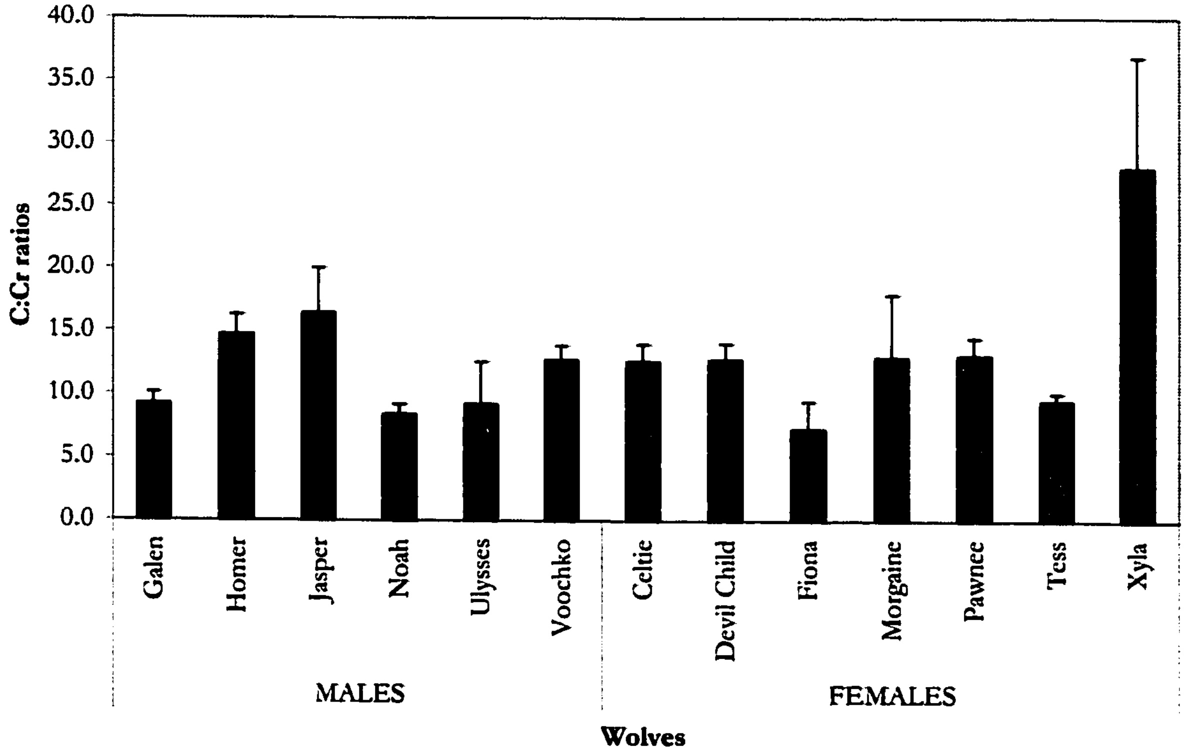
The pattern changed with Seasons 2 and 3. As noted earlier, there was a significant overall increase in C:Cr ratios between Season 1 and 2 and between Season 1 and 3. As with Season 1, there were significant differences among both males (F(4,15)=4.248, p< 0.0170) and females (F(5,16)=5.978, p< 0.0027) in Season 2. Within males, the difference between Homer's high cortisol levels and Noah's low cortisol levels were identified as significant by a Tukey-Kramer post hoc test. In females, similar to Season 1, the difference was between Xyla and each of the other females.

Figure 3.4. Mean C:Cr ratios for individual males and females for Season 2 (± sem). See Table 3.1 for sample size.



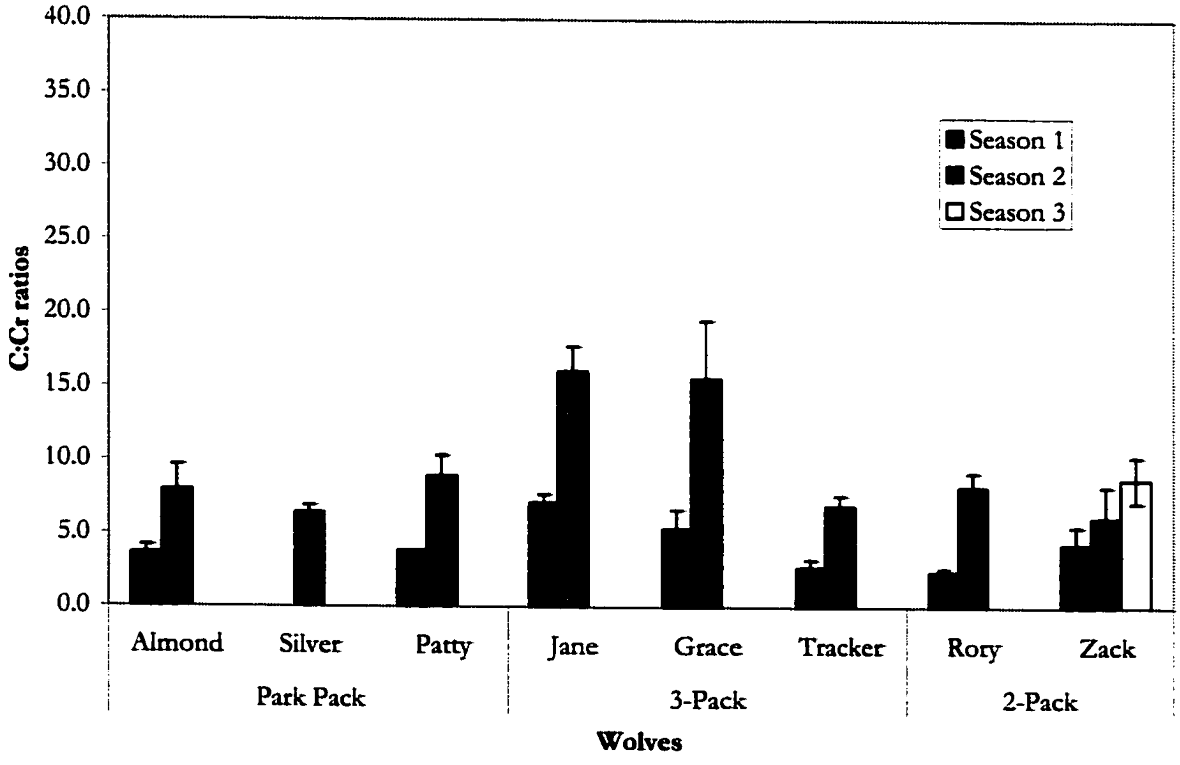
Season 3 (see Figure 3.5) was also characterized by an overall higher C:Cr ratio level for the pack (as compared to Season 1) but the within sex pattern was not as clear as for the previous seasons. There was a marginal difference within males ($F_{(5,16)}=2.963, p< 0.0443$) with no individual pairwise comparisons identified as significant by the Tukey-Kramer. In females, significant pairwise differences were found only between Devil Child and Xyla and between Fiona and Xyla with a significant overall difference ($F_{(6,37)}=2.535, p< 0.0371$). Note that the Tukey-Kramer test identified a significant difference between Xyla and Devil Child and not between Xyla and Celtie, despite the fact that the absolute magnitude of each difference is the same. This is due to differences in the sample sizes (greater in Devil Child than in Celtie), which are used in computing the Tukey-Kramer.

Figure 3.5. Mean C:Cr ratios for individual males and females for Season 3 (± sem). See Table 3.1 for sample size.



In addition to the main pack, as explained in the Methods, three other packs were sampled on occasion during the first two seasons (and a few times in Season 3 for one individual, Zack). Figure 3.6 shows the values for these animals. There was an apparent increase in C:Cr levels in the second season. This may have been due to fairly unusual and systematic observations done by myself during the winter of that year. Indeed, members of the Park Pack (Shubenacadie Park Zoo) and the adjacent hand-raised 2-Pack and 3-Pack were observed for one hour on the days of observations by myself (in order to identify the "owners" of the samples). Unfortunately, between season behavioural data was not available in order to determine a behavioural origin to this increase in C:Cr, but it should be noted that in the smaller packs, especially in the Park Pack (Almond, Silver and Patty), behavioural interactions were virtually never intensively aggressive (Almond and Silver were castrated males). Since those packs were not the primary focus of this study, little more will be mentioned about them.

Figure 3.6. Mean C:Cr ratios for individual males and females for all Seasons for the smaller packs (± sem).



3.1.2 Testosterone

The same sequence of steps taken to analyse the cortisol data was applied to the testosterone data. T:Cr values were averaged by day for each wolf (see Section 3.1.1 above). The first step was to confirm that males and females varied in their levels of androgen. The second step was to determine if a seasonal effect could be identified with Testosterone. The third, and arguably most important step, was to look at the individual profiles. Table 3.2 shows the number of contributions (number of daily data points) from each animal for each of the three seasons of the study. The dominant male and female are also identified (α). Remember that there could be a number of potential reasons for a daily contribution of "0": No sample was produced by the wolf, the sample(s) produced were contaminated, overmarked or contained blood or there were no measurable levels of either or both creatinine and testosterone.

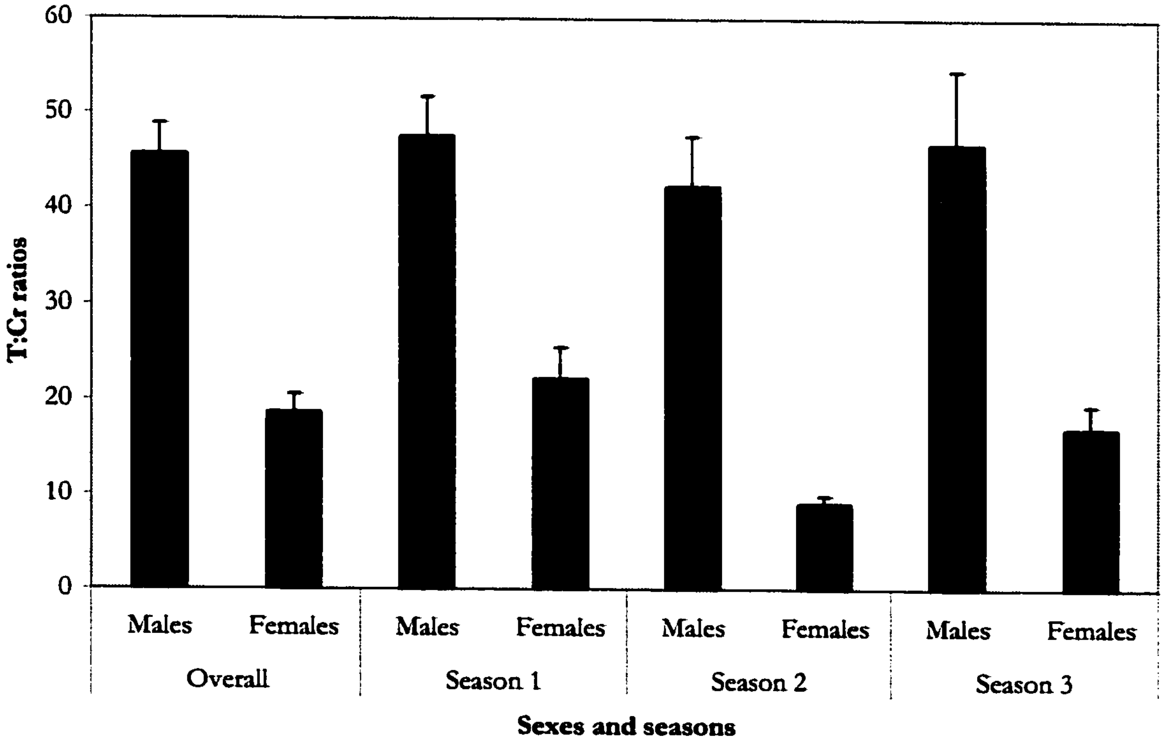
Table 3.2. Number of contributions from each wolf of the main pack per season. Note that one contribution could be the average of more than one urine sample on a given day.

Testosterone	**Season 1**	**Season 2**	**Season 3**
MALES			
Ashley	3	Deceased	Deceased
Galen (α)	6	6	8
Homer	2	3	4
Jasper	6 (yearling)	6	1
Noah	2	6	1
Ulysses	Unborn	Unborn	4 (yearling)
Voochko	5	2	3
Winston	3	Deceased	Deceased
FEMALES			
Celtie	5	0	3
Devil Child	2 (yearling)	1	13
Fiona	10	0	2
Morgaine	6	2	0
Pawnee (α)	9	2	5
Tess	0	1	2
Xyla	1	1	5

3.1.2.1 T:Cr ratios in males and females and between seasons

A gender difference was expected in androgen levels, with males having higher values than females. Figure 3.7 shows the expected pattern which was confirmed by unpaired t-tests comparing males and females collapsed across all three seasons ($t_{(138)} = -7.00, p<.0001$) and for each season of the study. In Season 1 ($t_{(58)} = -4.850, p<.0001$), Season 2 ($t_{(28)} = -3.439, p=.0018$) and, Season 3 ($t_{(48)} = -4.124, p=.0001$) males had significantly higher levels of Testosterone than females.

Figure 3.7. Global and Seasonal T:Cr ratios for males and females (± sem).



The next step is to determine if a season effect was present. I have already determined that there was a difference between males and females, so, in principle, the next step would be to examine the season effect within each sex (in other words, one repeated measures ANOVA for each sex). If I did this I would have lost more individuals than it seems reasonable[42]. Despite this reduction in subjects, the visually apparent differences in T:Cr levels from Figure 3.7 across seasons in females was confirmed ($F_{(2,\ 4)}$=13.368, p=.0169) and the absence of such a seasonal variation was confirmed in males ($F_{(2,\ 8)}$=.280, p=.7628)[43]. Tukey-Kramer post-hocs on the seasons within females identified a significant difference between Seasons 1 and 2 only. When sexes were collapsed, no main effect of season was found ($F_{(2,\ 14)}$=.215, p=.8088).[44]

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[42] For example, from 7 potential females, the data set would be reduced to 3 (less than half of the total number of females).

[43] 5 of the 7 males were included in this analysis.

[44] It should be noted that a one-way ANOVA on all of the samples, regardless of wolf, by seasons (not a repeated measures design, so no loss of individuals) still found no seasonal differences ($F_{(2,\ 138)}$ = .562, p= .5716).

3.1.2.2 Individual differences

The rationale used and steps followed in Section 3.1.1.2 for C:Cr values was followed for the T:Cr levels. Figures 3.8, 3.9 and 3.10 show the individual profiles season by season.

There were no significant differences within females ($F_{(5, 27)}$= 1.085, p=.3909) or within males ($F_{(6, 20)}$= 1.588, p=.2022) in Season 1. Figure 3.8 illustrates, in the context of those ANOVA's, highly variable T:Cr ratios within each sex.

Figure 3.8. Mean T:Cr ratios for individual males and females for Season 1 (± sem). See Table 3.2 for sample size.

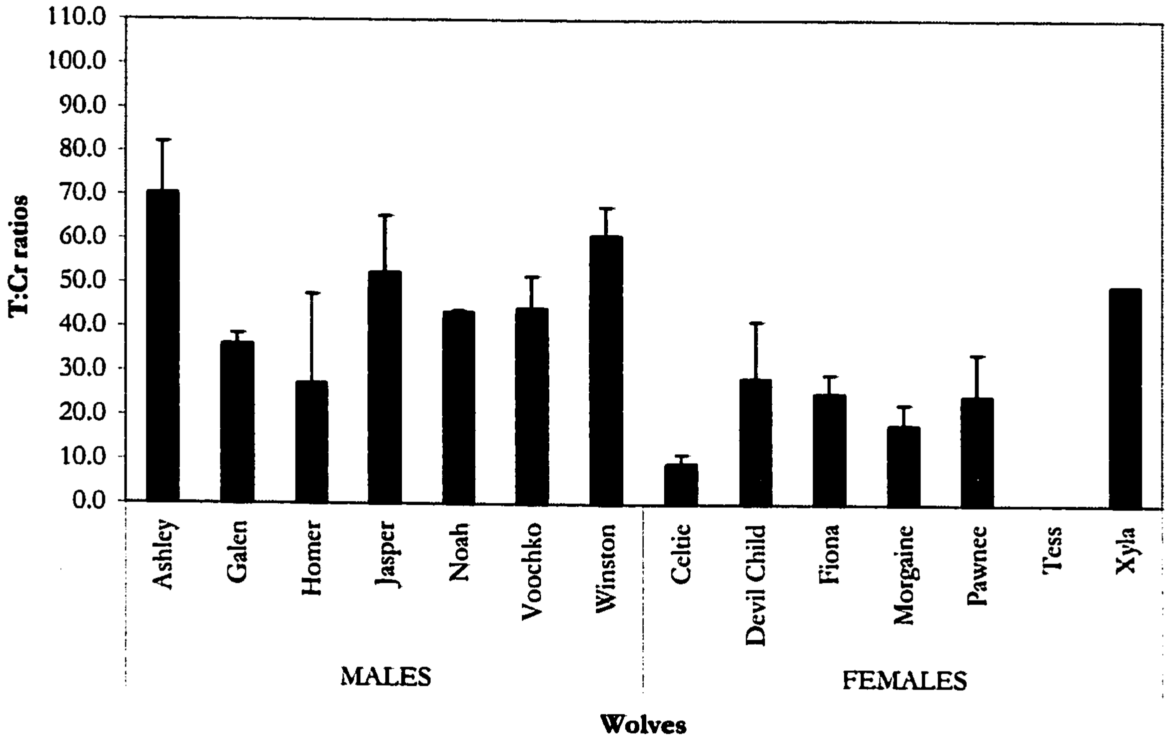


Figure 3.9 presents the data for Season 2. No differences among females were found ($F_{(4, 2)}$=.369, p=.8197). It should be noted that few T:Cr values contributed to this analysis (single values for Devil Child, Tess and Xyla, two values each for Morgaine and Pawnee and nothing for Celtie and Fiona). The situation in males was quite different. There was a significant difference among males ($F_{(4, 18)}$=4.783, p=.0083), and, more specifically, (from the Tukey-Kramer's) between Voochko and each of the other males. Consistent with these elevated values during Season 2, Voochko was engaging in very intense fights

with both Galen (the alpha male) and Homer (the beta of the previous year). Although Voochko maintained his rank, he was heavily challenged by Homer.

Figure 3.9. Mean T:Cr ratios for individual males and females for Season 2 (± sem). See Table 3.2 for sample size.

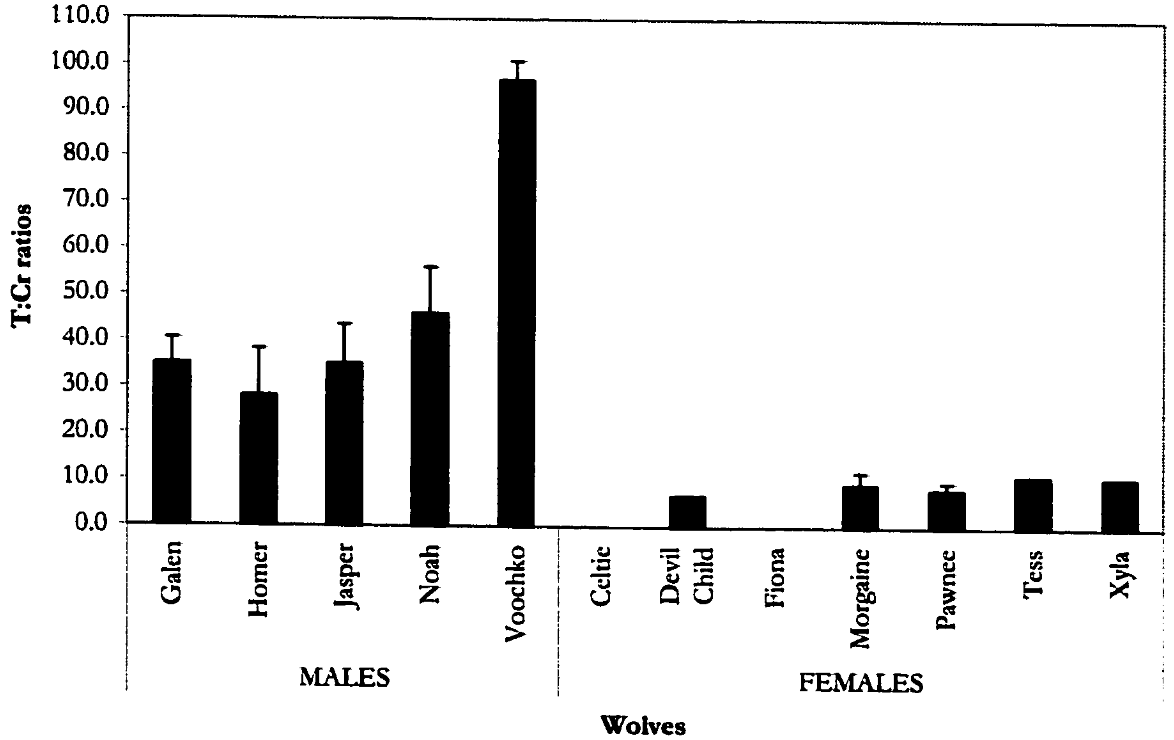
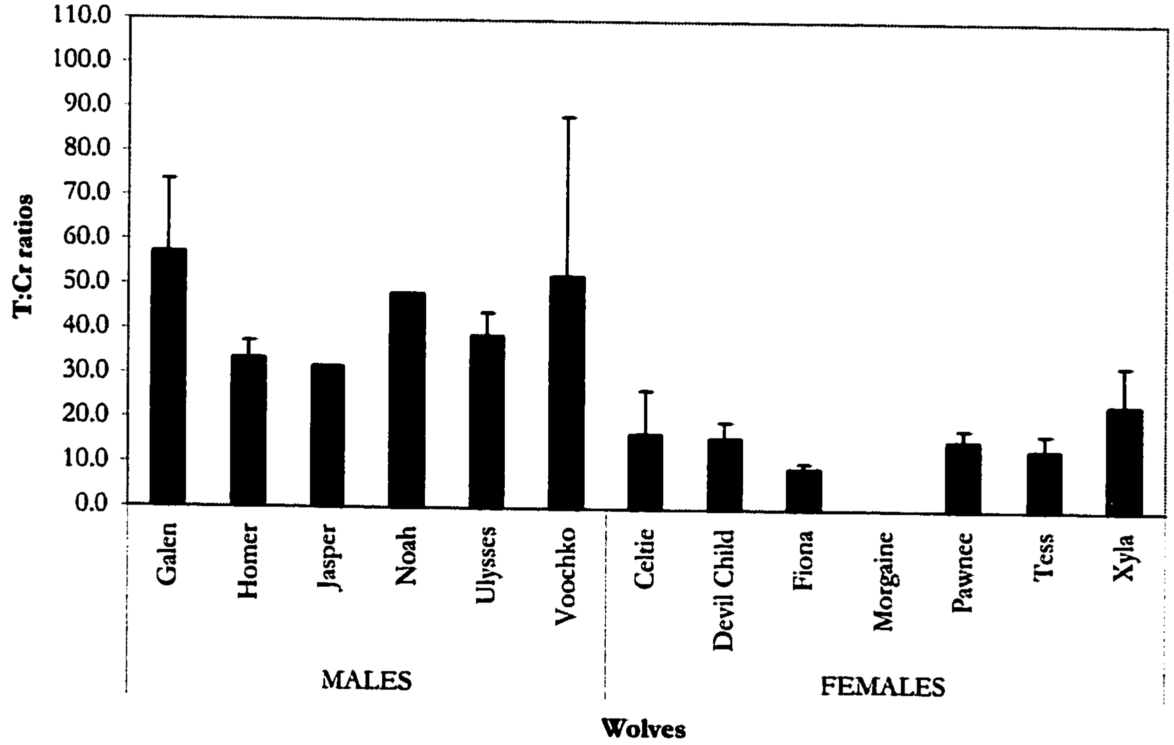


Figure 3.10 represents Season 3 and visually evokes Season 1. Indeed, no differences were found among females ($F_{(5, 23)}$=.684, p=.6403) or males ($F_{(5,}$

$_{15)}=.274, p=.9201)$[45]. It is interesting to note here that Voochko's levels were reduced by almost half relative to the previous year. In fact, Homer became the beta male sometime before the breeding season. It should be noted that Voochko appeared to be in poor health during that breeding season.

Figure 3.10. Mean T:Cr ratios for individual males and females for Season 3 (± sem). See Table 3.2 for sample size.



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[45] When data from all Seasons were collapsed, there were no overall differences among males $(F_{(7,63)}=1.231, p=.2996)$ or females $(F_{(6,62)}=.856, p=.5323)$.

3.2 Weather Data

Recall that information regarding the weather conditions for each of the three years of the study was obtained from Environment Canada. This was to control for the possibility that weather was a factor in influencing either behavioural or hormonal patterns.

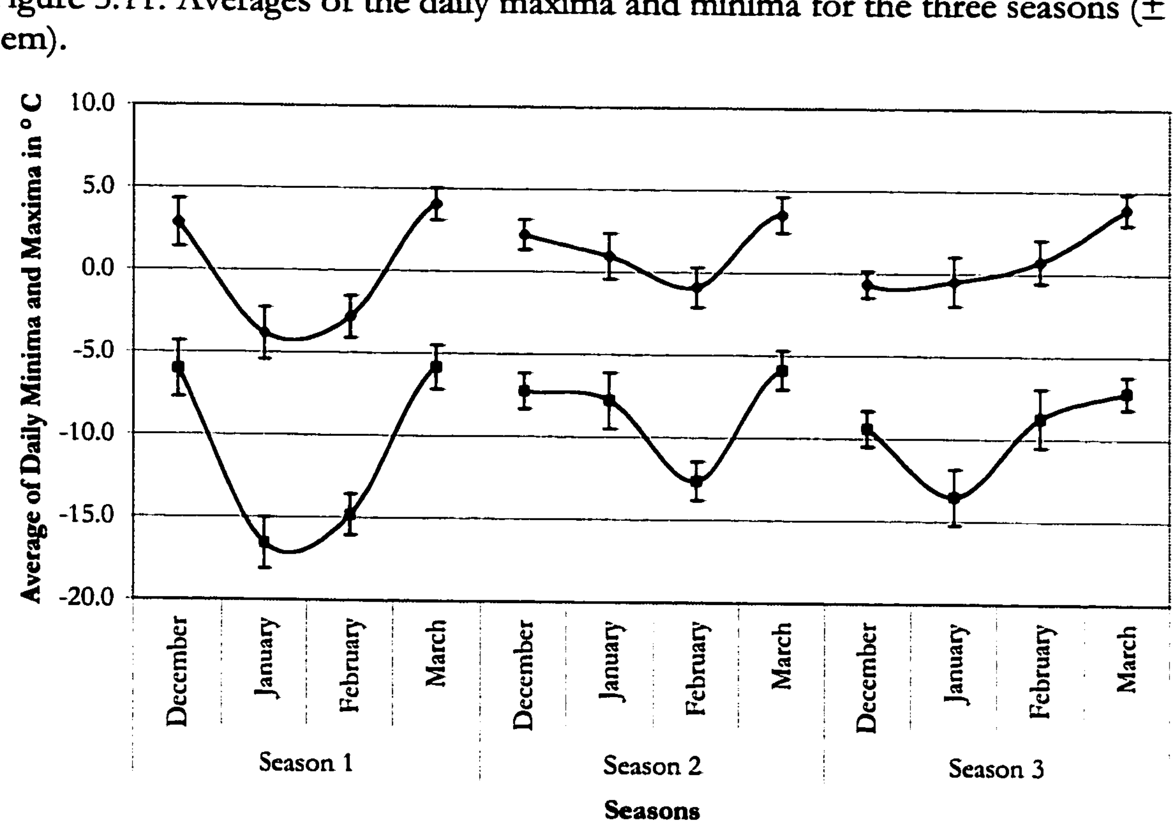
First, a subjective evaluation of the three seasons by the researchers involved in the field was of three remarkably mild winters with minimal precipitations overall, and especially modest amounts of snow. Environment Canada did not report any exceptional weather deviations or events during those three winters, with the exception of a slightly above average amount of rain, likely linked to the milder temperatures.

Recall that three types of weather data were requested from Environment Canada: temperature, precipitation, and barometric pressure. The records of precipitation were incomplete, and could be misleading. The remaining focus will be on the other two measures that are thought to have a potential impact on the behaviour and stress levels of the wolves. The potential effect of temperature is assumed to be direct (stress response caused by extremes, including the range between maxima and minima). The effect of barometric pressure is assumed to be by anticipation (i.e., reactions and adjustments to rises and falls in barometric pressure which precede weather changes).

In principle, a day to day account of these changes (or even hour by hour) would have been ideal, but since the corresponding behavioural and hormonal data was not available to that degree of detail, the weather parameters were examined month by month (December to March) for each year of the study (1994 to 1996).

Figure 3.11 shows the monthly average of the daily minima and maxima for the three breeding seasons. Season 1 had the lowest temperatures and the largest deviations between minima and maxima. January and February of that year, the key months for mating in Canadian wolves, showed the coldest temperatures of the three winters (-15°C and below). Allow me to remind the reader that the global stress levels of males and females were at their lowest that year.

Figure 3.11. Averages of the daily maxima and minima for the three seasons (± sem).



The second measure explored was the barometric pressure (in kPa)[46]. A limited amount of literature (e.g., Malechek & Smith, 1976)[47] has suggested that mammals and birds may have the ability to "predict" or anticipate, or at least behaviourally adapt to weather changes by "feeling" changes in barometric

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[46] The only meteorologic station with barometric pressure data available was Halifax' International Airport. The raw data was hourly (i.e., 24 data points per day) but was averaged for presentation by day.

[47] In this study, domestic cows would increase the duration of their grazing and ruminating after changes in barometric pressure.

pressure. Changes in barometric pressure happen frequently (within even a few days) and abruptly. Barometric pressure does not fluctuate between seasons. It is not a phenomenon characterized by seasonal or even monthly variations. The fluctuations are within shorter periods of time (within days or a few days) and do not vary significantly from summer to fall or fall to winter, etc. In other words, fluctuations are expected to be within a certain range with a specific average from month to month and from season to season. Variations are much less likely to vary between years (what we call breeding seasons). To demonstrate this, the average of the three breeding seasons or years are presented in Table 3.3, along with the month-by-month break down. Standard deviations are presented (not standard errors of the mean) in order to demonstrate that there is very little variance in the data. This table clearly shows that comparisons between years and between months are not informative.

Table 3.3. Means and standard deviations of barometric pressure for each of the three breeding seasons (in kPa).

	Season 1				Season 2				Season 3			
	Dec	Jan	Feb	Mar	Dec	Jan	Feb	Mar	Dec	Jan	Feb	Mar
Mean	99.6	99.9	99.8	99.2	100	99.5	99.2	99.9	99.1	99.9	99.2	99.5
St. Dev.	1.0	1.1	1.0	1.3	1.1	1.0	1.3	1.2	1.3	1.2	1.5	1.0
Mean	99.6				99.67				99.42			
St. Dev.	1.21				1.21				1.35			

More temporally detailed information is needed in order to evaluate the fluctuations potentially perceived by the wolves. In the case of this study, it is possible that the cumulative effects of such fluctuations could have a significant impact on stress levels or on agonistic behaviours. Two complementary graphs will be introduced: Figure 3.12 presents daily averages of barometric pressure (in kPa) from December to March of each year of the study and Figure 3.13 shows the corresponding (i.e., daily) standard deviations[48].

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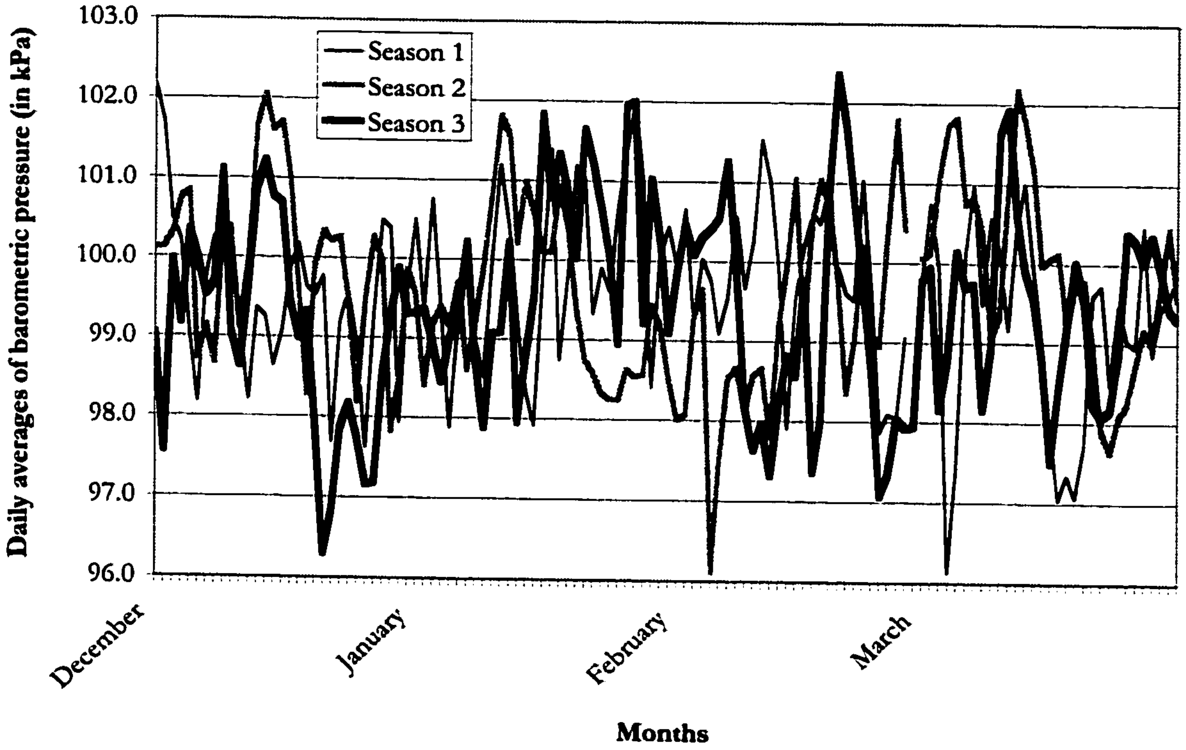
[48] Note that since kPa values were all centralized around 100 kPa, the standard deviations are almost identical to coefficient of variations (c.v. = (s.d./mean)*100).

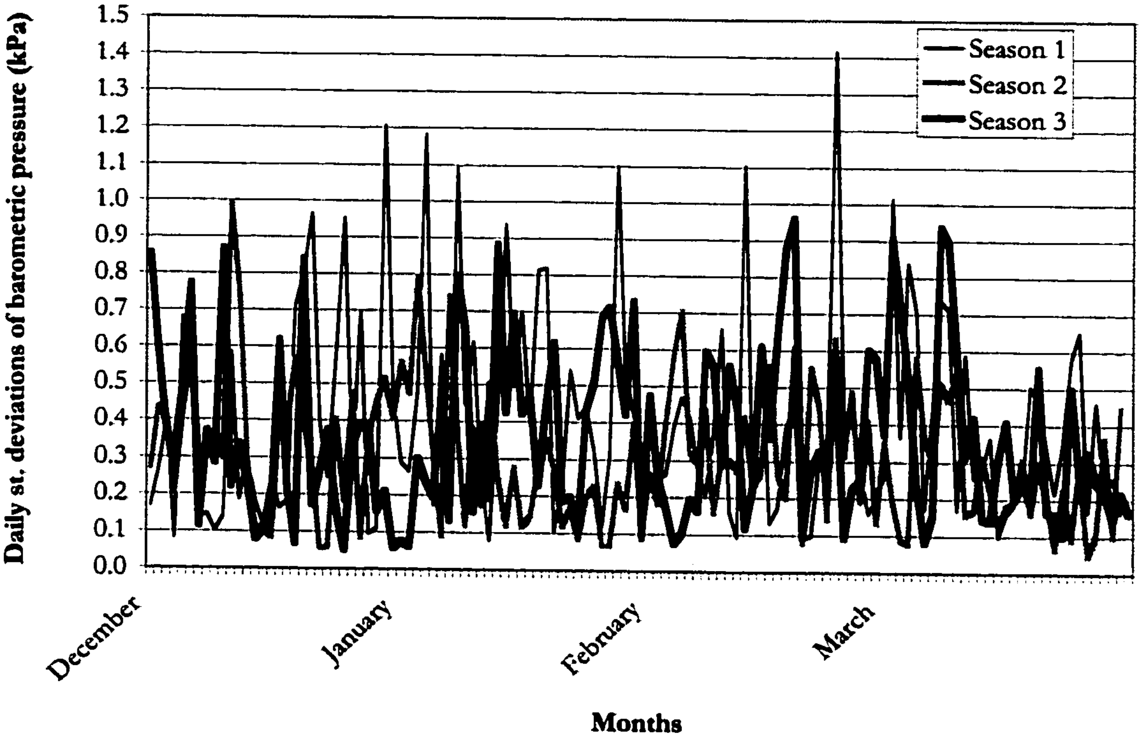
Figure 3.12. Daily averages of barometric pressure (in kPa) from December to March for the three breeding Seasons.



Note that in Figure 3.12 the range of values is 6.26 kPa. Globally, all three winters seem to present similar patterns of fluctuations with each winter having at least one low point (each below 97 kPa; occurring in March for Season 1, February for Season 2 and December for Season 3) each representing a dramatic drop in pressure. Of key importance here, no hormonal event could be associated with those drops in pressure in the day or days that followed. In Season 2, one fight (see Section 3.2, below for behavioural data) was temporally associated with the February drop (from 99.65 kPa to 96.12 kPa). It would be difficult to confirm that the fight was caused by the drop in pressure, because February was a busy month in terms of agonistic/aggressive interactions. More dramatic drops in pressure of this type followed by an increase in hostilities would be necessary to suggest that wolves respond agonistically to changes in barometric pressure.

More meaningful for a global (i.e., Seasonal) examination of atmospheric pressure data is Figure 3.13 showing the daily standard deviations of barometric pressure. This graph may actually parallel the temperature data presented above. Note that Season 1 (identified previously as having more extreme temperatures) has the highest variation. There are 10 data points with standard deviations above 0.90 (as compared to only 1 for Season 2 and only 3 for Season 3) and 6 data points with standard deviations above 1.0. It is reasonable to suggest that if wolves are sensitive (and responsive) to barometric pressure changes, they would be more likely to be influenced by the sharp and frequent changes occurring in Season 1 as compared to the other Seasons.

Figure 3.13. Daily standard deviations of barometric pressure (in kPa) from December to March for the three breeding Seasons.



If hormonal data are not sufficient in number to compare side by side (i.e., to correlate) with barometric data, it should be noted that no obvious relationship could be found (on a sample by sample basis) between extreme C:Cr values (i.e., those from Xyla or Voochko) and temperature (including daily fluctuations) or barometric pressure (including hourly fluctuations).

3.3 Behavioural data and synthesis.

The behavioural data were extracted using the principles explained in the introduction and the methodology described in Section 2 (Methods). First, the data collected from the analyses of videotapes and processed by the database were incorporated into sociomatrices. Two sociomatrices were completed for each Season of the study: the first compiled the observed frequency of inter- and intra-sexual aggressive interactions and the second compiled the observed frequency of inter- and intra-sexual submissive interactions. For each matrix, the initiators of interactions are identified at the left of the matrix and recipients of those interactions are identified at the top of the matrix. Because wolves have fairly distinct dominance hierarchies for each sex and because inter-sexual agonistic interactions are minimal, individuals are grouped by sex[49]. For each Season, the data included in the matrix are from the videotaped watches from December 1st to March 31st (see Appendix C for a detailed account). Because the number of watches varied from month to month and from Season to Season, the observed frequencies can not be compared from one matrix to another. Note also that since the pack composition changes between Seasons the matrices should not be contrasted or weighed against each other. Their purpose is akin to the use of similar, simpler matrices of wins and losses to determine dominance hierarchies in linear social networks (based on cumulated overthrows). In our case, the dominant animals were the same for all three Seasons (Pawnee among females and Galen among males) and the other ranks were fairly consistent across Seasons. The main purpose of the matrices was to determine which animal was the most aggressive and which was the most victimized. For our discussion of the impact of aggressive acts on stress levels, I focused on the matrices of aggressive acts. The matrices of submissive acts have significantly fewer interactions (see Appendix D). Both sets of matrices were used to determine the alpha, beta, other middle ranking (gamma, delta, etc) individuals, and omega animals.

I will now present the measures (see Methods) of agonistic behaviour that showed significant associations with the hormonal data. Other than the observed frequencies (number of occurrences) used for the sociomatrices, each agonistic interaction (aggressive or submissive) was analyzed for intensity on a scale of 1 to 3 for both initiators and recipients. Although durations of

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[49] This allows for an easier display of summaries and sub-summaries (sums) by rows and columns (for example, in order to determine how many times individual "x" was a recipient

interactions were measured, I believe that they were simply not sensitive enough to the subtleties of the dyadic encounters and that they basically mirrored the observed frequencies. Intensity, although slightly more subjective, seemed a better descriptor of the quality of the interaction between the two actors. As noted in the Methods section, a "1" was given to interactions of low intensity, typically Moynihan categories 2 and 3 of aggression (i.e., displays and other dimensions of ritualized aggression). A "2" (medium intensity) was given to interactions characterized by Moynihan's categories 3 and 4 (i.e., strong warnings or behaviours with physical contact not leading to potential injuries or actual injuries). Finally, a "3" (high intensity) was given to interactions from Moynihan's category 5 when injurious physical contact is observed or when the interactions have an estimated potential of leading to injury (if not observed). Group attacks and chases, which were observed mainly within females in this study, were also coded as a 3. Note that the length of the interaction was not a criterion in determining the intensity of the interaction. It is important to note that an intensity score (1, 2 or 3) was assigned to both the initiator and recipient of the interaction, and contributed to an intensity score for both animals. This means that a wolf could have been involved in high intensity interactions as an

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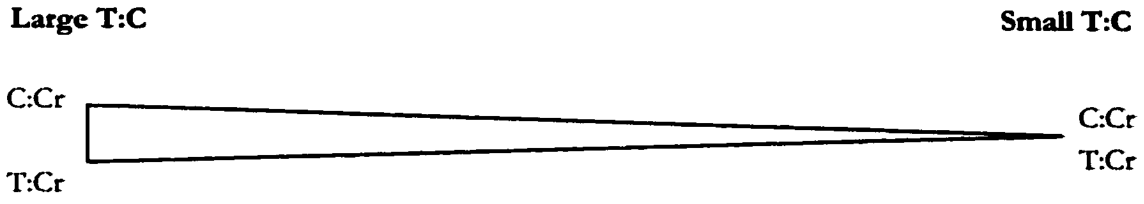
or initiator of aggressive interactions, within his or her own sex or overall).

initiator but in low intensity interactions as a recipient or vice versa. Individuals that were not initiators or recipients of an aggression were given a "0" value. Group chases and attacks were the exception to our focus on dyadic interactions in the sense that all the of the participants in a group attack were considered "initiators" and contributed to the score.

The T:C ratio (more precisely, the T:Cr/C:Cr ratio) was computed to identify associations between the levels of cortisol and the levels of testosterone in each wolf (see Figure 3.14 for more details). I decided to examine this association when I noticed that two highly stressed individuals, Xyla, an omega female and Voochko, a beta male, had high levels of both hormones. The reader may remember from the Introduction that most rodent theories and much of the data from non-cooperative breeding primates would suggest that chronic exposure to high levels of glucocorticoids tends to suppress, or at least inhibit, levels of reproductive steroids. In order to determine whether the same association exists in wolves, both C:Cr and T:Cr values will later be analyzed with correlations. Note that caution should be applied when interpreting T:C, because a ratio of ratios is an oblique or implicit representation of associations and therefore some accuracy is lost.

Figure 3.14. Illustration of the meaning of the T:C ratio.



A large T:C indicates a large discrepancy between C:Cr and T:Cr levels, i.e., one is low and the other is high.

This is what the current literature on rodents and non-cooperatively breeding primates would predict.

Small T:C means that C:Cr and T:Cr
1. are both low
OR
2. are both high

This pattern is observed in some of the wolves in this study as well as in some species mentioned in the discussion.

Table 3.4a is the social matrix for Season 1 of aggressive interactions between and within sexes. Table 3.4b presents the ranking for Season 1 of each individual wolf based on their C:Cr and T:Cr ratios as well as a combined T:Cr/C:Cr ratio (T:C). Table 3.4c ranks the wolves by observed frequencies of initiation and reception from the sociomatrix.

Table 3.4a. Observed frequency of inter- and intra-sexual aggressive interactions for Season 1.

	RECIPIENTS																
	Males								Females								
	A	G	H	J	N	V	W		C	D	F	M	P	T	X		Σ
INITIATORS																	
Males																	
Ashley [A]	•	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	**2**
Galen [G]	2	•	18	1	1	43	2	67	0	0	0	0	0	0	0	0	**67**
Homer [H]	1	0	•	3	2	12	4	22	1	0	0	0	0	1	0	2	**24**
Jasper [J]	0	0	0	•	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Noah [N]	0	0	1	0	•	1	1	3	1	0	1	1	0	0	0	3	**6**
Voochko [V]	5	4	75	1	11	•	12	108	1	1	0	2	0	0	0	4	**112**
Winston [W]	1	1	0	5	0	3	•	10	0	0	1	0	0	1	0	2	**12**
	9	6	95	10	14	59	19		3	1	2	3	0	2	0		
Females																	
Celtie [C]	0	0	0	0	0	0	0	0	•	0	11	16	0	0	0	27	**27**
Devil Child [D]	0	0	0	0	0	0	0	0	1	•	0	0	0	0	0	1	**1**
Fiona [F]	0	0	0	0	0	0	0	0	1	0	•	1	0	0	0	2	**2**
Morgaine [M]	0	0	0	0	1	0	0	1	3	0	16	•	0	0	0	19	**20**
Pawnee [P]	0	37	3	3	1	27	0	71	0	1	4	1	•	0	3	9	**80**
Tess [T]	0	0	3	0	3	1	1	8	2	1	8	1	0	•	1	13	**21**
Xyla [X]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	•	0	**0**
	0	37	6	3	5	28	1		7	2	39	19	0	0	4		
Total [Σ]	**9**	**43**	**101**	**13**	**19**	**87**	**20**		**10**	**3**	**41**	**22**	**0**	**2**	**4**		**374**

Most of the information contained in Table 3.4a has been extensively discussed by McLeod, Moger, Ryon, Gadbois, and Fentress (1996). First, as suggested by Table 2.1 in the Methods, Galen was the alpha male and he maintained his rank for all three years. Pawnee was the alpha female and she kept her rank for the duration of the study. We will see that Xyla, the omega female, kept her status for all three Seasons as well. The omega male was Ashley in Season 1. Ashley was an old wolf who died in the Spring of 1994 (following the end of Season 1) at age 14 years. Jasper, a yearling in 1994 (he was born in the Spring of 1993) took the omega status for the remainder of the Seasons. Another constant across Seasons was that subordinates rarely initiated aggression towards a dominant (in both males and females) and inter-sexual aggressions were extremely rare (see Fentress et al., 1987). When inter-sexual aggressions occurred, they were mostly from the dominant female (Pawnee) towards the dominant male (Galen).

Season 1 in males was characterized by many initiations of aggressive interactions (n=67) by Galen, the alpha, most of which (n = 43) were directed against Voochko, his main contender, and some of which (n = 18) were directed against Homer. Of all the males, Voochko initiated the most aggressive interactions (n = 112), most of which were directed towards Homer (n=75). During Season 1, and for the two following Seasons, this triad of animals was in a power struggle. Note, however, that the main contention was for the beta rank, that is, between Voochko and Homer; Galen was relatively secure in his alpha rank.

The pattern within the females was different. There was less of a power struggle for the beta rank and most of the aggression was from Pawnee towards Galen (the alpha male), and Voochko (the beta male). Celtie and Morgaine were trying to figure out the beta status. Celtie was dominant over Morgaine in January, but by February, Morgaine was dominant.

Note that the animals who received the most aggression within each sex, Homer (n=101) among the males and Fiona (n=41) among the females, were not the individuals with the highest C:Cr levels. In males, Voochko had the highest C:Cr levels and was the recipient of many aggressions (n=87). In females, the omega (Xyla), recipient of only 4 aggressions (most from Pawnee) had by far the highest C:Cr levels.

In order to investigate this further, T:Cr levels (see Table 3.4b; from which T:C, mentioned above, was calculated) and intensity of aggressive acts (see Table 3.4c) were collected. Ashley, the omega male, had the highest T:Cr levels of all males, and Galen, the alpha male, had the second lowest levels of T:Cr. This is a surprising result, because high T:Cr levels would be expected in a dominant, reproducing male (or a male that is about to reproduce). In contrast, an aging wolf at the bottom of the hierarchy (Ashley) should have low levels. Furthermore, T:Cr levels in females that are expected to be low (because of the theoretical lack of sensitivity and specificity of the assay to androgens in females), were found to be very high in Xyla, the omega female and in Devil Child, a yearling.

As mentioned earlier, these trends are what prompted me to consider the ratio between T:Cr and C:Cr, and to pursue the hypothesis that the relationship or association between Testosterone and Cortisol levels, especially in males, may be an alternative way to capture the hormonal status of the animal. With the ratio, two questions can be asked. Firstly, do wolves, like rodents and some primates (e.g., Sapolsky's baboons), have low testosterone in the presence of high glucocorticoids (and vice versa)? And secondly, is the size of this discrepancy (as reflected in the magnitude of the T:C), an informative individual difference variable that may correlate with behaviour or rank?

Table 3.4b. Ranking of individual wolves by ascending C:Cr, T:Cr and T:C ratios for Season 1.

	C:Cr		T:Cr		T:C	
MALES						
	Noah	4.2	Homer	27.1	Voochko	4.2
	Winston	4.7	Galen	35.9	Homer	4.5
	Galen	4.9	Noah	43.3	Galen	7.4
	Jasper	5.3	Voochko	44.2	Jasper	9.8
	Ashley	5.5	Jasper	52.3	Noah	10.3
	Homer	6.0	Winston	60.8	Ashley	12.8
	Voochko	10.5	Ashley	70.4	Winston	13.0
FEMALES						
	Fiona	4.3	Celtie	9.2	Celtie	1.7
	Tess	4.5	Morgaine	17.9	Xyla	2.0
	Morgaine	4.8	Pawnee	24.5	Pawnee	3.6
	Celtie	5.6	Fiona	25.0	Morgaine	3.7
	Devil Child	5.7	Devil Child	28.4	Devil Child	4.9
	Pawnee	6.9	Xyla	49.5	Fiona	5.8
	Xyla	24.4				

Table 3.4c. Ranking of individual wolves by frequency of initiations and receptions, and mean intensity of interactions as initiators and recipients for Season 1. A value of "0" suggests that the individual was not involved in any aggressive interactions as an initiator or recipient.

	Ranking by observed frequencies (see Table 3.4a)		**Intensity of aggressive dyadic interactions for:**			
	Initiations	**Receptions**	**Initiators**		**Recipients**	
MALES						
	Jasper (0)	Ashley	Jasper (0)	0	Ashley	1.3
	Ashley	Jasper	Ashley	1.0	Winston	1.5
	Noah	Noah	Noah	1.5	Noah	1.5
	Winston	Winston	Winston	1.5	Jasper	1.5
	Homer	Galen	Galen	2.6	Galen	2.0
	Galen	Voochko	Homer	2.7	Homer	2.6
	Voochko	Homer	Voochko	2.8	Voochko	2.8
FEMALES						
	Xyla (0)	Pawnee	Xyla (0)	0	Pawnee	0
	Devil Child	Tess	Fiona	1.5	Tess	1
	Fiona	Devil Child	Tess	1.6	Fiona*	1.2
	Morgaine	Xyla	Morgaine	1.6	Devil Child	1.5
	Tess	Celtie	Celtie	1.7	Morgaine*	1.6
	Celtie	Morgaine	Devil Child	2.0	Celtie*	2.0
	Pawnee	Fiona	Pawnee	2.5	Xyla*	3.0

* indicates recipients of group attacks/chases

From Table 3.4c we can see that males who were involved in high intensity interactions as initiators tended to be involved in high intensity interactions as recipients as well. This pattern was not observed in females. Interestingly, the same male triad had high ranks on all behavioural measures (frequency and intensity of interactions) and low ranks in the T:C ratio. Galen (the alpha), Voochko (the beta) and Homer (the gamma and main competitor with Voochko) were a common cluster on all ranked behavioural measures and on T:C, suggesting that the association between Cortisol and Testosterone levels (and not each independently) may be the most likely to be associated with the behavioural data. An examination of the rankings of individuals shows that the T:C ratio mirrors the intensity score for recipients, in other words, the lower the T:C ratio, the higher the intensity score when the animal is recipient. This suggests that being the target of intense aggressive acts was associated with hormonal levels. Specifically, being involved in interactions of high intensity as a recipient seems to be associated with high levels of C:Cr. This pattern is particularly evident in males.

In order to examine these relationships statistically, Pearson correlations were computed between all hormonal ratios (C:Cr, T:Cr, T:C) and behavioural indices: observed frequencies for initiations (OFI) and receptions (OFR), and intensities for initiators (II) and recipients (IR). To reduce the possibility of a type I error, no correlations with probability levels greater than p=.01 were considered significant[50]. Significant correlations were only identified with males. First, the T:C ratio is significantly correlated with the intensity of interaction as a recipient (IR; $r=-.952$, $p=.0002$) and observed frequencies of receptions (OFR; $r=-.921$, $p=.0014$). This is well illustrated by Voochko and Homer. They have the two lowest T:C (4.2 and 4.5 respectively) and both were involved, as recipients, in highly intense fights (2.8 and 2.6 respectively). Not surprisingly, IR and OFR were highly correlated with each other ($r=.974$, $p<.0001$). Despite the presence of an outlier (Xyla), there are no significant pairwise comparisons within the females data.

The same overall approach was adopted for the subsequent breeding seasons[51]. In Season 2, two males were deceased, the omega from Season 1 (Ashley) and a four year old mid-ranking male (Winston). This change in the composition of the male hierarchy did not change the overall pattern much. Voochko and Galen were still the primary aggressors (n=83 and n=81, respectively). Homer was still involved in a significant number of aggressions (n=59), mainly against Voochko (n=42). As in Season 1, Galen directed most of his aggressions to the beta, Voochko (n=51) and some to Homer (n=25).

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[50] The decision to select a more stringent alpha level was motivated by the high number of correlations.

Interestingly, there was a difference that year among males in terms of the recipients of aggressive acts. Among males, Voochko and Homer were now receiving equally high numbers of aggressive acts (n=94 and n=95, respectively). Most of the aggressive acts were from each other (Voochko to Homer=68; Homer to Voochko=42). Also noteworthy, Homer, like Galen and Voochko, initiated aggression against all of the other males. This kind of behaviour pattern is typical of a more dominant animal.

On the female side, Pawnee directed 79 aggressive acts towards males, half of which were towards Galen (n=40) and the rest were distributed between Homer (n=20) and Voochko (n=19). This much aggression against Homer was not observed in Season 1 and may explain Homer's high C:Cr levels in Season 2. Among females, Pawnee, Celtie, Morgaine and Tess initiated most of the female aggressions. Celtie and Morgaine were in fluctuation for the beta rank in Season 1 and that trend continued in Season 2. Morgaine was a recipient of aggression by Celtie (n=12) and Pawnee (n=10). As in Season 1, Fiona was a major target of aggressive acts, followed by the Celtie-Morgaine dyad. Devil Child started to affirm herself in Season 2. From 1 initiation of aggression in Season 1 she initiated 21 in Season 2, almost equally distributed towards males

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[51] More descriptive details for Season 1 can be found in McLeod et al. (1996).

and females. This is remarkable considering that in Season 1, Pawnee and Tess were the main females directing aggressions towards males. Field notes contained many references to Devil Child's boldness, because many of the aggression were towards males (and this is relatively uncommon), because of her size (she was a relatively small female) and because of the fact that most of her aggressions were unprovoked, that is, they were not mating rebuffs. Season 2 confirms the appropriateness of her name.

Table 3.5a. Observed frequency of inter- and intra-sexual aggressive interactions for Season 2.

	RECIPIENTS														
	Males						Females								
	G	H	J	N	V		C	D	F	M	P	T	X		Σ
INITIATORS															
Males															
Galen [G]	•	25	2	3	51	81	0	0	0	0	0	0	0	0	**81**
Homer [H]	10	•	4	3	42	59	0	0	0	0	0	0	0	0	**59**
Jasper [J]	0	0	•	0	0	0	0	0	0	0	0	0	0	0	**0**
Noah [N]	0	2	1	•	1	4	1	1	1	1	0	0	0	4	**8**
Voochko [V]	7	68	2	3	•	80	1	0	1	1	0	0	0	3	**83**
	17	95	9	9	94		2	1	2	2	0	0	0		
Females															
Celtie [C]	0	0	0	0	0	0	•	0	12	15	0	0	0	27	**27**
Devil Child [D]	0	2	3	3	2	10	5	•	3	2	0	0	1	11	**21**
Fiona [F]	0	0	0	0	0	0	2	1	•	2	0	0	0	5	**5**
Morgaine [M]	0	0	0	0	0	0	3	2	15	•	0	0	0	20	**20**
Pawnee [P]	40	20	0	0	19	79	1	2	7	10	•	2	0	22	**101**
Tess [T]	0	4	0	1	2	7	2	3	6	1	0	•	2	14	**21**
Xyla [X]	0	0	0	0	0	0	0	0	0	0	0	0	•	0	**0**
	40	26	3	4	23		13	8	43	30	0	2	3		
Total [Σ]	**57**	**121**	**12**	**13**	**117**		**15**	**9**	**45**	**32**	**0**	**2**	**3**		**426**

Table 3.5b. Ranking of individual wolves by ascending C:Cr, T:Cr and T:C ratios for Season 2.

	C:Cr		T:Cr		T:C	
MALES						
	Noah	7.5	Homer	28.0	Homer	1.4
	Jasper	8.5	Jasper	35.0	Galen	3.7
	Galen	9.3	Galen	35.0	Jasper	4.1
	Voochko	17.3	Noah	45.9	Voochko	5.6
	Homer	20.4	Voochko	96.7	Noah	6.1
FEMALES						
	Tess	7.8	Devil Child	6.7	Xyla	0.5
	Fiona	8.5	Pawnee	8.1	Devil Child	0.7
	Morgaine	9.7	Morgaine	9.2	Pawnee	0.7
	Devil Child	10.3	Xyla	10.6	Morgaine	1.0
	Pawnee	11.2	Tess	11.1	Tess	1.4
	Xyla	19.5				

Table 3.5c. Ranking of individual wolves by frequency of initiations and receptions and mean intensity of interactions as initiators and recipients for Season 2. A value of "0" suggests that the individual was not involved in any aggressive interactions as initiator or recipient.

	Ranking by observed frequencies (see Table 3.5a)		**Intensity of aggressive dyadic interactions for:**			
	Initiations	**Receptions**	**Initiators**		**Recipients**	
MALES						
	Jasper (0)	Noah	Jasper (0)	0	Noah	2.2
	Noah	Jasper	Noah	2.1	Jasper	2.5
	Homer	Galen	Voochko	2.6	Galen	2.6
	Galen	Homer	Galen	2.7	Voochko	2.7
	Voochko	Voochko	Homer	2.7	Homer	2.8
FEMALES						
	Xyla (0)	Pawnee	Xyla	0	Pawnee (0)	0
	Fiona	Tess	Fiona	1.6	Tess	1.2
	Morgaine	Xyla	Tess	1.6	Morgaine*	1.5
	Tess	Devil Child	Morgaine	1.6	Fiona	1.7
	Devil Child	Celtie	Celtie	1.8	Celtie	2.5
	Celtie	Morgaine	Devil Child	2.1	Devil Child	2.7
	Pawnee	Fiona	Pawnee	2.6	Xyla*	3.0

* indicates recipients of group attacks/chases

In Season 1, T:C appeared to be promising as a potential hormonal index of the dominance hierarchy. In Season 2, with the males, the only correlation that emerged as significant was between C:Cr values and observed frequencies as recipient (OFR) (r=.957, p=.0069). The Galen-Voochko-Homer cluster or triad was "broken" or disturbed by Jasper's intrusion in the ranking of hormones ratios. It is interesting to note following Ashley's death, Jasper became the obvious omega male. In conclusion, it seems that, in Season 2, being a male recipient of many aggressive acts was highly correlated with high C:Cr values. No significant correlations emerged between females' hormonal and behavioural ratings.

Season 3 did not deviate substantially from the previous breeding Seasons. It was especially comparable to Season 2. The major change was the presence of Ulysses, a pup from the previous year. Similar to Jasper and Devil Child in Season 1, Ulysses was involved in no initiations of aggression and was the recipient of very few aggressive acts (n=4; 1 from Voochko, 2 from Homer and 1 from Devil Child). Among males present from the previous Seasons, the most striking difference lay in Homer's proportional increase in initiation of aggressive acts (n=66) in comparison with Galen (n=40) and Voochko (n=24). In fact, there was no doubt that by the time breeding Season 3 started, Voochko had lost his beta rank to Homer. Voochko was the recipient of many aggressions (n=67 total) most of which (n=64) were from males, especially from Homer (n=52). Homer was attacked or threatened mainly by Galen (n=25) and proportionally significantly less by Voochko (n=10) than for the previous years. It is interesting to note that Homer's reception of aggressive acts from the dominant female, Pawnee, reached its peak (in proportion to the previous years and in comparison with Galen and Voochko) on Season 3 (n=39 for Homer, n=1 for Voochko). Recall that Homer was receiving aggressions from Pawnee much less than Voochko in Season 1 and was receiving proportionally an equal amount in Season 2. Overall, Homer received the most aggressions (n=78), followed by Voochko (n=67) and finally Galen (n=56, most of which were from Pawnee, n=51). There are reasons to believe that this ascension to beta status had its toll on Homer (see Figure 3.5) as it did in the transition in Season 2 (see Figure 3.4). Jasper's omega status was confirmed and at least one group attack may be able to explain his very high C:Cr levels for Season 3.

It is important to note that Voochko's C:Cr levels are lower in Season 3 than they were in Season 2, and this despite an adrenal condition that will be examined in the Discussion (see Moger, Ferns, Wright, Gadbois & McLeod, 1998). In Season 2, Voochko was still trying to mate with Pawnee (a few mounting attempts were observed), but this behaviour was noticeably reduced in Season 3.

Among females, aside from Pawnee's usual high rate of aggressive acts (n=93 against males, n=27 against females), Celtie and Devil Child were frequent initiators (n=34 and n=26 respectively). What was more surprising, was Devil Child's assertiveness with the males. Almost a third of her (unprovoked) aggressions were directed towards males. Aggressive interactions in January were high among females. On January 7th, a group aggression was directed towards Tess and a wound was observed on Celtie's side. On January 8th, Morgaine was stalked by Pawnee and later group-chased. Following that event, on the same day, Pawnee, Devil Child, Celtie and Tess all initiated aggressive acts against Morgaine. In fact, Morgaine's observed frequencies of receptions were the highest among females for the whole season. This is the first Season that Fiona was not the recipient of the most number of aggressive acts.

Table 3.6a. Observed frequency of inter- and intra-sexual aggressive interactions for Season 3.

	RECIPIENTS															
	Males							**Females**								
	G	H	J	N	U	V		C	D	F	M	P	T	X		Σ
INITIATORS																
Males																
Galen [G]	•	25	4	2	0	9	40	0	0	0	0	0	0	0	0	**40**
Homer [H]	3	•	5	2	2	52	64	1	0	0	1	0	0	0	2	**66**
Jasper [J]	0	0	•	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Noah [N]	0	2	4	•	0	3	9	1	0	0	1	0	0	0	2	**11**
Ulysses [U]	0	0	0	0	•	0	0	0	0	0	0	0	0	0	0	**0**
Voochko [V]	2	10	3	5	1	•	21	1	1	0	1	0	0	0	3	**24**
	5	37	16	9	3	64		3	1	0	3	0	0	0		
Females																
Celtie [C]	0	0	0	0	0	0	0	•	8	10	13	0	2	1	34	**34**
Devil Child [D]	0	2	3	2	1	2	10	4	•	3	4	0	3	2	16	**26**
Fiona [F]	0	0	0	0	0	0	0	0	0	•	5	0	2	2	9	**9**
Morgaine [M]	0	0	0	0	0	0	0	2	2	5	•	2	4	1	16	**16**
Pawnee [P]	51	39	1	1	0	1	93	3	5	3	12	•	1	3	27	**120**
Tess [T]	0	0	0	0	0	0	0	0	0	2	4	0	•	0	6	**6**
Xyla [X]	0	0	0	0	0	0	0	0	0	0	0	0	0	•	0	**0**
	51	41	4	3	1	3		9	15	23	38	2	12	9		
Total [Σ]	**56**	**78**	**20**	**12**	**4**	**67**		**12**	**16**	**23**	**41**	**2**	**12**	**9**		**352**

Table 3.6b. Ranking of individual wolves by ascending C:Cr, T:Cr and T:C ratios for Season 3.

	C:Cr		T:Cr		T:C	
MALES						
	Noah	8.4	Jasper	31.6	Jasper	1.9
	Ulysses	9.2	Homer	33.4	Homer	2.3
	Galen	9.2	Ulysses	38.7	Voochko	4.1
	Voochko	12.7	Noah	48.1	Ulysses	4.2
	Homer	14.7	Voochko	52.2	Noah	5.7
	Jasper	16.4	Galen	57.2	Galen	6.2
FEMALES						
	Fiona	7.2	Fiona	9.2	Xyla	0.9
	Tess	9.5	Tess	13.6	Pawnee	1.2
	Celtie	12.6	Pawnee	15.5	Devil Child	1.3
	Devil Child	12.7	Devil Child	16.0	Fiona	1.3
	Pawnee	13.1	Celtie	16.8	Celtie	1.3
	Xyla	28.1	Xyla	23.9	Tess	1.4

Table 3.6c. Ranking of individual wolves by frequency of initiations and receptions and mean intensity of interactions as initiators and recipients for Season 3. A value of "0" suggests that the individual was not involved in any aggressive interactions as initiator or recipient.

	Ranking by observed frequencies (see Table 3.6a)		**Intensity of aggressive dyadic interactions for:**			
	Initiations	**Receptions**	**Initiators**		**Recipients**	
MALES						
	Ulysses (0)	Ulysses	Ulysses (0)	0	Ulysses	1.4
	Jasper (0)	Noah	Jasper (0)	0	Noah	1.4
	Noah	Jasper	Voochko	1.5	Galen	2.3
	Voochko	Galen	Noah	1.6	Voochko	2.5
	Galen	Voochko	Homer	2.5	Homer	2.7
	Homer	Homer	Galen	2.6	Jasper*	2.8
FEMALES						
	Xyla (0)	Pawnee	Xyla (0)	0	Pawnee	1.2
	Tess	Xyla	Tess	1.2	Fiona	1.5
	Fiona	Tess	Morgaine	1.5	Tess*	1.9
	Morgaine	Celtie	Celtie	2.2	Devil Child	2
	Devil Child	Devil Child	Fiona	2.3	Celtie	2.8
	Celtie	Fiona	Devil Child	2.5	Morgaine*	2.8
	Pawnee	Morgaine	Pawnee	2.6	Xyla*	2.9

* indicates recipients of group attacks/chases

Among the males there were no significant correlations between the ratios, observed frequencies and intensities of interactions. In females, for the first time a correlation was found between C:Cr levels and T:Cr levels (r=.951, p=.0014) and, not surprisingly, C:Cr and T:C (r=-.941, p=.0024).

This trend had been observed within specific individuals, including some males, but this result confirms that being highly stressed does not prevent androgen levels from being high. This is somewhat difficult to interpret in females as our assay is lacking sensitivity to the female androgens.

In summary, we can say that omega status (Xyla) was associated with high C:Cr levels among females of this pack, but this pattern was not as clear in males. Fluctuations among beta/gamma ranks in males seem to have been associated with high levels of C:Cr or T:C. The trends with T:Cr are puzzling at best (with low ranking males and females often having the highest levels of T:Cr).

In the next section (Section 4) I will attempt to integrate this data with the current knowledge from studies and theories developed from Primate and Carnivore models.

4. Discussion

4.1 Overview

In this study, Cortisol (C:Cr) and testosterone (T:Cr) levels were examined in relation to sex, breeding season, weather, rank, and the frequency and intensity of aggressive acts, in an effort to understand the relation between stress and aggression in a pack of wolves. Overall, the data are characterized by high levels of variability within and between individuals, and fluctuations in the relations between factors across the seasons. Nevertheless, some patterns were extracted. Firstly, C:Cr ratios were higher in beta and omega animals, as were the T:Cr ratios in some of the same animals. Secondly, many of the individuals showed an unexpected positive correlation between T:Cr and C:Cr. Thirdly, in one of the three seasons, there was a positive relation between the number of aggressive acts initiated and the discrepancy between C:Cr and T:Cr (as reflected in the T:C ratio). There was an increase in C:Cr between Season 1 and the two subsequent seasons, and no difference in T:Cr across Seasons in males. The increase in cortisol could not be attributed to harsher weather patterns across Season. Season 1 was characterized by higher deviations between minima and maxima and greater fluctuations in barometric pressure, and this was the year with the lowest C:Cr levels. Factors that may have contributed to these results will be considered, and the findings will be placed in the context of other recent data and theories in behavioural endocrinology.

4.2 This study and others: similarities and differences

The goal of this study was to evaluate the impact of sociogenic stress (more specifically, aggression-mediated stress) in a captive pack of wolves. The inspiration for this study came from exceptionally thorough field studies conducted by Sapolsky in olive baboons (*Papio anubis*). The approach taken in this study was different from his in two respects. Firstly, the wolves are captive (Sapolsky's baboons were free ranging animals). Secondly, the methodology adopted here is significantly less invasive (darting and immobilization of individual wolves was not necessary). Captive studies with wolves have been criticized in the past (e.g., Haber, 1977, as cited in McLeod, Moger, Ryon, Gadbois, and Fentress, 1996; Constable, Hinchcliff, Demma, Callahan, Dale, Fox, Adams, Wack, & Kramer, 1998; Kotrschal, Hirschenhauser, & Möstl, 1998). I would suggest however, that captive conditions vary widely across studies and that those broader criticisms do not apply to this study.

Many of the criticisms of captive studies have pertained to general living conditions such as the size of the enclosure and human contact. The conditions at the CCWR were likely among the best in the world in these respects. The wolves had access to a full 8 acres of which only a fraction was cleared of trees. Because of the size of the enclosure, it is unlikely that the wolves would have suffered from "lack of exercise" (a characteristic of some captive packs as identified by Constable, Hinchcliff, Demma, Callahan, Dale, Fox, Adams, Wack & Kramer, 1998). Human disruption was kept to a minimum and visitors were almost exclusively a very small number of researchers and students. Dens, man-made shelters, and other safety zones (locations near the catching pens, observation trailer, and observation building) were scattered within the enclosure, giving a chance for harassed subordinates (including omegas) to hide and protect themselves if necessary (i.e., following group chases or attacks and other group unrests).

Some have also raised concerns about inbreeding in captive wolves. Although Mech (1970) and Shields (1983) suggested that that wolves in the wild appear to be very resistant to inbreeding, Laikre and Ryman (1991) do not agree and found evidence in Scandinavian captive wolves to suggest deleterious effects on longevity, reproduction, juvenile weight, and eyesight (i.e., an hereditary form of blindness). Peterson, Thomas, Thurber, Vucetich, and Waite

(1998) argue that inbreeding depression was a factor in at least one population crash among the isolated wild population of wolves on Isle Royale.

Note that in the years following the completion of this study (from 1996 to 1998), there was a high mortality rate in the pack. From the start of the pack in 1974 to the end of this study, a reduction in the percentage of whelping females (see Figure 2.2) was observed. The main pack and two of the peripheral smaller packs were from a stock that was at least 20 years old (when the pack was established in Nova Scotia in 1973-1974). The increased social instability and mortality observed in the years post-1996 as well as the possible decrease in "global fertility" of the pack may have been influenced by the direct effects of inbreeding.

4.3 Health of the pack

The question of inbreeding is raised to introduce the possibility that the high testosterone and high cortisol levels in our low ranking wolves could be originating from pathologies, such as congenital adrenogenital syndromes. Although this is unlikely and I could not find any references to a canine equivalent of human congenital adrenal hyperplasia, it should be noted that such disorders often manifest themselves in humans (men and women) by a deficiency in cortisol (and aldosterone) and an overproduction of adrenal androgens[52] (Greenspan & Strewler, 1997). Adrenal androgens and cortisol can also be increased by adrenal carcinomas.

Recall that Voochko had high cortisol and high testosterone levels for each of the three seasons. In 1998, we (Moger, Ferns, Wright, Gadbois, & McLeod) published information from Voochko's necropsy and the histology of his adrenal glands. An adrenal tumour was found (cortical adenoma) that could explain Voochko's high cortisol levels (especially in Season 2) and high testosterone levels (which were very high in Season 2 and variable in Season 3). Devil Child died around the same time as Voochko and her autopsy (unpublished) suggested a "thickening of the [adrenal] cortex, with a somewhat nodular appearance" (pathology report. Dr. L. Ferns, February 26, 1997). Devil Child's general ratio of Zona glomerulosa to Zona reticularis and fasciculata (1:5 or 1:6) is suggestive of chronic stress. It is interesting to note that Devil Child's C:Cr levels, although average, increased consistently from season to season and that her T:Cr levels were quite high during Season 1.

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[52] Mainly androstenedione and DHEA.

4.4 Could dominance be associated with high cortisol levels?

Recall from the Introduction that until about a dozen years ago (circum 1990) the main theory of social stress came from the rodent literature and was strongly suggesting that dominant animals have high reproductive hormones levels and low glucocorticoid levels and that subordinate animals have low reproductive hormones levels and high glucocorticoid levels. Furthermore these data have been used to develop the notion that reproductive suppression is hormonally mediated. The current literature on the endocrinology of social mammals includes several reports of a lack of association between dominance and cortisol levels or between dominance and testosterone levels. Moreover, a number of papers find patterns that, until recently, were not considered orthodox, i.e., low testosterone levels or high cortisol levels in dominant animals.

For example, Bercovitch and Clarke (1995) could not differentiate low and high ranking rhesus macaques (*Macaca mulatta*) based on their cortisol levels. Female cynomolgus monkeys (*Macaca fascicularis*) were shown to have no relationship between rank and cortisol levels (Stavisky, Adams, Watson, & Kaplan, 2001). Dominant female common marmosets (*Callithrix jacchus*) were more stressed than subordinates (Abbott, Saltzman, Schultz-Darken, & Smith, 1999; Saltzman, Schultz-Darken, & Abbott, 1996; Saltzman, Schultz-Darken, Scheffler, Wegner, & Abbott, 1994; Saltzman, Schultz-Darken, Wegner, Wittwer, & Abbott, 1998). Black tufted-ear marmoset (*Callithrix kuhli*) dominants and subordinates could not be differentiated by their cortisol levels (Smith & French, 1997; Smith, Shaffner, & French, 1995). The same was observed in cottontop tamarins (*Saguinus oedipus oedipus*) by Ziegler, Guenther, and Snowdon (1995) as well as Ginther, Ziegler, and Snowdon (2001). High cortisol levels were found by Creel et al. (1996, 1997) in dominant African Wild Dogs (*Lycaon pictus*) and by Sands and Creel (2001) in the Yellowstone wolves. Cavigelli (1999) found that dominant female ring-tailed lemurs (*Lemur catta*) are significantly more stressed than subordinate females. And finally, Kreeger, Seal, and Plotka (1992) found that exogenous glucocorticoids (2.2 mg/kg of cortisol acetate) do not modulate LH levels, suggesting that reproductive steroids (such as testosterone) may not be modulated by stress, at least not by transient stress. Each of these studies is suggestive of the idea that stress and glucocorticoids may not act as suppressors of reproduction in all carnivores and primates, and that dominance and subordination may not be highly correlated with the distribution of stress in a social group.

In the Introduction, I suggested that the mating system (monogamous versus polygamous, individual versus cooperative breeding, singular versus plural breeding) could be a determining factor in the distinction between species-specific hormonal profiles. The examples above suggest a surprising diversification of species–specific patterns between and even within mating/breeding systems. It has been suggested (Creel, 2000; French, 1997) that cooperative breeders, either extended family based (e.g., African Wild Dogs), or immediate family based (e.g., common marmosets) do not exhibit reproductive suppression of subordinates by the dominants, and that therefore, cortisol levels are undifferentiated on the basis of rank, or even have the potential of being higher in dominants. On the other hand, individual breeders (ring-tailed lemurs, rhesus macaques, olive baboons)[53] would tend to follow the early rodent literature that suggests the presence of high glucocorticoid levels in subordinates and low to normal levels in dominants (although this would be true only in stable hierarchies among social primates).

According to Creel et al. (1996, 1997), French (1997), Abbott, Saltzman, Schultz-Darken, and Smith (1999), as well as Sapolsky in his more recent work (Sapolsky, 2000), wolves, as cooperative breeders, singular breeders, and

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[53] With the exception of cynomolgus monkeys (*Macaca fascicularis*).

monogamous carnivores, should not have stressed subordinates and relaxed dominants. Instead, there should be no differentiation in stress between animals of different ranks, or even a pattern of high stress in dominants even when the dominance hierarchy is stable. Sapolsky (2000) identified a trend emerging in the primate literature: in most species of macaques and baboons (corresponding to the "individual / plural / polygamous breeder" group), suppression of reproduction in subordinates is behaviourally controlled by the dominants, more specifically, aggression from the dominants increases the levels of stress in subordinates. Conversely, in marmosets and tamarins (members of the "cooperative / singular / monogamous breeder" group), subordinates are part of an immediate or fairly small extended family (similar to wolves and most other monogamous canids). As characterized by Sapolsky (2000) "subordinates [in callitrichids] are usually younger siblings or offspring of the dominant female, free from redirected aggression, aiding in cooperative breeding and ultimately rising in rank by waiting their turn" (p. 114).

It is my belief that only careful comparative studies of the social and mating systems of canids and callitrichids (marmosets and tamarins) will allow us to determine if wolves, lycaons, dholes and other monogamous carnivores have similar patterns as this group of singular, cooperatively breeding mammals.

Precise hormonal profiles and detailed quantitative and qualitative evaluation of social interactions (including affiliative behaviours) would be an important next step towards integrating this literature. French's (1997) literature review for callitrichids and Asa's (Asa, 1997; Asa & Valdespino, 1998) review for canids, as well as my attempt to synthesize more current information for canids (Section 1.4) are potentially important first steps towards an integration of the socioendocrinology of family-based groups of mammals. Field and laboratory (when possible) comparative studies may also point towards important group differences (e.g., differential troop, pack, and family dynamics based on individual differences, including temperament-based differences and other factors). For instance, our pack did not demonstrate a trend of high intensity of aggression in females and high frequency of aggression in males as found by Zimen (1976). One can only start to imagine the multiple factors that can contribute to different group dynamics.

4.5 Dominance, reproduction, testosterone and cortisol

A troubling and unexpected result was the observation of both high testosterone and high cortisol levels in some individuals. Voochko (all three seasons) and Xyla (Season 1) are particularly notable for this. Also difficult to interpret, are the high levels of testosterone in: an omega male, Ashley (Season 1) and very low ranking male, Jasper (also in Season 1) who in fact would "replace" the late Ashley in the omega rank the following year. In comparison, especially in Season 1, Galen, the dominant male, has relatively low levels of testosterone.

In the introduction, I discussed data that suggest that high cortisol levels were associated, in some species, with high sexual interest and activity as well as aggressiveness (see Zillman, 1998, for a review). For example, Chambers and Phoenix (1981) found that high cortisol levels in rhesus macaques were associated with increased sexual activity. Squirrel monkeys experience an increase in cortisol levels as the breeding season starts and progresses (Schiml, Mendoza, Slatzman, Lyons, & Mason, 1996). High cortisol levels are necessary for the induction of sexual behaviour in the female musk shrew (*Suncus murinus*; Schiml & Rissman, 1999). Some species, such as Tufted Capuchin monkeys, do not even show elevations in testosterone or cortisol levels among males during the breeding period, and dominant and subordinate animals do not differ on measures of either hormone (Lynch, Ziegler, & Strier, 2002). Male muriquis (*Brachyteles arachnoides*) do not show any significant variations in their testosterone levels between breeding and non-breeding periods but they do show higher levels of cortisol during and following the breeding season (Strier, Ziegler, & Wittwer, 1999).

It seems that stress and reproduction may be linked in a positive way in a number of non-cooperatively breeding mammals. The same can be said of sex and aggression or stress and aggression (Zillman, 1998). For instance, Beerda, Schilder, Van Hoof, De Vries, and Mol (1999) found that chronic stress in dogs induces aggression (no endocrine measures were used, but we can assume that cortisol levels must have been elevated considering that social and spatial restrictions were imposed on the experimental group).

4.6 Predictability and controllability

Sapolsky's (1992, 1994, 1998, 2002) extensive discussion of predictability and controllability factors were recently found valuable by Wingfield and Ramenofsky (1997) and by Creel (2001) to explain the absence of stress in seasonal breeders (including, we have to assume, wolves). In fact, they claim that mating seasons, because they are cyclical, are predictable and therefore not stressful. They further argue that simply because breeding seasons are "taxing" or difficult for animals, it does not follow that they are stressful. They also seem to think that because the animals know the mating season is on its way, that they can control their stress levels[54]. This is, in my view, like trying to tell undergraduate students that they should not be stressed by the final exam period because they know it is coming[55]. In fact, knowing a stressor is coming but not knowing which form it will take (e.g., intensity, duration) is likely much more stressful than having all of the possible information or knowing nothing at all. If wolves had an implicit knowledge of the coming period of strife and social tension, they would still have to guess who is going to "play politics" (cf., de Waal, 1982) that year and with what determination and perseverance. Moreover, there is no doubt that Sapolsky's arguments apply to many short term, mildly stressful events, but they likely do not apply to largely disruptive events, especially when social strife is involved (including competition and aggression between former friends). Based on the quote in footnote 54 (from Creel, 2001) I would argue that Creel and Wingfield are too quick to attribute mental and cognitive abilities to birds and mammals. Both authors seem to

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[54] From Creel (2001): «There is a tendency to consider any difficult or energetically demanding situation a stressor. As Wingfield and Ramenofsky point out: "phrases such as 'the stress of reproduction' or 'the stress of migration'... are inaccurate, because these processes occur on predictable schedules and an individual can make necessary preparations"».

[55] The reader, at this point, should realize that the author of this dissertation would certainly not be stressed before his defence because he knew it was going to happen. In fact, he had months to prepare, years to witness similar events (some successful, some less) and he

assume that their subjects engage in conscious anticipation, prospective memory (from experiences of previous seasons), awareness of their circannual rhythms, and of their own coping strategies. In fact, despite their so-called "knowledge" of the impending mating season, wolves still increase their aggressive behaviours (McLeod, Ryon, & Fentress, unpublished manuscript) until the breeding season subsides (circum end of March).

4.7 Do we even agree on the concept of dominance?

When dominance is discussed in lycaons, Creel et al. (1996, 1997) report using a win/loss criterion to determine dominance yet do not provide us with any useful ostensive definitions of aggression. Extracting dominance data from win/loss matrices can be problematic and is a relatively unorthodox way to compute and determine dominance in social animals. It is well documented, even in introductory textbooks on ethological methods, that an animal who wins more fights than all the others is not necessarily the dominant individual. To demonstrate the limitations of a win/loss approach, the following matrix is inspired by and expanded from Martin and Bateson (1993). From Table 4.1, we

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expected the event to be like a walk in the park on a beautiful July afternoon after a morning of massotherapy. This is a well known attitude in doctoral candidates...

could conclude, based on a strict wins-versus-loss perspective, that animal A is the dominant individual since he wins more agonistic interactions than any other in the group. In fact, the number of “wins” is meaningless in this example because animal A never managed to win against C. Although the example used here is a simplified one, illustrating a perfectly linear dominance hierarchy, the same principle would apply to a more complex hierarchy.

Table 4.1. Simple dominance matrix with wins and losses.

		Recipient/ “loser”					
		A	B	C	D	E	Wins
Initiator, “winner”	A	•	21	0	29	11	61
	B	0	•	0	0	0	0
	C	22	11	•	8	18	59
	D	0	11	0	•	6	17
	E	0	2	0	0	•	2
	Losses	22	44	0	37	35	

Table 4.2 shows the more conventional way to extract dominance information from a dominance matrix. The matrix is re-structured so that the minimum number of overthrows appears on the lower left side of the diagonal, or, in this example, so that all "0"s are below the diagonal ("0"s are present since we have a perfectly linear hierarchy, i.e., with no reversals).

Table 4.2. Reorganized dominance matrix with the corresponding ranks.

Initiator, "winner"	Recipient/ "loser" C	A	D	E	B	
C	•	22	8	18	11	alpha
A	0	•	29	11	21	beta
D	0	0	•	6	11	gamma
E	0	0	0	•	2	delta
B	0	0	0	0	•	omega

Following the re-organisation of the matrix, it is easier to see that C literally "dominated" every other animal in the group in the sense that he was successful in overthrowing all of them. This is not to say that a cumulative number of losses would not increase cortisol levels, or that a cumulative number of wins would not increase testosterone levels. In other words, wins and losses can be informative if we want to focus on the consequences and effects of accumulated agonistic (aggressive or submissive) acts in an initiator as well as provide an index of rank stability. This is not an appropriate way, however, to determine dominance hierarchies.

Creel et al. (1996, 1997) also point out that they use "displacements at resources" as a criterion for dominance. This is a potentially a serious problem if lycaon pups are like wolf pups, who displace adults at the food site very easily.

Males and females "displace" each other over food, without in fact, any need for ritualized aggression.

4.8 Reproductive suppression

In the Introduction, I discussed the potential mechanisms of reproductive suppression, from exclusively behavioural mechanisms (e.g., mate-guarding[56]) or physiological mechanisms (natural hormonal fluctuations) to behavioural-physiological mechanisms (e.g., stress inducing agonistic interactions). In the light of rodent research, scent-marking or urine-marking may be important factors (see Brown, 1979, 1985). At the behavioural level, we know that urination postures are good indices of status (low postures in subordinates, e.g., squat urination, and high postures in dominant animals, e.g., raised-leg urination) and therefore could act as "displays" of ritualized aggression among wolves (Asa, Mech, Seal, & Plotka, 1990; Ryon & Brown, 1990). At a more physiological level, pheromonal mechanisms may also be important with urine as well as faeces (canids have anal glands or sacs that can impregnate faeces with social odours; Macdonald, 1985). Canids also use other outputs, including

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[56] Dunbar (1995) argues that even females callitrichids tend to behaviourally control the males, coercing them to remain monogamous.

their foot glands, their supracaudal gland (conveniently "marked" by a darker coat coloration in wolves and coyotes[57]) and likely their perioral and cheek glands (Macdonald, 1985). The literature on rodents (see Brown, 1979, 1985 for reviews; see also Baum, 2002; Crews 2002; McCarthy & Becker, 2002; Silver & Kriegsfeld, 2002) is rich in data suggesting a number of pheromonal mechanisms influencing and modulating reproduction (e.g., the Bruce effect and the Vandenbergh effect). Unfortunately, such mechanisms are virtually impossible to investigate in non-laboratory conditions and we can only hypothesize that they are influential. Some have also suggested that high testosterone levels in females can shorten proestrous and decrease attractiveness (Packard, 1980; Packard, Seal, Mech, & Plotka, 1985). This hypothesis is interesting considering high testosterone levels found in some of our subordinate females.

The view that wolves do not have behaviourally-mediated reproductive suppression has been suggested in the past. For example, at the population level, Packard and Mech (1980) identified food supply as an important regulation mechanism. This would not have been a factor with our captive wolves. Packard (1980), Packard, Mech, and Seal (1983) and Seal, Plotka, Mech,

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[57] This gland, in red foxes, also called the violet gland, produces much of their musky smell.

and Packard (1985) suggested that reproductive failure in subordinate females is simply failure to breed, that is, deferred reproduction, and not stress-induced suppression. This perspective is based on an individual selection principle, suggesting that delayed maturation would take place in a social group that is characterized by high social competition. It recognizes the idea that individual subordinate wolves make a "cognitive assessment" of the social dynamics of their pack and adjust their reproductive strategy accordingly. This mirrors Sapolsky's (2000) acknowledgement that marmosets and tamarins will simply be "rising in rank by waiting their turn" (p. 114) and will help in the raising of the progeny of the group in the meantime. Individuals may delay reproduction increasing the survival of the younger members of the pack (yearlings, subadults[58]) and increasing at the same time their own reproductive success. Baker, Abbott and Saltzman (1999) notice that in immediate families of common marmosets, fathers and sons do not differ in their hormonal profiles.

As we think that the picture is becoming tidier, it should be noted that the early literature on marmosets strongly suggested reproductive suppression of subordinates (Abbott, 1984, 1993; Barrett, Abbott, & George, 1993), at least in captivity. But regardless of the current conclusions on captive studies with

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[58] A subadult wolf is considered to be 20 months old or younger.

callitrichids, as Snowdon (1998) warns "there is as yet no evidence in the field of the mechanism of reproductive suppression..." (p. 448).

Furthermore, Asa (1997), after pointing out that subordinate males and females are, in fact, able to reproduce, also suggests that a mechanism akin to incest taboo (i.e., a reduced likelihood of reproduction by close relatives) restricts the mating to the dominant pair. As mentioned earlier, there is a fair amount of inbreeding in a typical wolf pack (wild or captive) suggesting that, even if this were true, it could not be the main mechanism underlying group size regulation of a pack.

4.9 Future directions

The present study is a typical example of "ethoendocrinology," behavioural endocrinology with an ethological perspective, that is, a focus on the non-invasive and unobtrusive study of wolves in their (quasi-) natural environment. Most research focuses on either laboratory studies (the majority of the rodent research and much of the research on callitrichids) or field studies (e.g., lycaon research). A synthesis of data gathered using all approaches will be necessary for the understanding of the proximate mechanisms behind reproductive suppression, social and mating systems, and social dynamics.

As discussed previously, I acknowledge the limitations that are inevitable in captive studies, mainly the partially controlled environment and the debatable ecological validity of the approach. As argued in Section 4.2, however, the study location and setting were quite exceptional for a captive pack. Moreover, the state of the social dynamic and environment of the pack was analysed with thoroughness and precision that is virtually impossible to attain in the wild. New techniques for analyzing the faeces of wolves in the wild are making field research a promising alternative and augmentative approach to captive studies. DNA fingerprinting methods are being developed to identify individual wolves through their faeces (see for example, Barr, 1999), and methods of extracting levels of steroid hormones (glucocorticoids, androgens, estrogens, progestogens, etc) from faeces already exist. This is a great advance in behavioural endocrinology. The main limitation, of course, is that detailed behavioural observations and analyses are more of a challenge in the wild.

Comparative studies among canids are also needed, including studies of foxes (e.g., *Vulpes vulpes* or *Alopex lagopus*) and coyotes or jackals (i.e., canids with a more transient immediate family system or permanent pair-bond immediate family system). Red foxes, arctic foxes, and coyotes are common throughout Canada and could be studied with our methods (or by substitution of urine with faeces). Koren, Mokady, Karaskov, Klein, Koren, & Geffen (2002) present a method for measuring hormone levels in hair which is interesting considering that DNA information can often be extracted from hair. Hair may be, in some cases, easier to collect (with traps that "comb" the animal at entry), and would certainly be easier to store, move around, ship, and handle in the laboratory. In canids, hair can also be found around dens and rendez-vous sites.

Considering the state of the literature and the current state of knowledge on social stress in carnivores and primates, the combination of thorough, non-invasive, unobtrusive captive and non-captive studies, in parallel with comparative approaches (as already common in the rodent literature) will be essential to our understanding of the role of sociogenic stress in reproductive suppression.

4.10 General conclusion

The investigation of social stress as a means of reproductive suppression in relation to aggression is proving to be a difficult endeavour. It may be time to close the chapter on aggression-mediated stress in wolves as a means of group-size regulation and to recognize that wolves may be part of a special group of monogamous, singular, and cooperative breeding mammals that do not show hormonal reproductive suppression of subordinates.

Since reproductive hormones do not provide strong evidence of physiological reproductive suppression (or even inhibition), examining pheromonal factors may not even prove to be informative, unless pheromones, like ritualized aggression, fights, and urine postures (as displays) act as reminders of one's status in the pack.

McLeod, Ryon, and Fentress (unpublished manuscript), as well as Fentress, Ryon, McLeod, and Havkin (1987), remind us that aggression increases during the mating season in wolves. It is unlikely that individuals, dominants and subdominant animals alike, would engage in such potentially damaging and injurious behaviours if they did not serve a purpose.

I am not suggesting that aggression is not an important factor. I am simply suggesting that aggression-mediated stress is not the primary factor in hormonal reproductive suppression. The complexity of the mechanisms discussed here should incite behavioural endocrinologists to focus on non-captive animals and on comparative studies of canids' and callitrichids' social behaviours (agonistic, affiliative, sexual) and their hormonal correlates.

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Appendix A

Levels and intermediary levels of reproductive, social, parental, and alloparental patterns of canids: species by species account.

Tables 1a and 1b. Levels and intermediary levels of reproductive, social, parental and alloparental patterns of canids: species by species account.

Table 1a. Legend for Table 1b

LEVEL	**DESCRIPTION**
Level 0	Solitary species: Maned wolf; *Chrysocyon brachyurus.*
Level 1	Transiently social species: *Urocyon*, many *Vulpes* species.
Level 1.5	Transiently social species with flexibility towards more stable groups: *Nyctereutes Cerdocyon*, *Vulpes macrotis* & *velox.* Species at this level could arguably fit within Level 1 or 2 and more field data may help to determine this.
Level 2	Permanent, stable pair bond, frequent cooperative breeding, evidence of reproductive suppression in subordinates: *Canis* (except for the dog and the wolf), *Alopex*, *Fennecus*, *Otocyon*, *Vulpes vulpes* & *zerda.*
Level 3	Pack structure canids with cooperative breeding and evidence of reproductive suppression in subordinates: *Canis lupus, Lycaon pictus, Speothos venaticus.*
Level 4	Pack structure canids with superseding clans: *Cuon alpinus.*
Level 5	Loose structure canids with high flexibility and adaptability: *Canis lupus familiaris.*
Undetermined	Status (level) unknown: Many South American canids.

Table 1b. Levels and intermediary levels of reproductive, social, parental, and alloparental patterns of canids: species by species account.

1. **Species** (scientific & vernacular names)	2. **Mating System**	3. **Social system**	4. **Paternal & alloparental care**	5. **Reproductive suppression** (in subordinates)	6. **Notes**
LEVEL 0					
Chrysocyon brachyurus Maned wolf	Monogamous	Solitary, mated pair. Thought to be facultatively monogamous.	Minimal (if any) paternal care. No evidence for alloparental care.	No evidence.	Not very social, typically the most solitary of all canids.
LEVEL 1					
Pseudalopex gymnocercus Pampas fox, Paraguayan fox, Azara zorro	Monogamous	Mated pair and immediate family group.	Some paternal care. No evidence for alloparental care.	No evidence.	Very little is known on this species. Formerly labelled *Dusicyon gymnocercus*.
Urocyon cinereoargenteus Gray fox	Monogamous, Polygynous	Mated pair, immediate family group.	Minimal paternal & alloparental care.	Uncertainty. (Anecdotal only.)	
Urocyon littoralis Insular gray fox	Monogamous	Mated pair, immediate family group.	Minimal paternal & alloparental care.	Uncertainty. (Anecdotal only.)	

1. Species (scientific & vernacular names)	2. Mating System	3. Social system	4. Paternal & alloparental care	5. Reproductive suppression (in subordinates)	6. Notes
Vulpes bengalensis Bengal fox	Monogamous, Polygynous?	Mated pair. Possibility of immediate family groups.	Possibility of more than one lactating female in a group. See Moehlman & Hofer (1997).	Uncertainty. (Anecdotal only.)	
Vulpes cana Blanford's fox Hoary fox Afghan fox	Monogamous, Polygynous?	Solitary, mated pair. Possibility of immediate family group. Not a very social fox.	Minimal paternal care. Females from previous year may stay with parents but will not assist (Geffen & Macdonald, 1992).	Uncertainty. (Anecdotal only.)	
Vulpes chama Cape fox	Monogamous	Solitary, mated pair, maybe immediate family groups? Communal denning observed.	Minimal paternal care. Possibility of more than one lactating female in a group. See Moehlman & Hofer (1997).	Uncertainty. (Anecdotal only.)	
Vulpes ferrilata Tibetan (sand) fox	Monogamous	Mated pair, immediate family groups.	Some paternal care. Lack of data.	No information.	
Vulpes pallida Pale fox	Monogamous	Immediate family groups.	Some paternal care. Lack of data.	No information.	

1. Species (scientific & vernacular names)	2. Mating System	3. Social system	4. Paternal & alloparental care	5. Reproductive suppression (in subordinates)	6. Notes
Vulpes rueppellii Sand fox	Monogamous	Solitary, mated pairs or immediate family groups. Often found in small groups.	Some paternal care. Lack of data.	No information.	
LEVEL 1.5					
Cerdocyon thous Crab-eating fox or dog	Monogamous	Mated pair and immediate family group. Lasting pair bond?	It seems that some paternal care is provided. No evidence for alloparental care.	No evidence.	Shares behavioural characteristics with the genera *Canis* and *Vulpes*. Formerly labelled *Dusicyon thous*.
Nyctereutes procyonoides Raccoon dog	Monogamous (Polygynous?)	Mated pair, immediate family group. Polygyny observed in captivity.	Paternal care, although limited to care for female.	No conclusive information.	Only canid to hibernate (semi-torpor). Use of latrines.
Vulpes macrotis Kit fox	Monogamous, Polygynous	Immediate family groups. Occasional polygynous groups.	Some paternal care, some alloparental care.	Uncertainty (see Moehlman & Hofer, 1997). Some evidence of reproductive suppression in multi-female groups despite the fact that multiple litters groups are found.	Purrs like the Fennec.

1. **Species** (scientific & vernacular names)	2. **Mating System**	3. **Social system**	4. **Paternal & alloparental care**	5. **Reproductive suppression** (in subordinates)	6. **Notes**
Vulpes velox Swift fox	Monogamous, Polygynous?	Mated pair, immediate family groups. Groups composed of 1 male & 2 females have been seen: tendency towards polygyny?	Some paternal care, alloparental care or shared care?	No information.	
LEVEL 2					
Alopex lagopus Arctic fox	Monogamous, Polygynous?	Mated pair, immediate family group; Solitary off breeding season; Hersteinsson & Macdonald (1982): temporary pack structure? Mated pair for life (Chesemore, 1975)?	Alloparental care (with female helpers) common. Some paternal care (Hersteinsson & Macdonald, 1982).	At least one study with supporting evidence (Kullberg & Angerbjörn, 1992).	Seem to be more social than initially thought. Among the most gregarious of the vulpines with *Vulpes vulpes*, *Vulpes corsac* & *Fennecus zerda*.
Canis adustus Side-striped jackal	Monogamous	Solitary, mated pairs, immediate family group. Likely similar to *Canis aureus* & *mesomelas*.	Likely similar to *Canis aureus* & *mesomelas*.	Likely similar to *Canis aureus* & *mesomelas*.	Not very well known.

1. Species (scientific & vernacular names)	2. Mating System	3. Social system	4. Paternal & alloparental care	5. Reproductive suppression (in subordinates)	6. Notes
Canis aureus Golden jackal, common jackal, Asiatic jackal	Monogamous, Polygynous?	Mated pairs, immediate family group, occasional extended family group (with helpers) & pack structure.	Parental care, alloparental care (Moehlman, 1983).	Uncertainty (see Moehlman & Hofer, 1997), but possible (Estes, 1991).	Common in the Balkans (Bulgaria), and as North as Austria. Similar behavioural pattern to *Canis mesomelas* although more social than *Canis mesomelas*. (Moehlman, 1983)
Canis latrans Coyote	Monogamous*	Solitary, mated pairs, immediate family group, occasional extended family group & pack structure. *Sometimes multiple pairs.	Some paternal & alloparental care (Bekoff & Wells, 1982).	Uncertainty (see Moehlman & Hofer, 1997), but possible.	Exceptional social flexibility, in the Northeastern range, could be attributed to hybridisation with Canis lupus (as in the extreme case of the Algonquin "wolves", see Wilson et al., 2000).
Canis rufus (or *Canis lycaon*?) Red wolf	Monogamous	Solitary, mated pairs, immediate family group, occasional extended family group & pack structure. Much like wolves and the most social coyote groups.	Paternal care & alloparental care (Riley & McBride, 1975), although minimal (even less than coyotes).	Likely similar to coyotes (*Canis latrans*).	Confirmed a distinct species according to a recent study (Wilson et al., 2000); behaviourally more similar to coyotes than wolves (Wilson et al, 2000)

1. **Species** (scientific & vernacular names)	2. **Mating System**	3. **Social system**	4. **Paternal & alloparental care**	5. **Reproductive suppression** (in subordinates)	6. **Notes**
Canis mesomelas Black-backed jackal, silver-backed jackal	Monogamous, Polygynous?	Mated pairs, immediate family group, occasional extended family group (with helpers) & pack structure.	Parental care, alloparental care (Moehlman, 1983).	Uncertainty (see Moehlman & Hofer, 1997), but possible.	Similar behavioural pattern to *Canis aureus* although less social than *Canis aureus* (Moehlman, 1983).
Canis simensis Simien jackal, Ethiopian jackal or wolf, Abyssinian jackal	Monogamous	Solitary, mated pair, immediate family group, occasional extended family group (with helpers) & pack structure.	Parental care, alloparental care.	Some evidence.	
Fennecus or *Vulpes zerda* Fennec fox	Monogamous	Mated pair, immediate family group, extended family group (rudimentary pack structure, up to 10 individuals).	Paternal care (minimal).	Unknown but possible.	Tail wagging and other affiliative behaviours typical of larger, very social species such as wolves. Also purrs, like the kit fox. Among the most gregarious of the vulpines with *Alopex lagopus*, *Vulpes vulpes* & *Vulpes corsac*.

1. **Species** (scientific & vernacular names)	2. **Mating System**	3. **Social system**	4. **Paternal & alloparental care**	5. **Reproductive suppression** (in subordinates)	6. **Notes**
Otocyon megalotis Bat-eared fox	Monogamous, Polygynous?	Mated pair, immediate family group, small extended family group. Groups with 1 male & 2 females have been seen; tendency towards polygyny?	Some paternal care; Alloparental care (cooperative breeding in the females).	Uncertainty (see Moehlman & Hofer, 1997).	Mainly insectivorous.
Vulpes corsac Corsac fox	Monogamous	Mated pair, immediate family groups, maybe even extended family group & rudimentary pack structure. Will actually hunt in groups (unlike all other *Vulpes* species). Communal denning.	Paternal care, alloparental care (Buehler, 1973).	No evidence.	Among the most gregarious of the vulpines with *Vulpes vulpes*, *Alopex lagopus* & *Fennecus zerda*. May even form small hunting packs in the winter.

1. **Species** (scientific & vernacular names)	2. **Mating System**	3. **Social system**	4. **Paternal & alloparental care**	5. **Reproductive suppression** (in subordinates)	6. **Notes**
Vulpes vulpes Red fox	Monogamous, Polygynous	Mated pair, immediate family groups, maybe even extended family group & rudimentary pack structure.	Some paternal care. Alloparental care (aunting: Macdonald, 1979).	Evidence of reproductive suppression in multi-female groups (Macdonald, 1980) but occasionally multiple litters are found in a group. Polygyny has been observed (e.g., Macdonald, 1983).	Among the most gregarious of the vulpines with *Alopex lagopus*, *Vulpes corsac* & *Fennecus zerda*.

1. Species (scientific & vernacular names)	2. Mating System	3. Social system	4. Paternal & alloparental care	5. Reproductive suppression (in subordinates)	6. Notes
LEVEL 3: *CANIS LUPUS, LYCAON PICTUS, SPEOTHOS VENATICUS*					
Canis lupus Wolf	Monogamous*, Polygynous, Polyandrous	Mated pairs, immediate family group, and pack structure as extended family group. Dual parallel dominance hierarchies within packs for males & females. * Sometimes multiple pairs.	Extensive paternal care & alloparental care (known since Murie, 1944).	Evidence for behavioural reproductive suppression (Packard et al 1985). Uncertainty regarding physiological reproductive suppression in this species (see Moehlman & Hofer, 1997), but possible.	Mech (1999) actually questions the dual-parallel dominance hierarchy in this species and suggests a leadership advantage of the alpha male and minimizes the importance of agonistic behaviour in wild packs. Polygyny in wild wolves: Mech & Nelson, 1989). Polygyny in captive wolves: Harrington et al., 1982).

1. **Species** (scientific & vernacular names)	2. **Mating System**	3. **Social system**	4. **Paternal & alloparental care**	5. **Reproductive suppression** (in subordinates)	6. **Notes**
Lycaon pictus African hunting dog or Cape hunting dog	Monogamous*, Polyandrous	Pack structure, extended family group. Packs of 20 or more, up to 40 or 60. Dual parallel dominance hierarchies within packs for males & females. * Sometimes multiple pairs.	Extensive paternal care & alloparental care (Malcolm & Marten, 1982).	Uncertainty (see Moehlman & Hofer, 1997), but possible.	Female emigration is common. In most social, carnivores, male emigration is the rule. Sex ratio in packs also unusual: significantly more males than females in many packs (i.e., extreme case of 8 males, 1 female). Little overt aggression.
Speothos venaticus Bush dog	Monogamous	Pack structure, extended family group. Up to 10 animals.	Some paternal care.	Evidence of reproductive suppression in captive families (Porton, Kleiman & Rodden, 1987).	Information available mainly from captive studies.

1. **Species** (scientific & vernacular names)	2. **Mating System**	3. **Social system**	4. **Paternal & alloparental care**	5. **Reproductive suppression** (in subordinates)	6. **Notes**
LEVEL 4: *CUON ALPINUS*					
Cuon alpinus Dhole	Monogamous	Clans of packs (2-3) (Fox, 1984). 2-15 (more frequently 5-12) animals per pack, up to 50. Dual parallel dominance hierarchies within packs for males & females.	Paternal care, alloparental care (Davidar, 1975).	Uncertainty (see Moehlman & Hofer, 1997), but possible (Johnsingh, 1982).	As first recognized by Fox (1975) and Davidar (1975), dholes have a complex social organization with a social unit superseding the pack; they form clans of 2 or 3 packs. This is similar to the "troop" unit in some monkeys (e.g., baboons).

1. Species (scientific & vernacular names)	2. Mating System	3. Social system	4. Paternal & alloparental care	5. Reproductive suppression (in subordinates)	6. Notes
LEVEL 5: *CANIS LUPUS FAMILIARIS*					
Canis (lupus) familiaris Dog	Polygynous	Contextually-defined… Very flexible. The pack structure is found in dingoes with cooperative breeding.	No (domestic) or little (dingo) paternal care, no (domestic) or little (dingo) alloparental care (Corbett & Newsome, 1975). Dominant female dingoes will kill progeny of subordinate females (Corbett, 1988).	No evidence of reproductive suppression but lack of data on physiological suppression. Possible behavioural suppression (e.g., infanticide).	Includes the dingo, New Guinea Dog, etc.
UNDETERMINED: *SOUTH AMERICAN CANIDS*					
Dusicyon culpaeus Culpeo or Andean fox	?	?	?	?	Sometimes classified in genus "*Pseudalopex*".

1. **Species** (scientific & vernacular names)	2. **Mating System**	3. **Social system**	4. **Paternal & alloparental care**	5. **Reproductive suppression** (in subordinates)	6. **Notes**
Dusicyon griseus Chilla fox, Argentine (gray) fox, gray zorro	Polygynous?	Mated pair and immediate family group?	Non-breeding adults and female helpers observed.	Possibility of reproductive suppression in females	Sometimes classified in genus "*Pseudalopex*".
Dusicyon microtis Small-eared dog or fox	?	Solitary, mated pair?	?	?	Almost nothing is known about this species. Sometimes labelled *Atelocynus microtis.*
Dusicyon vetulus Hoary fox	?	?	?	?	Sometimes classified in genus *Pseudalopex* or *Lycalopex.*
Pseudalopex sechurae Sechura fox, Peruvian desert fox	?	?	?	?	Formerly classified as *Dusicyon sechurae.*

Appendix B

Narrative account of the personality of major figures in the main pack.

Name/Birth	Personality
Devil Child (1993)	Assertive and aggressive, with females and males alike, Devil Child had an attitude and plenty of confidence despite her small size. Her name could not have been more appropriate.
Fiona (1992)	Good natured and tolerant, Fiona eventually replaces Pawnee after her death. She continued to be good natured and tolerant in her new role.
Galen (1988)	Elegant, calm, respected but quite in control, he was a very diplomatic alpha male.
Homer (1988)	Voochko's enemy, very much interested in the beta rank until Voochko conceded it in the third season of the study. Homer took his beta role seriously although in a tamer manner than Voochko.
Jasper (1993)	Brother of Devil Child, although quite opposite in personality. He was playful and not very interested in the politics of the pack.
Noah (1990)	Gentle and somewhat shy, although like Xyla, was often the first to show himself to humans.
Pawnee (1984)	Pawnee was a good natured and diplomatic alpha female. A good match for Galen.
Ulysses (1995)	Ulysses was curious and playful. He got plenty of attention from the whole pack during his puppyhood. He never seemed bothered by the politics of the pack.
Voochko (1984)	Assertive male (for most of the time of the study) until the very last year (1996). Voochko then seemed sick and actually died soon after. In his contention for the alpha rank, Voochko would be described as "stubborn" but he may have had a hard time accurately perceiving threat. His main competitor was Homer.
Xyla (1988)	Gentle and shy (although, like Noah, often the first to arrive and the first to leave). Despite harassment from others, Xyla seemed to have good spirits, as long as she could avoid the other members of the pack.

Note: Ten of the fifteen wolves are described here. The descriptions originate from field notes and personal memory. The information contained here applies only to the three years of the study (1993-1996) and has the sole purpose of orienting readers interested in a more subjective evaluation of each wolf's personality.

Appendix C

Days for which behavioural and hormonal data were available, organized by Season.

Note: For all the figures below, the drop bars show the days for which both the hormonal and behavioural data were available.

Table 1. Number of watches and start date/end date of each Season.

	Season 1	Season 2	Season 3
December	7	4	7
January	14	9	16
February	14	9	7
March	8	8	6
Total	**43**	**30**	**36**
Start date/end date	December 8th to March 31st	December 3rd to March 22nd	December 2nd to March 31st

Figure 1. Watches and samples available for Season 1.

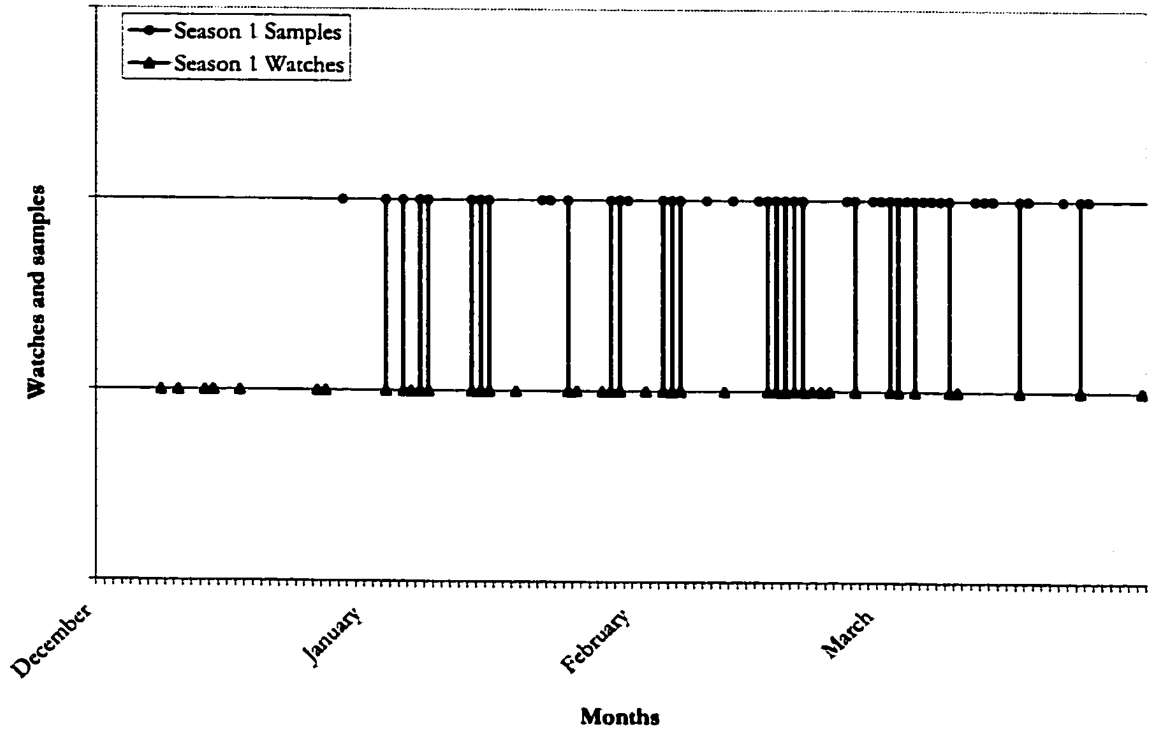


Figure 2. Watches and samples available for Season 2.

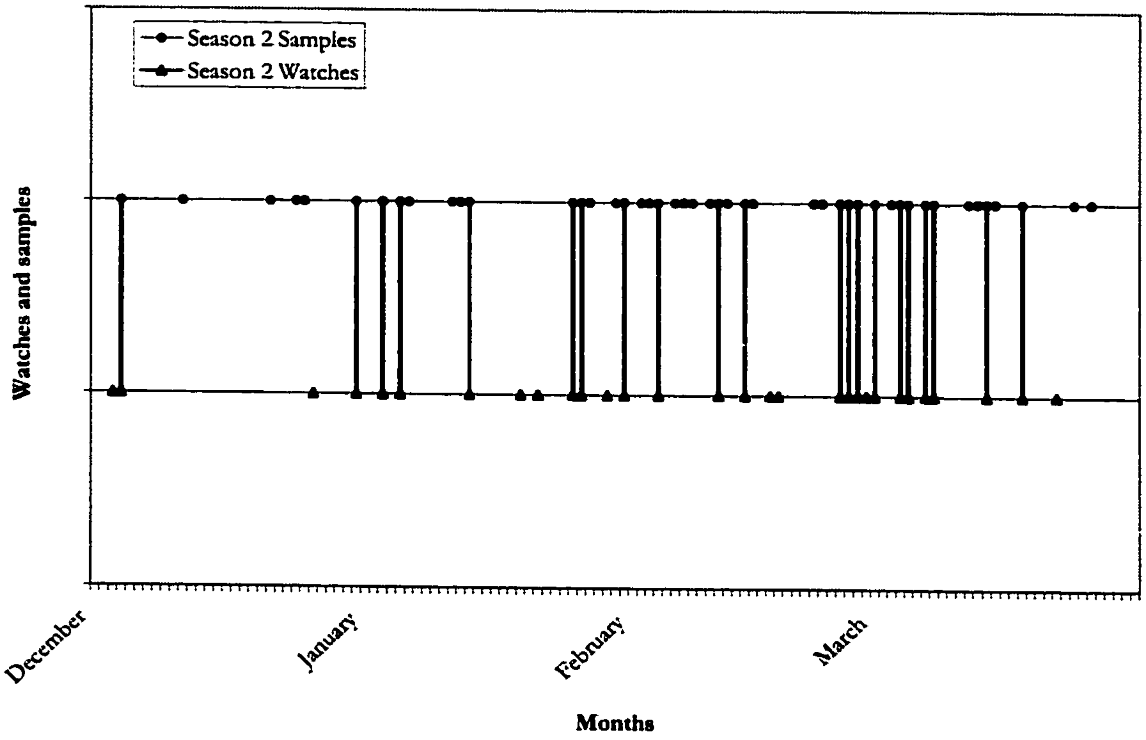
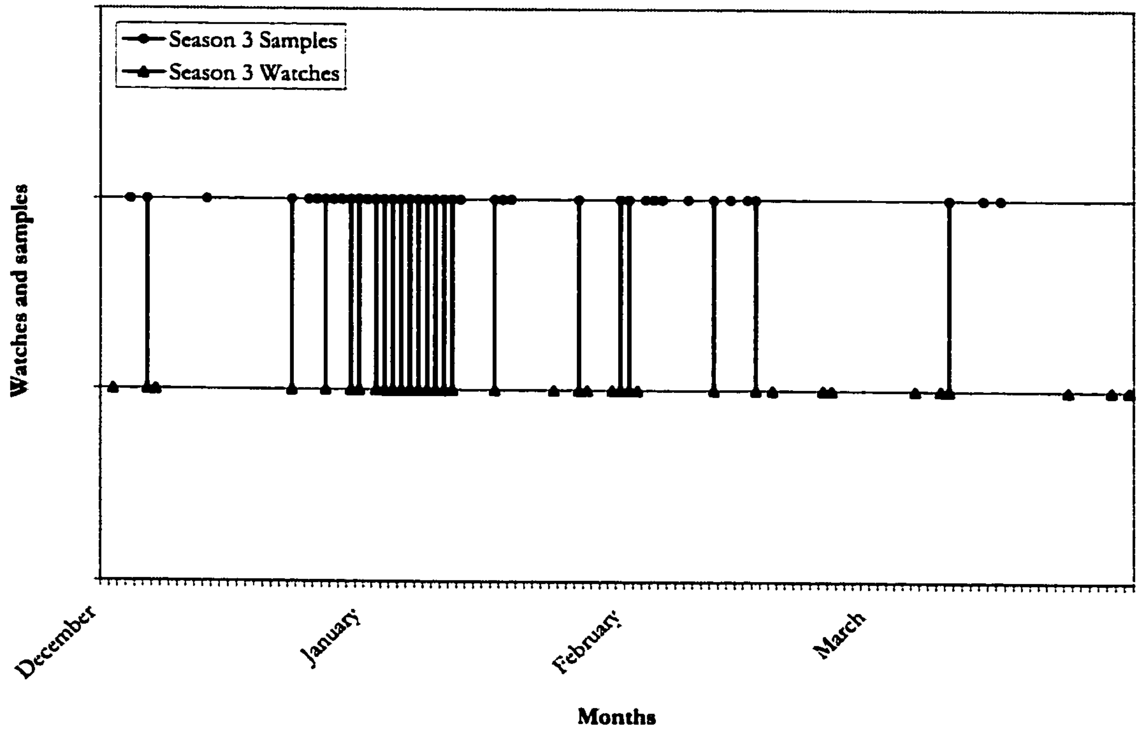


Figure 3. Watches and samples available for Season 3.



Appendix D

Behavioural matrices: Observed frequency of inter- and intra-sexual submissive interactions for Season 1.

Table 1. Observed frequency of inter- and intra-sexual submissive interactions for Season 1.

RECIPIENTS

	Males								**Females**								
INITIATORS	A	G	H	J	N	V	W		C	D	F	M	P	T	X		Σ
Males																	
Ashley [A]	•	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	**1**
Galen [G]	0	•	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Homer [H]	0	1	•	0	0	0	0	1	0	0	0	0	0	0	0	0	**1**
Jasper [J]	0	0	0	•	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Noah [N]	0	0	0	0	•	0	0	0	0	0	0	0	0	0	0	0	**0**
Voochko [V]	0	5	0	0	0	•	1	6	0	0	0	0	0	0	0	0	**6**
Winston [W]	0	4	0	0	0	0	•	4	0	0	0	0	0	0	0	0	**4**
	0	11	0	0	0	0	1		0	0	0	0	0	0	0		
Females																	
Celtie [C]	0	0	0	0	0	0	1	1	•	0	0	8	0	3	0	11	**12**
Devil Child [D]	0	0	0	0	0	0	0	0	0	•	0	0	0	0	0	0	**0**
Fiona [F]	0	0	2	0	0	0	0	2	0	0	•	1	0	1	0	2	**4**
Morgaine [M]	0	4	0	0	0	0	0	4	0	0	0	•	1	0	0	1	**5**
Pawnee [P]	0	1	0	0	0	0	0	1	0	0	0	0	•	0	0	0	**1**
Tess [T]	0	0	0	0	0	0	0	0	0	0	0	0	1	•	0	1	**1**
Xyla [X]	0	0	0	0	0	0	0	0	0	0	0	0	2	2	•	4	**4**
	0	5	2	0	0	0	1		0	0	0	9	4	6	0		
Total [Σ]	**0**	**16**	**2**	**0**	**0**	**0**	**2**		**0**	**0**	**0**	**9**	**4**	**6**	**0**		**39**