REPTILIAN WELFARE IN A BIOLOGICAL CONTEXT

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ABSTRACT

At the interface between human association with reptiles and the resultant impacts on these animals resides the issue of artificial pressures and effects on organismal coping strategies and biological outcomes - in other words, their welfare. As a platform, this thesis takes the position that welfare is a fundamental component of evolutionary biology by postulating that adaptational processes have selected biological strategies in service of individual wellbeing, because the wellbeing of the individual is important both to its fitness as well as to the success of its genetic continuity. This thesis presents an overarching hypothesis that reptiles and their wellbeing are locked-in to lifestyles under natural conditions, and that the reptilian adaptational landscape to non-natural situations is highly limited, and that these animals do not adapt or at best adapt poorly to the general conditions of captivity. Commonly reported signs concerning abnormal behaviour and behaviour-related injury, as well as clinical evidence of stress-related immunocompromise, opportunistic infection, morbidity and mortality, supports the argument that reptiles do not adapt or adapt poorly to common conditions of captivity. It is hypothesised that strong ancestral innate traits or genotypic ‘hard wiring’, ectothermic dependency, low metabolic and energetic rates, and common nocturnalism, are causally-related to the poor welfare observed in many captive reptiles. Other factors relevant to poor welfare include deficiencies and errors of provision concerning humidity, nutrition, and light. Strong ancestral innate traits and associated precosity are dominant in determining reptilian psychological and behavioural profiles for an evolved lifestyle under natural conditions. The Aims and the Study questions for this thesis, were to investigate: the scope of reptilian adaptability or nonadaptability to artificial environments - that is, whether reptiles are adaptable to captivity; and the welfare-relevant endpoints or

'consequences' of captivity for reptiles - that is, whether typical captive husbandry practices are consistent with reptile welfare. The thesis relates to its Aims and Study questions by outlining essential adaptational principles as well as exemplifying issues of captivity- associated stress and stressors, as well as failures of coping mechanisms and adaptive plasticity, to conclude that reptiles are not adaptable to captivity and thus the artificial conditions in which they are routinely confined; and also that typical captive husbandry practices are inconsistent with reptile welfare.

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1. INTRODUCTION

1.1 **Summary hypothesis**

At the interface between human association with reptiles and the resultant impacts on the latter resides the issue of artificial pressures and effects on organismal coping strategies and biological outcomes - in other words, their welfare. As a platform, this thesis takes the position that welfare is a fundamental component of evolutionary biology by postulating that adaptational processes have selected biological strategies in service of individual wellbeing, because the wellbeing of the individual is important both to its fitness as well as to the success of its genetic continuity. This postulate places wellbeing, or welfare, as a necessary priority both under natural conditions and under human control in captivity. On this platform is laid a summary of concepts and principles for animal welfare in general to emphasise current approaches to understanding and providing for welfare factors generally. In refinement of this foundational information is included further reptile welfare-relevant biological features, concepts and principles. These features, concepts and principles are important to understanding and providing for reptile welfare. Endpoints or consequences of captivity and typical husbandry practices are also considered, and these involve frequent manifestations of stress, morbidity and mortality. Captivity-stress, morbidity and mortality are important to assessing issues of welfare because they may indicate an animal's ability or failure to cope with environments, particularly those that are at odds with the animals' free-ranging environments.

Collectively these thematics suggest an overarching hypothesis that reptiles and their wellbeing are locked-in to lifestyles under natural conditions, that the reptilian adaptational landscape to non-natural situations is highly limited, and that these animals do not adapt or at best adapt poorly to the general conditions of captivity. Behavioural and clinical evidence of captivity-stress, morbidity and mortality supports the argument that reptiles do not adapt, or adapt poorly, to captivity.

It is hypothesised that strong ancestral innate traits or genotypic 'hard wiring', ectothermic dependency, low metabolic and energetic rates, and common nocturnalism, are elements causally-related to the poor welfare observed in many captive reptiles. Other factors relevant to poor welfare include deficiencies and errors of provision concerning humidity, nutrition, and light. It is in particular argued that the strong ancestral innate traits and associated precocity, which are dominant in determining reptilian psychological and behavioural profiles for an evolved lifestyle under natural conditions, may significantly inhibit reptilian coping mechanisms and adaptive plasticity towards artificial environments. In the following sections, each of the above themes will be discussed and key evidential examples included.

1.2 **Concepts, principles and protocols for animal welfare**

In the Western world, animal welfare concepts, principles and protocols have a history of legal debate and implementation extending to over 400 years, commencing with the introduction of Parliamentary Acts in Ireland in 1635 (1) and England in 1822 (2). Since these early structures innumerable legislative and practical bases for animal welfare governance have been introduced across all use sectors (3). It is not possible to include all relevant animal welfare developments herein, thus emphasis is on some key concepts, principles and protocols with extant applications particularly relevant to the aims of this thesis.

Modern concepts, principles and protocols for animal welfare can be traced back to early foundational themes largely co-emergent between the 1950s-90s that developed ideas and approaches regarding stress (4-6), adaptation (4, 7), behaviour (7-17) pain (6, 18), and related issues of measurement (6, 19-25). Expectedly, over time some of these ideas and accompanying evidence have been developed and adapted as novel information arose and, fortunately, several authors of these seminal works have continued to build on their original materials, for example (17, 26-36), thus ensuring consistency of interpretation. However, the evolution of concepts principles and protocols for animal welfare has essentially been one of incorporation rather than replacement. Accordingly, the early foundational works referred to herein can be regarded as relevant not only in terms of historical context, but also in terms of contemporary relevance, not least because other key authors continue to borrow from and further develop these foundational examples, for example (37-42).

Broom (6, 19, 20) suggests that an individual's welfare is its state as it attempts to cope with its environment, and that the less the individual has to do to cope then the more satisfactory may be its life, and conversely, that morbidity and premature mortality may result from failed coping abilities. Reduced life expectancy is an indication that animals have experienced stress and poor welfare, and that body damage (i.e. injuries) and disease (as well as susceptibility to it) are important indicators in welfare assessments as well as indicators of poor husbandry (6, 14, 43). However, Broom (6) also emphasises that certain physical and behavioural signs, growth rate and reproduction, may be normal whereas concomitant welfare may be poor, thus these superficially positive potential welfare indicators are ambiguous. Broom (6, 19) also points out that attempts to cope with challenging environments may widely and diversely manifest a range of signs from abnormal excessive amounts of normal regulatory behaviours (essential primary activities such as feeding and basking), to abnormal inactivity, to stereotypies, and self-harm. Accordingly, animals facing overwhelming challenges in captivity may revert to basic self-maintenance biological needs or homeostatic management as a possible means to gain control over interactions with their environment and homeostasis. Hart (44, 45) adds to this ‘back to basics in a crisis’ idea by proposing that such activities involve redirection of energy to fundamental operations as a ‘stress-releasing’ mechanism.

Dawkins (21) and Broom (6) explain that welfare and suffering can be considered separately, in that, for example, an animal may be immunocompromised and harbouring imminent disease due to a poor welfare state while at the same time experiencing no adverse feelings from sickness, and a clinically sick animal that may experience adverse feelings when awake may not do so when asleep. Dawkins (21) expressly states that animal welfare involves the subjective feelings of animals. Combined, Dawkins (21) and Broom (6) infer that subjective feelings are unpleasant emotional states that include pain, fear, loneliness, frustration, boredom, thirst, and hunger. In addition, these authors infer that body damage, disease, behavioural responsiveness, expressed preferences, and life expectancy constitute examples of physical measures or indicators of poor welfare; thus, welfare relates to evolved mechanisms for the individual’s state, and suffering relates to evolved mechanisms for the avoidance of danger and threats to fitness and survival.

The issue of an animal's control over interactions with its environment are relevantly further investigated. For example, Dawkins (21) states that suffering often occurs in captivity where animals are prevented from carrying out something that they are motivated to do. Broom (6) described five factors where control, or lack of control, may impact welfare: '*Difficulties in movements*', refers to restrictive features of an environment (such as inability to move normally or adopt normal postures or positions); '*Frustration*', refers to animals knowing how to control interactions with their environment, but being prevented from performing them normally; '*Absence of specific input*', refers to absence of certain essential stimuli; '*Insufficient stimulation*', refers to a situation where an animal is programmed (i.e. involving innate psychological and behavioural characteristics) to explore and respond to certain stimuli, but where overall environmental complexity is low - essentially, sensory deprivation; and '*Overstimulation*', refers to overload of novel stimuli for a situationally naïve animal.

1.2.1 ***Stress, stressors and coping mechanisms***

Stress is a response or result of one or more real or perceived threats or challenges affecting the stability of organisms, and can be divided into three basic groups: environmental (e.g. predatory threats, heat, cold); internal (e.g. emotion, thirst, hunger, fear, lack of rest, disease); and cognitive (frustration of psychological drives) (46, 47). Stressors are stimuli that result in stress (48). Stress is a normal part of healthy functioning and may be considered only truly problematic when stressors are frequently repeated, prolonged or extreme, where, for example, chronic presence of high-levels of glucocorticoids can result in organ impairment and dysfunction (48, 49). Stress responses that succeed in stabilising an organism (i.e. allow it to meet its needs) are adaptive, whereas those that fail to stabilise an organism are non-adaptive (46, 48) (see also: 'Normal, abnormal and maladaptive behaviours' and 'Abnormal, maladaptive and stress-related behaviours in reptiles'). Zanette and Clinchy (50) imply that animals in their natural habitat would unlikely have adapted to chronic stress, and thus chronic stress in captive animals indicates maladaptive and pathological states.

Physiological contexts of stress relate to release of adrenaline from the adrenal cortex in order to enhance tolerance or performance in a crisis such as during anti-predator behaviour (49, 51, 52). There are also psychological contexts of stress - e.g. situations that do not pose a clear physical threat - that include social pressures (46, 53-55) and conditions such as depression (7, 11, 46, 51, 56-59). Accordingly, within its evolved natural context, stress is biologically valuable in challenging situations. In captive animals, while the processes and functions associated with stress remain allied to those under natural conditions, the context of stress can become altered to involve disproportionately frequent and abnormal stressors that essentially result in, among other things, physical deterioration, physiological imbalance and loss of homeostasis, immunological compromise, behavioural alteration, psychological disturbance, morbidity and mortality (60-62). All these stressor- and stress-related factors are known to occur in reptiles (47-49, 63-79), and this will be further explored below.

Coping mechanisms are elements of the general stress-response concept that involve elevated biologically strategic adjustment when one response strategy fails to regain stability (46). In other words, when one level of an organism's adaptive scope is exceeded, the organism must 'up' its strategic response to another coping mechanism (46). Coping mechanisms include physiological, behavioural and psychological strategies (46, 48, 65, 80). For example, within coping mechanisms, physiological responses include shifts from elevation of melanocyte-stimulating hormone (colour-changing) to high-level stimulation of the adreno-corticoid axis (49, 81); behavioural responses include shifts from defensive posturing to physical aggression (82, 83); and psychological responses include shifts from dominant status to post-combat social defeat and hierarchical subordination (54).

1.2.2 ***Normal, abnormal and maladaptive behaviours***

Normal behaviours can be regarded as those that are naturally occurring, and act to enable an animal to control or modify its environment, and to maintain homeostasis (14, 16, 21, 80). Normal behaviours are contextualised to acquiring or achieving what an animal needs or wants to do at any given point, and that only it may be able to determine. Context is an important factor when considering the nature of behaviour. For example, under natural conditions locating food and water would involve a range of locomotor, ambush or search behaviours. In zoo and pet animals, essential requirements of food and water are provided, which means that normal food and water locating behaviours are unnecessary. However, artificial provision of nutrition does not assure that inherited drivers of behaviours are redundant (24).

Abnormal behaviours can be regarded as those that differ in pattern, frequency or context from the species norms (6, 14). Abnormal or 'functionally redundant' behaviour may constitute part of a coping system, but it is also an indicator of poor welfare (6), and often associated with animals housed in environments where chronic aversive stimuli are involved, and where an animal cannot perform essential behaviours as it would under natural conditions, or where behaviour is unsuccessful in achieving homeostasis (80). Accordingly, abnormal behaviours are enduringly and widely regarded to constitute indicators of stress in captive animals, for example (6, 8, 14, 65, 80, 84), as well as acting as indicators of poor welfare and internal experiences (or subjective feelings) (84).

Maladaptive behaviours are considered to be consequences of poor species adaptability to artificial environments (65), and represent normal behaviours that fail to regulate a stressor (80). However, while these behaviours may be normal, their functional inability to regulate a stressor implies that they are being used improperly and therefore can be considered abnormal (14, 80). Therefore, maladaptive behaviours have an arguably 'circular' component in that they may be both normal and abnormal at the same time.

There are three key types of stereotypies: 1. normal/natural repetitive behaviours, such as displayed in courtship routines; 2. so-called maladaptive stereotypies (as reviewed by Garner (80) and others), such as repeated normal behaviours by normal animals under abnormal conditions (e.g. because they are thwarted by spatial constraints/attempts to escape); and 3. mulfunctional stereotypies (as reviewed by Garner (80) and others), such as abnormal behaviours resulting from altered (damaged) brain development and neurochemistry caused by captivity-stress. This latter category is further divided (as reviewed by Garner (80) and others) into categories of abnormal behaviour, such as functionless sham mouthing movements on a cage bar, jumping, and route-tracing, none of which have been described in reptiles.

In reptiles, ITB can be regarded as a stereotypy because it is a repetitive behaviour. However, the term ‘stereotypy’ does not infer any particular aetiology. Also, there are no scientific descriptions in the literature of ITB in the context of type 3 above. Thus, reptilian ITB in relation to captivity stress/welfare falls into the category of type 2. Furthermore, the term ‘maladaptive’ (as in ‘maladaptive behaviours’ and ‘maladaptive stereotypies’) as used in the thesis is not a term preferred by this author, but it is now generalised in the literature so it has been used herein. Strictly speaking, ‘maladaptive’ means ‘bad-adaptive’ - which one could smooth-out to say ‘badly-adaptive’, which then implies some degree of adaptation/coping, whereas no amount of adaptation or coping may be involved. There is no evidence that any adaptive result is occurring with reptilian ‘maladaptive’ ITB, but according to Garner (80) and others, because of its nature (fitting into type 3 above), ITB technically emerges as a ‘maladaptive behaviour’.

1.2.3 ***Aetiology of abnormal animal behaviours relevant to sub-optimal environments, and their potential function***

Garner (80) divides abnormal behaviours into two primary groups: maladaptive behaviours and malfunctional behaviours. Maladaptive behaviours refer to those behaviours that result from normal animals under abnormal conditions. Thus, even though the behaviours may fail to regulate a stressor or achieve homeostasis, they essentially remain intact behaviours (80). Neuroanatomy and physiology of maladaptive behaviours is unclear, but is thought to relate to thwarted expression of normal behaviour (15), and mental understimulation (85). A range of maladaptive behaviours have been described, including: high-level locomotor activity (hyperactivity) (26, 28, 80); escape activity (6, 55, 80, 86-88); exploratory behaviour (6, 16, 89); aggression/repulsion (90); infanticide (80); anorexia (inappetence) (16, 91); tonic immobility (motion-freezing); and learned helplessness (behavioural despair) (7, 11). Accordingly, maladaptive behaviours can broadly and collectively (although variously) be described as representing two response strategies to stressors: physically active or inactive responses.

Locomotor, exploratory, search and escape behaviours (essentially physically active behaviours), are perhaps exemplified by animals experiencing preferences for alternative environments, whether to avoid aversive conditions or respond to migratory or environmental search drives (6, 16, 26, 28, 64, 80, 89). Sedentarism and biological shut-down behaviours (essentially physically inactive behaviours), are perhaps exemplified by 'learned helplessness' (behavioural despair), a phenomenon in which animals experiencing stressful conditions over which they cannot gain remedial control adopt passive or immobile behaviour rather than persist in attempts at avoiding or escaping aversive situations (7, 11). Psychologically, animals may recognise the futility of intentionally remedial behaviour (thus their 'helplessness') and experience depression (indicated by the presence of pro-depressive chemicals; and administered anti-depressants limit the behaviour), thus affected animals essentially 'shut down' active behaviour (7, 11, 21). Broom (6, 20) reports that withdrawal from normal responses to an environment may constitute an attempt at coping with suboptimal conditions, and is an indicator of poor welfare.

As suggested previously, while the common examples of behaviours described as abnormal and maladaptive (e.g. hyperactivity, exploratory and escape, and hypoactivity) also represent normal behaviours (e.g.

locomotor, exploration, sedentarism), this does not infer their normality in artificial environments, because they may be noncontextualised. For example, behaviours that do not functionally enable an animal to express a preference for leaving an environment or locating an alternative environment can be considered non-contextualised and abnormal (14, 16, 21, 24, 80). Transparent boundaries, which will be returned to later (see also 'Abnormal, maladaptive and stress-related behaviours in reptiles'), are implicated in stressful conditions among numerous animals. For example, hens prevented by a transparent boundary from reaching visible food showed behavioural frustration (stereotypies and aggression), presumably because their control over interactions with their environment were thwarted (6).

Malfunctional behaviours refers to abnormal repetitive behaviours (ARBs) that occur in captivity, and that result from animals with altered psychology, brain development and neurochemistry induced by captivity (21, 80, 92, 93). However, certain repetitive or 'stereotypical' behaviours occur naturally in free-living animals, for example, ritualised courtship displays (80, 82), and require separate consideration. ARBs have been further divided into two groups: stereotypical behaviours that are functionless and goal-less, unvarying, repetitive, inappropriate body movements or postures – i.e. the behaviour is inflexible in its action (e.g. cage route-pacing or somersaulting); and impulsive/compulsive behaviours that are repetitive, inappropriate actions with varied goals – i.e. the behaviour is flexible in its action (e.g. feather or fur plucking) (80). Neuroanatomy and physiology of stereotypical ARBs (which in some interpretations are also regarded as maladaptive) are unclear (93). However, ARBs are thought to relate to dysregulation of the brain's (in particular basal ganglia) executive behavioural control (i.e. goal and response) systems that would normally regulate balance between 'drive and satisfaction', but which are thwarted by confounded normal behavioural sequences in artificial conditions, leading to 'recurrent perseveration' – arguably a form of psycho-behavioural 'lock-in' (21, 80, 93-95). A range of ARBs have been described, including: self-harm (self-mutilation) (16); fur or feather-plucking (self or others) (80, 96); pica (consumption of typically inedible items) (63); head-weaving (80); and route-tracing (26, 28, 80).

Table 1 provides a summary of abnormal behaviours that will later be used for comparative purposes in relation to selected examples of normal and abnormal stress-related behaviours in reptiles (Tables 6,7,8).

Table 1. Selected stress-related behaviours in animals.

Behaviour	Background	Resources (e.g.)
High-level locomotor activity (hyperactivity)	Stereotypical behaviour, high-level (i.e. not 'mild'-level [Broom, 1981] exploratory behaviour), pacing.	(26, 28, 80)
Escape activity	Fear, anti-predator behaviour.	(6, 55, 80, 86-88)
Exploratory behaviour	Low overall complexity of environment, search for novel environment.	(6, 16, 89)
Learned helplessness (behavioural despair)	Loss of control over interactions with environment.	(7, 11)
Aggression/repulsion	Fear, anti-predator behaviour.	(90)
Anorexia	Fear, injury, disease.	(16, 91)

1.2.4 *Scientific approaches for assessing or measuring welfare*

As indicated by Broom (19), Dawkins (21) and others, measurement of welfare and suffering is guarded by current inability to objectively determine degrees of subjective feelings. Thus, even if other assessment options (e.g. behavioural and physiological) were complete in determining observable health and welfare, an individual animal's feelings remain at least partially, and potentially relevantly and importantly, obscured. Nevertheless, scientific protocols for assessing or measuring welfare have steadily developed, and while diverse, these possess numerous common threads of concept and principle (84).

While it is not possible to state with certainty what another animal or indeed another human may feel, it is possible to make evaluations based on critical anthropomorphism and presumptions based on many cross-species similarities of physiology and behaviour (13, 37, 97, 98).

Measuring animal welfare by attempting to estimate the individual's internal subjective state (i.e. its feelings), rather than merely assessing welfare indicators such as the animal's physical health and fitness, is increasingly accepted as a valid scientific approach. (21, 36, 99, 100). As reviewed earlier (see 'Behavioural versus physiological measures of welfare'), there is an increasing wealth of research into the assessment of animal emotions through passive and experimental behavioural investigations. Motivation and preference studies in captive animals assume a definition of emotion that can be measured by how hard an animal works to achieve a reward (giving it a 'positive feeling') and conversely how hard it works to avoid a punishment (giving it a 'negative feeling') (30). This allows for quantifiable measurement in preference studies that can help us understand an individual's internal state. There are obvious limitations to such subjective studies and some of these issues are raised in Table 5.

With these caveats in mind, it is unlikely that feelings would have evolved to be functionless. Rather, feelings may be central to functioning, because they involve motivational states (8, 21, 101-103). For example, pain is a negative or 'bad' feeling that may motivate against being injured or re-injured, and feeling ill is a bad feeling that may motivate against consuming future toxic items (56, 104); whereas sexual engagement is a positive or 'good' feeling and may motivate successful reproduction, and finding important or 'favoured' foods is a good feeling and motivates consuming life-sustaining nutrition (56, 104).

The Five Freedoms

In 1979, The Five Freedoms (Table 2) were proposed as foundation aspirational protections widely incorporated into welfare assessments (105) and this model has become integral to global guidance and law.

Table 2. The Five Freedoms. Derived from FAWC (105) and Webster (106)
1. Freedom from hunger and thirst - by ready access to fresh water and a diet to maintain full health and vigour; 2. Freedom from discomfort - by providing an appropriate environment including shelter and a comfortable resting area; 3. Freedom from pain, injury, or diseased by preventing animals from getting ill or injured and by making sure animals are diagnosed and treated rapidly if they do; 4. Freedom to express normal behaviour - by providing sufficient space, proper facilities, and company of the animal's own kind; 5. Freedom from fear and distress - by ensuring conditions and treatment, which avoid mental suffering.

With the exception of Freedom 4 (Freedom to express normal behaviour), the model focuses on preventing negative physical and affective states rather than promoting positive physical and affective states. Arguably, at the time of the conception, the Five Freedoms model relevantly reflected prevalent aspirations for 'cruelty prevention' philosophy, whereas subsequent models would reflect intrinsic welfare criteria.

The '3 Fs' (freedom, function & feelings)

In 1997, Fraser et al. (24) investigated three commonly expressed ethical concerns for quality of life in an animal – i.e. what freedom it has, how it feels, and how it functions ('the 3 Fs'), and presented these concerns as essentially overlapping concepts in animal welfare science (summarised in Table 3).

Table 3. The 'Three Fs' (freedom, function & feelings). Derived from Fraser et al (24)
1. Freedom: that animals should lead natural lives through the development and use of their natural adaptations and capabilities; 2. Function: that animals should feel well by being free from prolonged and intense fear, pain, and other negative states, and by experiencing normal pleasures; 3. Feelings: that animals should function well, in the sense of satisfactory health, growth and normal functioning of physiological and behavioural systems.

The first of these 'F's raises the issue of freedoms and their importance by exemplifying that using value judgements involving empirical measurements such as, physiological criteria, immune competence, fitness and morbidity to define animal welfare may not accurately represent an animal's underlying state or quality of life in respect of the freedoms it may be able to express – a scruffy mongrel farm dog in charge of its own life may experience better welfare than a mollycoddled in-bred lap-dog. The second 'F' raises the issue of feelings and emotions or the affective states experienced by an animal – an animal that 'feels' comfortable or good with its life may signal a satisfactory standard of welfare regardless of what else is going on around it or in it. The third 'F' raises the issue of importance in providing for an animal's biological functionality and thus its general environmental, nutritional and clinical safeguards – an animal that experiences good 'enviro-physical' provisions is generally 'well'. However, Fraser et al. (24) suggest that each 'F' should not be singly deterministic of good welfare, rather, that in combination the conceptions provide foundation for animal welfare science.

The Five Welfare Needs

In 2005, The Five Welfare Needs (Table 4) were proposed as enhanced protections, advancing The Five Freedoms principles from aspirational to outcome-led welfare qualities, and are also widely incorporated into assessments, global guidance and law (107). The Five Welfare Needs model also focuses on promoting positive physical and affective states, and incorporates a greater applied nature over the conceptual underpinnings of the 3Fs.

Table 4. The Five Welfare Needs. Derived from RSPCA (107)
1. Need for a suitable environment;
2. Need for a suitable diet;
3. Need to be able to exhibit normal behaviour patterns;
4. Need to be housed with, or apart, from other animals;
5. Need to be protected from pain, suffering, injury, and disease.

Conceptual advancement in welfare extended in 2015 to accept the paradigm for achieving positive affective states in animals, which infer such behaviours as calm interaction, relaxation and play (38, 39). Also in 2015, The Five Freedoms (although still used as a standalone model) was further refined to produce The Five Domains (40-42). The Domains were intended to provide more robust means of assessment against negative welfare and focused specific criteria including nutrition, environment and health aimed at achieving positive affective states and a 'life worth living' for all animals (40-42). These approaches, although widely accepted and well rationalised, indicate that the scientific measurement of animal welfare is a complex area with no simple or universal way to evaluate individual (subjective) wellbeing (108). Several reasons underlay why measuring animal welfare is complex, and can be briefly exemplified by selectively examining (in no order of importance) some relevant considerations. Human measurement of animal welfare is essentially observational, because we cannot accurately experience life from the perspective of an individual animal (22, 30), or even another human (30).

The above available recognised fundamental approaches allow for investigation of welfare via agreed criteria regarding observational indicators (i.e. observable signs) and presumptive affective states (i.e. we cannot be certain what feelings or emotions are being experienced by individuals). As Broom (6) notes, subjective states (feelings and emotions) can be separated from other welfare measures. Thus, whereas an individual may experience positive mental and emotional states from consuming regular or large quantities of favourite foods, its physical state may be negatively affected due to obesity related morbidities.

Ultimately, as Mendl (30) reminds us, the 3Fs (and probably relevantly also other current concepts in animal welfare) are human constructs of animal welfare designed to evaluate both physical and mental state, thus it is unsurprising that animal welfare science continues to refine its approach to both understanding and assessing what constitutes – to use another perhaps relevant term 'holistic wellbeing'.

1.2.5 ***Applied welfare assessment tools***

While the above concepts and principles provide fundamental elements for welfare they do not provide applied welfare assessment tools. In 2000, Schuppli and Fraser (31) developed a species suitability framework for 'companion' animals in which a self-assessment checklist of 12 questions raise awareness for animal welfare, human health and safety, species conservation, and invasive species issues. In 2014, Warwick et al. (109) introduced a pet suitability algorithm that scores animals as 'easy', 'moderate', 'difficult' or 'extreme' (EMODE) according to six animal welfare and human health and safety factors relating to animal husbandry challenge. Also, in 2014, Schuppli et al. (32) produced a further proposal that prioritised four welfare concerns regarding pet animals, namely that 'animals function well biologically', are 'free from negative psychological states' are 'able to experience normal pleasures', and to 'lead reasonably natural lives'; zoonotic risks and invasive species potentials were also raised as key considerations. In 2016, Koene et al. (110) devised a model algorithm that utilised an evidence-based decision tree for pet suitability based on animal biology, behaviour, husbandry, welfare, health, zoonoses, and human-animal relationship. In 2018, Warwick et al. (111) proposed a pet-labelling scheme based on the EMODE system providing a traffic light type advisory scale appended to all pet shop animal enclosures, notifying prospective purchasers of the potential degree of challenge associated with keeping specific animals. Also, in 2018, Warwick et al. (112) published applied husbandry- and inspector-centred guidelines broadly relevant to a wide variety of companion-animal sectors and that introduced a novel approach to animal husbandry based on safety net criteria derived from best practice evidence, as well as biological and global climate parameters.

The Five Freedoms, The 3 Fs, and The Five Welfare Needs models, as well as Schuppli and Fraser (31), Schuppli, et al. (32), EMODE (109), Koene et al. (110), the pet-labelling scheme (111), and husbandry- and inspector-centered guidelines (112) are all applicable to reptile welfare assessment. However, certain welfare protocols are reptile-specific, and include approaches regarding animal assessment, involving awareness for behavioural and physical signs of health and welfare (67, 113, 114) and keeper assessment, involving self-evaluation (114). A specific Welfare Quality® Protocol has also recently been developed that uses behavioural, health and husbandry based indicators for scincid lizards that may have foundation for general application to reptiles (67). Collectively, these developments in applied welfare underscore the message that welfare is also fundamentally recognised in societal frameworks (*ergo* by nature and humanity).

Over time, both as results of trial and error and scientific development (115, 116) numerous advances have materialised intended to understand and structure captive animal welfare and husbandry in terms of concepts, principles and protocols. Essentially, current concepts, principles and protocols for animal welfare generally are also relevant and widely applied to reptiles specifically. However, certain concepts and principles, as well as applied and anthropogenic considerations are more specific and relevant to reptilian biology and welfare.

1.2.6 *Behavioural versus physiological measures of welfare*

Behavioural measures

Behavioural measures of welfare are widely used in various situations, for example, veterinary clinics, zoos, laboratories and farms using passive observation (27, 117-121) as well as active experimental conditions pertaining to aversion and preference tests (99, 122-129). Although investigations involving behavioural assessment have primarily focused on mammals and birds, reptiles are also represented (passive observation (118-121); active experimental (125-129)). Example advantages and disadvantages of using behavioural measurements of welfare are summarised in Table 5.

Behavioural assessments of animal welfare may have become increasingly favoured over physiological indicators (84) although many researchers agree that assessing welfare is complex and best approached using a variety of measurements (6, 20, 24, 25, 33-35, 108, 123, 124, 130-132). The objectivity and validity of behavioural welfare assessments are argued by Meagher (117) and Broom (33) although there is much discussion regarding the reliability of certain behavioural assessments. For example, historically animals performing stereotypies were generally assumed to be suffering poorer welfare than individuals not exhibiting such behaviour when in reality many other factors may complicate such an 'oversimplified' conclusion (27). Certain individuals may use stereotypic movement as a coping strategy (6) and may arguably be coping better than conspecifics not performing these behaviours due to physical or psychological limitations (27, 84). Many behavioural studies such as 'preference' and 'consumer demand' tests have limitations. Preference tests may in fact lead to reduced welfare because of an individual's poor choices (6, 16) and in many cases the studies only illustrate partial or variable preference (16, 124, 133), and interpretation relating to welfare can be problematic (23, 124). Further research is needed to ascertain conclusive behavioural indicators of welfare for any specific group of animals (84) (if indeed this is possible). However, there are significant advantages to behavioural studies to assess welfare, including: they are noninvasive and easy to undertake (133), provide immediate feedback (121, 132-134), they are cost efficient (117), and they are probably the most sensitive measure of an animal's state at any given time (35, 121). In reptiles, although exploratory behaviour is recognised as being associated with aversive stress-related situations under both natural conditions (48, 135), the behaviour is also associated with some mental and physical arousal states and presumed positive welfare under conditions of 'mild' stress (67), a phenomenon known as the Yerkes-Dodson principle (136). Implicitly, therefore, measurement of welfare using exploratory behaviour requires a degree of observer judgement to evaluate whether a behavioural sign 'crosses the line' from being a positive to negative welfare indicator, a judgement that may require experiential context. Nevertheless, in reptiles, behavioural observation is regarded as the preferable and most a reliable indicator of stress and welfare (48, 49, 66).

Table 5. Example advantages and disadvantages of using behavioural measures of welfare.	
Advantages	**Resources (e.g.)**
Observability can be uncomplicated and can also benefit from identifying signs under conditions of multiple influences.	(6, 16, 34)
Non-invasive observation allows for minimised interference with objective and quick assessment.	(120, 121, 132, 134, 137)
Facilitation of critical comparative thinking based on limited interspecies biological similarities may allow reasonable presumptive insight into subjective feelings.	(16, 34, 137)
Relevance and applicability across diverse situations (e.g. natural conditions, clinical health, zoos, laboratory).	(49, 64, 72, 117, 126, 138, 139)
Cost efficient.	(117, 120)
Disadvantages	**Resources (e.g.)**
Requires good data on natural behaviour, which can be difficult to acquire and interpret taking account of many possibly 'unobserved' factors (abiotic and biotic).	(16, 121, 131, 132, 140)
Can be subject to observer subjectivity or over-anthropomorphism.	(17, 24, 117, 134)
Interpretation of behaviour at species and individual level is problematic.	(27, 33, 84, 108, 131, 132)
Individual variation of observers, ambiguous behavioural descriptions and presuppositions may influence analyses.	(17, 24, 25, 121)

Physiological measures

Advantages of physiological biomarkers include their well-documented associations with the stress response, and thus their values (presence and context) can be informative (48, 49, 66). However, there is a major lack of data and context for what constitutes normal physiology across the range of reptile species (at least 1,100) in captivity (48, 66).

Over 20 stress-related physiological biomarkers are used in reptile laboratory science (48), the most common of which is corticosterone (48, 49, 66). Despite its commonness as a potential stress-biomarker in reptiles, corticosterone may not reliably represent actual environmental suitability and stress (48, 128). For example, Case et al. (128) studied box turtles (*Terrapene* sp.) in enriched versus barren environments and found that in enriched conditions turtles showed lower heterophil to lymphocyte ratios (indicating less stress) (and less escape behaviour), whereas corticosterone values were unchanged. The broad range of known biomarkers in general presents possible opportunities for cross-marker confirmation of potential factors involved in stress, but as with corticosterone, understanding of the possible interactive nature of these markers is currently low (48). Physiological biomarkers are also often highly transient and thus considered by some to be inherently salubrious (56). Although corticosterone is well-studied in reptiles (both for its association with stress and metabolism regulation), for the above reasons, its reliability as a singular indicator of stress is considered to be low (48, 66, 74, 141).

In reptiles, sampling for physiological biomarkers is possible using several means, including venous blood, faecal material and ecdysis detritus (48, 49, 66, 142). Blood sampling for raised corticosterone values has been found useful for indicating chronic social stress in Anolis lizards (a well-studied ‘laboratory’ species) (48, 143), and faecal material and ecdysis detritus sampling for raised corticosterone values has been found to have limited potential use for indicating temporally undefined environmental stress in wild (Natricine) and captive Pythonid and Colubrid snakes (142). However, blood sampling involves invasive needle aspirations, which can artifactually elevate biomarkers (48, 66, 74); faecal material sampling and ecdysis detritus are non-invasive, but involve temporal disconnection between stress-related events and chemical deposits in sampled materials, thus contextualisation of stress is complex (48, 113). Some authors consider physiological biomarkers to be important during field studies of stress in reptiles, while expressing caution regarding possible misinterpretation due to contextual complexities (48, 142). Sampling of biomarkers at necropsy can be informative, not least because major concomitant clinical signs may offer insight for stress-associations, but again temporal disconnection limits interpretation of historical acute stress events (48, 63, 66, 74). Relatedly, biomarker sampling and analysis requires specific field or laboratory experiment and analytic equipment, thus opportunities to examine these potential indicators is possible only under very limited circumstances (48, 66, 74). Various experimental investigations of well- studied laboratory Anolis lizards indicate simultaneous observed stress-related behaviours and elevated corticosterone (48, 135, 143-148). Accordingly, although combined behavioural, physical and physiological parameters may be jointly utilised for the measurement of welfare, behaviour is commonly the preferred indicator of stress and welfare in captive reptiles (48, 64, 66, 67, 74, 82, 115, 125, 126, 138, 139, 149, 150).

1.3 **Adaptation, adaptive plasticity and biological strategies**

1.3.1 ***Adaptation***

Adaptation typically refers to the ways in which organisms fit and manage within their environments based on evolutionary processes, stability, and flexibility (adaptive plasticity) when faced with change (151, 152). Classical biology defines three categories of organismal adaptation: behavioural, physiological, and structural (153). Individually and collectively adaptational elements exist to promote survival (48). Again classical biology emphasises 'survival and reproduction' as co-equal primary outcomes for adaptive success (survival) (48). However, reproduction is arguably not as essential as survival because most species will not sacrifice or expose themselves to harm in order to save offspring from predatory attacks (154-156), also individuals in poor physical condition may hold off from reproduction (49, 63) or even resorb developing offspring (157-159), and reproductively nonfunctional individuals typically lead otherwise normal lives (48, 115). Conversely animals suffering stress due to non-adaption will also reproduce (6, 22). Accordingly, it has been argued that realisation of maximum biological potential or inclusive fitness, and not reproductive state, indicates true success (48). Therefore, while reproduction is essential in order to promote genetic continuity, the well-being and thus fitness of the individual is also a key part of the evolutionary process (even though non-reproductive individuals effectively commit biological suicide). Accordingly, the groundwork is set for the concept of individual self-preservation as the paramount biological target consistent with normal evolutionary parameters. Essentially, individual self-preservation signals the foundation of welfare.

1.3.2 ***Adaptive plasticity and biological strategies***

Adaptive (in particular behavioural) plasticity enables an organism to better survive in novel environments (160). Currently, there is a lack of a universally-accepted conceptual framework for predicting why different species manifest adaptive or maladaptive responses to new (e.g. artificial conditions of captivity) conditions (161), although attempt has been made to use phylogenetic comparative methods to identify links between species characteristics and susceptibility to welfare problems in captivity (162). Also, there appear to be no dedicated reptile *versus* other animal class comparative studies for relative adaptive plasticity (160). However, consideration can be given to several aspects of evolution, adaptedness and adaptive plasticity into which known evolutionary and biological features of reptiles can be contextualised to offer potential clarity and explanations to support the hypothesis that their adaptive plasticity in suboptimal captive conditions is low.

For some species, the potential ability to develop novel traits in response to novel environments (e.g. artificial conditions of captivity) are so strong that concern is raised regarding concomitant abilities to invade local ecologies in the event that they escape captive conditions (29). Organisms born with intact innate environmental preferences, but which are experimentally denied access to those preferences, may seek out alternative similar items to their innately preferred (or biologically anticipated) ones (160, 161, 163); thus in those examples, early adaptive plasticity is apparent because individuals target and accept items similar to abnormal items. Essentially, animals tend to prefer environments that they have ancestrally experienced (160). Because innateness is a strong component of reptilian biology (see 'Innateness'), environmental conditions are strongly biologically anticipated - or perhaps 'pre-preferred'.

As Snell-Rood (160) comments, an organism and its physiology, morphology and behaviour may constitute an integrated suite of traits developed to match a particular environment. Furthermore, generalist species (e.g. those with naturally greater diversity of diet, habitat, sociality, and temperature) rather than specialist species (e.g. those with naturally lesser diversity of diet, habitat, sociality, and temperature) show greater adaptive plasticity towards novel, i.e. artificial, environments (164-167). However, generalist (especially neophillic or 'novelty-seeking') species may also change rapidly and unfavourably within novel environments, whereas specialised species, for example reptiles (82, 150, 168, 169) are less susceptible to change and retain greater 'naturalness' (161). Reptiles are categorically specialist animals (82, 168, 170), which could account both for their relative lack of change in purity or 'naturalness' between wild and captive counterparts, and this further supports the perspective that they do not fit the profile of being adaptive to novel conditions.

Snell-Rood (160) suggests that adaptive plasticity can be viewed as a transient costly evolutionary process culminating in reduced plasticity. Integration of novel behaviours into innate traits is resistant to sudden changes in environment, and requires long periods to reach adaptive outcomes (160). Reptiles have a long evolutionary timeline, which could be viewed as offering that prior plasticity levels and 'trial and error' adaptation have settled on reduced plasticity today. Because, as mentioned elsewhere in this thesis (see 'Innateness'), new traits may only emerge where they are in the right evolutionary-biological direction (37, 171, 172), suboptimal conditions in captivity are unlikely to promote adaptive change.

Thus, behavioural plasticity that leads to changes in innate behaviour is costly because evolutionary change is expensive, and requires lengthy trial and error forces (160). Successful adaptive plasticity may also require evolutionary investment in larger brains to manage increased demands on motor dexterity and sensory outputs, again making plasticity neurologically expensive (160, 161, 173). For example, mammals and birds with large forebrains are more likely to adapt to urban environments (160, 164, 165, 174). In comparison, French et al. (175) applied 77 conceived indicators relating to increased, similar, indeterminate or decreased successfulness for reptiles in greater *versus* lesser urbanised areas, with results scoring that reptiles did: better = 15; worse = 43; similar = 13; and indeterminate = 6, suggesting that across the range of indicators reptiles generally do relatively poorly in urban environments. Also, artificial environmental features, such as a secluded paving slab or hedge reasonably mimic natural features such as a flat basking rock or vegetation border, and can, as argued elsewhere in this thesis, represent an alternative habitat that is adaptively within 'the right evolutionary-biological direction' (see sections: 1.3.2, 1.4.3, and 2. Aims). Accordingly, even limited success within an urbanised environment does not infer generalised adaptability of reptiles to captivity. In addition, none of the urbanised environments in the study involved spatial restrictions, which, as argued elsewhere in this thesis, constitutes a major obstacle to for reptilian adaptation to captivity. Furthermore, no specific artificial urban features were imposed, such as minimalist habitat variation or controlled deprivation, which are common to captive conditions. Thus, reptiles within urban settings were able to express preferences across differing conditions, and maintain control over their environments, which are elements considered important to animal welfare (see section 1.2).

The reptilian brain has historically been mistakenly considered morphologically and cognitively simplistic and incapable of complex learning (12, 37, 176-180). Nevertheless, the reptilian brain is proportionately smaller than that of mammals and birds (180), suggesting that significant evolutionary investment would be required for reptiles to change course towards greater mammalian- or avian-like adaptive plasticity. Accordingly, some animals (e.g. reptiles), rather than evolutionarily pursue cognitive plasticity, appear to have instead invested in a stable ‘adaptedness’ model, where there is low probability of change (37, 169, 181).

An individual’s welfare (wellbeing) is thus dependent on its ability (adaptedness or adaptability) to cope with life. Adaptive or phenotypic plasticity refers to an individual’s suite of capacities to cope with its environment and essentially describes evolutionary investment for possible, rather than certain, conditions facing an organism (182-184). Adaptive plasticity involves costs inherent to maintaining potential responses that may or may not be utilised, although for some species in changeable environments higher plasticity is manifestly cost efficient, whereas for other species adaptedness (i.e. lower plasticity) is more efficient assuming low-level environmental change (182). An individual’s welfare is definitively linked to its state within its environment, and may to some extent be measured by its control over its environment and its ability or inability to cope (6). Adaptation, adaptive plasticity and biological strategies govern an organism’s place in its environment, including how far from a regular stable environment it can venture, its stability, and psycho-behavioural states and physiological homeostatsis (56, 182-186). Combined, these elements of evolutionary concepts and principles for adaptation to novel environments can be viewed as indicating that reptiles have invested in the stable-adaptedness model. Given that captivity is an extreme novel environment, reptilian adaptive plasticity under such conditions may be expectedly low or non-emerging.

In the context of this thesis, biological strategies refer to organised physiological or behavioural responses (coping mechanisms) evolved for prevention, stabilisation or recovery relevant to physical and psychological states in challenging situations (44, 45, 56, 185-189). Diverse biological strategies manifest across species boundaries, and with numerous commonalities, for example in response to pain and stress associated with predator-prey interactions, environment-associated deprivations (e.g. drought and starvation), and injury and disease (56, 185, 186). Existing within organisms is an array of anatomical, physiological and psychological mechanisms associated with perception of aversive stimuli, and which are capable of allowing significant pain and stress (44, 45, 56, 185-189). Human understanding of pain and stress is predominantly set against a facultative background. Arguably, facultative pain and stress occurs quasi-idiopathically rather than within a holistic context. However, any assumption that pain and stress would have evolved to naturally diminish life quality is incongruent with biological success – why would nature aim to accommodate a life of misery and failure? Survival 'for its own sake', for the individual, has to be hedonically balanced (190) or 'worth it' and this implies that any pain or stress within normal daily life is proportionate and tolerable – *ergo* in concert with the recognised welfare principle of 'a life worth living' (41, 186). Many animals, for example, migrating spawning salmon (191, 192), combative lizards (46, 193), and predatory species in general voluntarily undertake arduous or dangerous activities in pursuit of valuable goals - and all these activities exemplify animals biologically balancing degrees of risk or discomfort with near-future hedonic benefits. Accordingly, below are presented some considerations regarding aversive stimuli in nature, and probable evolved mechanisms for ameliorating pain and stress in a natural context.

Predator-prey interactions

Relatively little work has been done regarding the effects of stress on individual animals in the wild, not least because objective non-invasive sampling is challenging. However, overt predator attack strategies and covert predator and prey biological strategies require close consideration regarding their apparent potential regarding stress. Effects on prey of exposure to predators may include chronic physiological results and reduced birth rate survival, potentially implying long-term consequences for adaptive state at the individual and species levels (194), whereas observations (mostly behavioural) suggest acute psychological, physiological and physical stressors from such events probably do not have enduring negative sequelae at the individual level (64, 186, 195-197). Predatory and prey species are well-known to co-occupy microhabitats and even to manifest contextualised 'facultative mutualistic' relationships (198), thus stress is not an implicit consequence of predator-prey encounters. Measurement of cortisol in deer hunted and killed by humans suggested that this mode of attack was less stressful than, for examples, deer killed by cars (199). Assessment of small cetaceans during human capture by herding was declared inhumane due to prolonged use of noise and entrapment methods (200). Although not like-for-like observations, *prima-facie* this research would support the view that where predatory attacks are more naturally contextualised they are also less stressful (185, 186).

Observations of predatory attacks frequently describe short-duration pursuits, after which predators abandon the chase or prey escapes (185, 186). Therefore, pursuit strategy itself is not an enduring stress –prey is either caught and despatched or escapes. Captured prey manifest one or more of the three 'fight, flight, freeze' strategies (5, 201). In principle, from the individual prey animal's perspective fight, flight, freeze strategies may be interpreted to reflect three psychological strategies: 'I can hurt this menace back and make it go away' = psychological optimism (otherwise why fight?); 'I can out-run this menace' = psychological optimism (otherwise why run?); 'I am caught, nothing can be done, so shut-down' = desensitise (otherwise why not run or fight?) (186). It is not within the predator's interests to tackle and become injured by a violently responsive prey (56, 186).

Several hormones and neurotransmitters including dopamine, serotonin, oxytocin and endorphin are associated with predatory attack and prey escape strategies, and are regarded to provide positive, even rewarding, stimuli during and after dramatic interactive episodes (56). Within an entirely human perspective, research and anecdotal reports of major predatory (e.g. shark or crocodile) attacks on people include common accounts by victims who despite experiencing severe tissue damage or limb loss report that pain was minimal until post-event (56, 185, 186, 202-204).

Essentially, it appears that in stressful situations the body becomes sensitised to pain relieving mechanisms (56, 205). Biological strategies for predator and prey are consistent with evolved systematic protections limiting pain and stress for the individual, and arguably it would be inconsistent that evolved stress and pain moderating mechanisms should fail to serve purpose for the individual's welfare under extreme conditions (185, 186).

Environment-associated deprivations

Environment-associated deprivations variously affect animals in the natural world and include seasonal challenges associated with heat, cold, drought, flooding, and available nutrition. Within a harsh environment search behaviours and cognitive challenges continue, and these activities arguably represent stabilising elements of normality (56, 185, 186). Environmental deficiencies (e.g. water, food) arguably become a priority psychological drive state (perhaps turning the deficiency into a goal and positive focus), and detracting from an individual's entrenchment in a problematic situation (56, 185, 186). Where a malnourished or dehydrated wild animal locates food or water the experience may be highly rewarding and perhaps compensatory against preceding physiological stress (56, 185, 186).

Injury and disease

During injury or disease in humans (185, 187-189), dogs (44, 45), and wild animals (56, 186) biological strategies are readily observable. Selye (4) introduced the concept of the general adaptation syndrome (GAS) as a three-stage stress response process. Stage 1 refers to a situation where a stressor is perceived or experienced, and includes an 'alarm' reaction that elicits the 'fight or fight or flee' response. Stage 2 refers to a situation where the body attempts to resist or compensate for a stressor. Stage 3 refers to a situation where the body is exhausted due to failures of stages 1 and two to stabilise the individual. Collectively, GAS concept is integral to how or whether an organism successfully or unsuccessful copes with stressors.

Injury-associated pain may result in temporary disuse of a limb; pain is dissuasive of limb use and protective against re-injury - promulgating rest and healing (187). Thus, in principle, pain is thought to be useful (18, 206). Disease (e.g. infection) may result in an individual experiencing adverse stimuli or 'feeling ill' (e.g. fever, vomiting and / or nausea), and becoming relatively inactive (44, 45, 187). Elevated body temperature enhances immunocompetence and inhibits microbial activity, vomiting ejects potentially contaminated contents from the body, and nausea avoids further ingestion of causally related material (187). Feeling ill and its associated inactivity (a behavioural response) results in reduced caloric expenditure and redirection of energy towards high-caloric fever and other recovery costs (44, 45, 187). Thus, biological strategies may contribute to regulating normal activities, and even temporarily contra-balance short-term ‘feeling good’ to benefit medium- and long-term health and wellbeing

However, adverse physical stimuli (‘symptoms’ in humans or ‘signs’ in non-human animals) are not necessarily caused by microbial invasion itself, but by physiological responses to infection – the body makes itself feel bad (44, 45, 187). Initially, the idea that the individual’s own body should instigate feeling bad through pain or disease, appears illogical. However, in both injury and disease physiological responses theoretically could act to remedy discomfort via a suite of elements (e.g. endorphin, cortisol or adrenaline elevation) that would enable an individual to resume more normal activities (56, 104), but, suppression of pain and other ‘bad’ (or ‘aversive’) feelings, would not serve dynamics of recovery because an active animal that is oblivious to its damaged or diseased state may inadvertently add to its problems by re-injuring itself or consuming items that caused its original problems - thus inhibiting healing or recovery (44, 45, 187).

Collectively, the presence and purpose of adaptation, adaptive plasticity and biological strategies are consistent with the concept of evolved mechanisms for the regulation of stress and pain in nature. Non-adaptation manifests when conditions (e.g. gross environmental or subtle physiological) change to the point where an organism no longer fits or manages stability, and thus any adaptive plasticity is exceeded (207). Where nonadaptation or maladaptation (adaptive malfunction) occurs, stress results, and uncontrolled poor welfare commences (55, 65, 66). Under artificial conditions or captivity, adaptation, adaptive plasticity and biological strategies (i.e. the natural welfare regulators) may be recontextualised by human control over most elements essential to survival and welfare – or controlled deprivation. Where ‘short-term optimism’ associated with adaptive behaviours is exhausted ‘learned helplessness’ may impose itself as a result of animals losing long-term control over their environments and they essentially ‘shut down’(7, 11). The concept of absence of control by individual animals within their environment (6) provides a reasonable and over-arching summary of the fundamental problem and explanation relevant to why many animals succumb to conditions of captivity.

Within the environment to which an organism is adapted, along with its plasticity reach, stressors manifest at the levels of macro- and microhabitat, predator-prey interactions, and injury or disease, among other factors. Biological strategies are major tools evolved to cope with the diversity of challenges faced by organisms in the natural world, and arguably deliver a scheme of ‘incidental compassion’ (185, 186). Therefore, welfare-promoting systems arguably exist as a target of evolutionary biology. Inherent to the messages of this is the fundamental importance of welfare and thus its relevance to captive situations.

1.4 **Concepts and principles for reptile welfare**

Reptiles have been 'kept' in captivity by humans for at least 4,000 years (195), with the 'modern' era of reptile keeping being facilitated largely by the development of amenable glass panels facilitating elementary climate controlled enclosures (208). The first book to include care of kept reptiles appeared in 1797 (209), and the first dedicated book on 'herpetoculture' was published in 1897 (210). Since then, scientific understanding of numerous relevant issues has steadily increased, including: nutrition (63, 211-219), environmental lighting (115, 220-223), temperature (68, 112, 115, 223-225), humidity (112, 225), disease (63, 211, 212, 214, 215, 226), physiology (49, 66), behaviour and psychology (37, 64, 66, 68, 82, 113, 115, 127, 227, 228), and enrichment (37, 82, 115, 118, 119, 125, 229-236). Relatedly, in environmental preference experiments, reptiles select larger more naturalistic conditions (67, 125-129, 237-239), suggesting the problematic nature of typically spatially restrictive and minimalistic habitat conditions of reptile enclosures.

However, these advances predominately follow the presumption and conceptual limitations of servicing biological needs within the context of a life behind glass, rather than seeking to understand and meet biological needs in a holistic and naturalistic environment (115, 185, 239). Therefore, the fundamental physical characteristics of enclosed-environment ('caged') reptile husbandry have remained largely unchanged in over 200 years. Furthermore, in respect of all the above-cited advancements, co-emergent evidence conveys that the more is learnt of reptilian biology and biological need complexity, the more apparent are the deficits in their husbandry and welfare (115, 195). These deficits in welfare are significantly associated with certain reptile specific welfare factors, discussed later.

Even using best evidence-based practice, there is only ‘so much’ that can be accomplished, especially within the limitations of a small, enclosed, ‘vivarium’ environment system. Placing reptiles in captivity may constitute the most challenging environment in which they might be expected to survive (64). Welfare is an implicitly positive state - if welfare is good then all else is probably in place (64, 196), and a target of husbandry has been achieved (240).

1.4.1 *Biology of stress in reptiles*

Concepts and principles for stress biology in reptiles essentially resemble those of other animals (46, 48, 49, 66, 168). As for other animals, the effects of stress in reptiles can be wide-ranging and include behavioural, social, reproductive and immunity issues (48, 49). The two classically described internal (physiological) stress-response systems of reptiles involve the sympathetic adrenomedullary (SAM) and hypothalamic-pituitary-adrenal (HPA) axis, although in reptiles this latter system is called the hypothalamic-pituitary-interrenal axis (48, 49, 241, 242). The SAM axis is the body’s first-responder, and on perception of a threat releases adrenaline and other chemicals to facilitate the fight or flight reaction, whereas the HPA axis is the body’s energy moderator, and typically acts within minutes or hours to regulate or balance the cost of a perceived threat (48, 49, 241, 242). In reptiles, the HPA axis and in particular the glucocorticoid hormone biomarker (typically corticosterone), is the most well-studied, and thus often used modality of physiological stress measurement (48, 49, 241, 242). However, although frequently used in measurements of stress, physiological biomarkers in reptiles are widely agreed to hold limited relevance due to lack of normal baseline comparative data, sampling effects, species diversity, and temporal disconnections between stressors and sampling, among other considerations (48, 63, 66, 74, 113, 141) (see also: 'Behavioural versus physiological measures of welfare').

1.4.2 ***Stereotypies and reptiles***

As for other animals, ritualised and repetitive 'stereotyped' behaviours (e.g. courtship or combat routines) occur in reptiles under natural conditions (80, 82, 243). Numerous studies investigating, or relevant to, captivity-stress in reptiles have recognised and identified a range behavioural responses and indicators of stress in suboptimal conditions (37, 49, 53, 64, 66-68, 82, 113, 115, 125, 126, 138, 150, 176, 226, 244-248). However, malfunctional stereotyped behaviour, as described above (see 'Aetiology of abnormal animal behaviours relevant to sub-optimal environments, and their potential function'), have not been reported and appear non-existent in captive reptiles (64, 67, 68, 113).

As indicated earlier, classically, stereotyped behaviour is regarded as inferring sustained or prolonged 'fixed sequences performed repetitively and with no obvious function' (21), and 'functionless goal-less, unvarying, repetitive, inappropriate body movements or postures' (80). Essentially, using classical definitions, malfunctional stereotyped behaviour has not been observed in captive reptiles, thus evidence to date suggests that the possible features of stereotyped behaviour as a coping mechanism under stressful or suboptimal conditions does not occur in reptiles.

References to ‘stereotypies’ and reptiles in literature are not always clear. For example, Rose et al. (249) refer to stress-related repetitive behaviours in reptiles involving interaction with transparent boundaries (ITB) and boundary exploration, and abnormal behaviour patterns. However, any behaviour that is noncontextualised (e.g. functionally unable to regulate a stressor) may include ‘abnormal’, and this does not infer malfunctional stereotypies. Benn et al. (67) refer to reptiles performing stress-related repetitive behaviours, including ITB and boundary exploration, but draw no conclusions regarding ‘maladaptive stereotypies’ in reptiles, other than to conclude that there are no descriptions of the phenomenon in reptiles. This conclusion is consistent with the earlier comments herein, that the term ‘maladaptive’ may overstate true adaptive or coping capacities). Relatedly, because historical or extant abnormal and repetitive behaviours in reptiles resolve with improved conditions, this also shows consistency with an absence of malfunctional stereotypies (249). Martínez-Silvestre (66) refer to reptiles performing stress-related ‘stereotypical’ behaviours, which again does not infer any meaning beyond repetitiveness.

Accordingly, whereas interaction with transparent boundary (ITB) behaviour is an example of a reptilian stereotypy, because it is a repetitive behaviour, the term ‘stereotypy’ itself does not infer any particular aetiology. Also, there are no scientific evidence-based studies describing ITB in the context of malfunctional behaviour - i.e. animals neurologically damaged by partial or failed attempts to cope with captivity. Thus, whereas reptiles manifest stereotypies under natural conditions, reptilian ITB in relation to captivity stress and welfare only falls into the category of ‘maladaptive stereotypies’, because this involves repeated normal behaviours by normal animals under abnormal conditions that show no adaptation to captivity (see also '*Normal, abnormal and maladaptive behaviours*' for note on use of term 'maladaptation').

It may be argued that although none of the identified studies provide evidence of malfunctional stereotypies in reptiles, such lack of description, definition, and context might simply constitute evidential under-ascertainment rather than absence of malfunctional stereotypies. However, replacing absence of evidence with presumption of its possible existence does not offer counter argument to the point that malfunctional stereotypies remain undocumented in reptiles. Relatedly, one can consider the issue of adaptability (even partially) to captivity through coping mechanisms, even where these result in neuropsychological damage. In other words, if an animal shows some form of psycho-behavioural change (whether positive adjustment or damage), this can be interpreted as indicating some form of adaptational response (see section 1.2.3 '*Aetiology of abnormal animal behaviours relevant to sub-optimal environments, and their potential function*'). In mammalian zoo animals, maladaptive and mulfunctional stereotypical behaviour reportedly occurs less in animals that were wild-caught as adults (250, 251); thus younger captive individuals are more likely to formatively develop problematic stereotypical phenomena. Also, as captive animals age they are thought to become increasingly resistant to remedial enrichment for problematic stereotypical phenomena (251, 252). These points imply that mammals are changed by captivity, and the more they change, the less they revert to normality. Although negative, these changes are nevertheless adaptations as part of coping mechanisms. In comparison, as indicated above, observations of captive reptiles (chuckwalla lizards [*Sauromalus* sp.]), show that previous abnormal stereotypical behaviour (ITB and 'pacing'), ceased when individuals were transferred to improved naturalistic conditions (249). Thus, the reptiles had not adjusted to deprived captive environments or manifested any adaptations as part of coping mechanisms, and had remained psycho-behaviourally intact - i.e. their repetitive behaviours were consistent with ‘type-2’ stereotypies, and had not developed into malfunctional types. Therefore, it may be that the greater the ‘wild-conservedness’, i.e. an animal’s inherited and naturally learned characteristics, then the less (or possibly no) maladaptive and mulfunctional stereotypical behaviour is manifested.

1.4.3 ***Reptile learning***

Relatively few studies have been conducted into, and therefore little is known about, the learning abilities of reptiles compared with mammals and birds (177, 179, 180). In mammals and birds, phenotypic adaptive plasticity is known to be aided by parent-offspring sociality (253), whereas in reptiles such learning is absent or highly peripheral – i.e. typically not required for survival (82, 150).

However, reptiles are capable of learning and cognitively demanding problem solving on a par with mammals and birds (177, 179, 180, 254-256), (as well as successful handling of novel atypical challenges (125, 180, 257)), including habituation, classical instrumental conditioning, maze learning, food aversion learning, predator avoidance learning, discrimination learning, visual/colour discrimination, chemical discrimination, imprinting-like phenomena and critical periods, geomagnetic imprinting, navigation cues, spatial learning, reversal learning, social learning, social facilitation (reviewed in Font et al. (180)). All these examples relate to adaptive learning in relation to challenges that are grounded in functionally similar contexts to natural and normal behaviour and thus are importantly in the right biological direction, as has been emphasised elsewhere. Relatedly, behaviours that involve expression of exploratory, escape or shutdown behaviours continue to involve ancestrally-successful traits, although immediately unsuccessful. In contrast, learning to adapt to diminutive artificial environments or challenges that offer depauperate conditions (37, 171, 172) may constitute functionless maladaptive responses; thus, an organism may be resistant to adapting to such conditions.

1.4.4 ***Key welfare factors relevant to reptiles***

Welfare factors common to non-reptilian animals, as referred to above, are also broadly relevant to reptiles. However, several biological features and other considerations common to reptiles are relevantly and briefly discussed below, because these issues have regular importance for welfare.

Normal stress-related behaviours in reptiles

A range of behaviours associated with probable stress-related situations have been described in free-living reptiles (see Table 6 for examples). Observations of these behaviours under natural conditions confirms their normality as responses, and their occurrence under natural conditions involving harsh environmental (e.g. drought, excessive heat), anti-predator, fear, anti-social, pain and morbidity situations indicates that their contexts are probably aversive and stress-associated. Accordingly, the presence of these probable stress-associated behaviours under unnatural conditions of captivity can be considered undesirable, especially where identified as common, frequent and recurring.

Table 6. Normal behaviours commonly observed in free-living reptiles under conditions of stress.

Behaviour	Background	Resources (e.g.)
High-level locomotor activity	Threat (e.g. perceived or real predatory) avoidance, fear.	(82, 126, 138, 258)
Escape activity	Threat avoidance, excessive heat, excessive noise, entrapment.	(64, 66, 82, 126, 138, 258, 259)
High-level exploratory activity	Unsuitable environments (e.g. drought, social pressure), environmental searches.	(48, 72, 135)
Hypoactivity	Pain, morbidity, social competition.	(48, 63, 72)
Aggression/repulsion	Fear, defence, social competition.	(66, 82, 143)
Anorexia	Inappetence, stress, fear, disease.	(63, 66)

Abnormal, 'maladaptive' and stress-related behaviours in reptiles

Stress-related behaviours (behavioural responses to stressors) occur under natural and normal conditions. Similarly, some stress-related responses that also occur under unnatural conditions, such as captivity, remain normally contextualised, inferring that although occurring in an abnormal situation, such behaviours are nevertheless also biologically normal (e.g. food searching, courtship, anti-predator, defence, activities). Concern regarding stress among captive animals may, therefore, involve normal and stress-related or abnormal and stress-related issues.

Over 30 behaviours have been reported as abnormal, maladaptive and stress-related, and therefore problematical, in reptiles, and is listed in Table 7.

Table 7. Behaviours reported as abnormal, maladaptive and stress-related in reptiles.

Behaviour no:	Behaviour	Resources (e.g.)
1	Anorexia	(48, 63, 64, 66-68, 82, 113, 125, 126, 128, 138, 150, 237, 245, 260)
2	Hyper-alertness	
3	Rapid body movements	
4	Flattened body postures	
5	Head-hiding	
6	Inflation of the body	
7	Hissing	
8	human-directed aggression	
9	Clutching	
10	Death-feigning	
11	Loop-pushing	
12	Tonic immobility	
13	Hesitant mobility	
14	Wincing	
15	Prolonged retraction of head, limbs and tail	
16	Squirting blood from eye	
17	pigmentation change	
18	Cloacal evacuations	
19	Projection of penis or hemi-pene	
20	Voluntary regurgitation of food	
21	Tail-autotomy	
22	Vocalisation/pseudo-vocalisation	
23	Venom-spitting	
24	Open-mouth breathing	
25	Panting	
26	Interaction with transparent boundaries (ITB)	
27	Hyperactivity (high-level) locomotor activity	
28	Escape	
29	High-level exploratory activity	
30	Hypoactivity	
31	Aggression/repulsion	
32	Atypical locations	

Of the behaviours listed in Table 7, nos. 1 – 23 are biologically commonly grounded in reptilian (and other) animals' fear and anti-predator responses (63, 82, 168), and nos. 24 – 25 are commonly associated with heat stress (63, 82, 168). The occurrence of these same behaviours in both free-living and captive situations has functionally similar purposes – to act as countermeasures against potential predators, with many human actions (even passive handling) probably being perceived as predatory threats (261) or, for example, to shed heat as part of normal thermoregulation (63, 168). However, behaviours nos. 26 – 32, although occurring under natural and normal conditions, fall outside meeting functional normality in captive situations. For example, interaction with transparent boundaries (ITB) cannot occur in nature because the behaviour requires interaction with a transparent boundary such as glass or clear plastic, is non-remedial, and thus is not occurring within its natural and normal context; hyperactivity (high-level) locomotor activity infers 'too much' or redundant activity, is non-remedial, and thus is not occurring within its natural and normal context; escape activity is non-remedial (the animal cannot escape, but persists with futility), high-level exploratory activity is non-remedial, and thus is not occurring within its natural and normal context; hypoactivity (self-imposed sedentarism) is non-remedial, and thus is not occurring within its natural and normal context; aggression/repulsion, while arguably functionally directed at human handlers, results in both co-occupant injuries and self-injuries from provoked retaliatory actions and is non-remedial, and thus is not occurring within its natural and normal context; and anorexia is non-remedial, and thus is not occurring within its natural and normal context.

Mench (16) comments that exploratory behaviours (which include locomotor, search and escape activities) are rewarding in nature and thus probably have some reward value in captivity (e.g. exercise and relief from understimulation or 'boredom'). However, in reptiles, high-level exploration-associated behaviours often emerge at cost of regulatory behaviour (eating, drinking) resulting in clinical emaciation due to calorific cost and concomitant anorexia (63, 113, 247). Accordingly, this group of hyperactivity-related behaviours are non-beneficial, non-contextualised, and abnormal.

For comparative purposes, the same six common examples of normal stress-related behaviours in reptiles used for Table 6 are also used in relation to common examples of behaviours that are considered to be abnormal and maladaptive and stress-related (Table 8), which shows strong overlap between stress-related behaviour in wild and captive reptiles. On the one hand, it may be argued that because numerous common abnormal and maladaptive behaviours are shared between other animals (e.g. mammals and birds) (Table 1) and reptiles (Table 8), that this could imply that both groups of animals can be considered to share the same or similar levels of coping mechanisms, adaptability or non-adaptability to suboptimal and stressful captive conditions. However, on the other hand, shared manifestations and aetiologies for cross-group abnormal and maladaptive behaviours may only reflect the commonality of these behaviours (e.g. locomotion, food search, sedentarism) in animals generally and not represent coping strategies or adaptive plasticity. In this thesis, it is argued that despite similarity among certain abnormal and maladaptive behaviours, a key consideration distinguishing the two animal 'groups' above is the issue that whereas Table 1 (mammals and birds) signs are strongly associated with maladaptive or malfunctional stereotyped behaviours, Table 8 (reptiles) signs are not associated with maladaptive or malfunctional stereotypical association (see also: 'Normal, abnormal and maladaptive behaviours', 'Aetiology of abnormal animal behaviours relevant to sub-optimal environments, and their potential function', 'Stereotypies and reptiles', Abnormal, maladaptive and stress-related behaviours in reptiles', 'Innateness').

Table 8. Abnormal and maladaptive behaviours commonly observed in captive reptiles under presumed conditions of stress.

Behaviour	Background	Resources (e.g.)
Hyperactivity (high-level) locomotor activity.	High-level physical activity, surplus or redundant activity, often associated with ITB, overcrowding, self-compounding and frequently injurious, overly restrictive, deficient and inappropriate environments.	(64, 66-68, 82, 113, 126, 138, 237)
Escape activity.	Animal observed clawing, climbing or snout rubbing at boundaries, corners and other points, related to entrapment and exploratory activity, often associated with ITB, overcrowding. self-compounding and frequently injurious, overly restrictive, deficient and inappropriate environments.	(64, 66, 68, 82, 113, 125, 126, 128, 138)
High-level exploratory activity.	Frequent searches of environment and boundaries, high-rate of tongue-flick/other scenting, often associated with ITB, overcrowding, self-compounding and frequently injurious, overly restrictive, deficient and inappropriate environments.	(48, 64, 66-68, 82, 113, 125, 126, 138)
Hypoactivity.	Reduced activity relative to normal, hypothermia, co-occupant harassment, infection/organic dysfunction, disease, injury, pain, transport trauma.	(48, 63, 64, 66-68, 82, 113, 125, 126, 138, 237)
Aggression/repulsion.	Aggressive or defensive displays, biting, chasing cage mates, often related to courtship routines, inability to avoid cage-mates when required, overly restrictive, and exposed deficient and inappropriate environments, hunger.	(64, 68, 82, 113, 237)
Anorexia.	Loss of appetite, emaciation, weakness, inactivity, hypothermia, pain, fear, co-occupant harassment, organic dysfunction, disease, injury, transport trauma.	(63, 64, 66, 82, 113, 211, 257)

Innateness

Innateness has several definitions, meanings, and interpretations. Simplistically, innateness is commonly described as implying information ‘in’ an organism that is programmed, inborn, inherited, or hard-wired that allow actions to be performed despite the individual having no pre-existing experience of them (262-264). This area of science can relate to widely varied subjects, for example, innate immunity (49), innate behaviour (262, 264), and (presumptively given that subjective mindsets are difficult to assess) innate psychology (263); and all these subjects have been investigated in reptiles (49, 82, 180). Although all these descriptions and subjects have validity, closer inspection reveals that early acceptance of innateness to mean genetically inherited information (10) is inconsistent with contemporary perspectives that consider innate information to involve both genetic and epigenetic processes (265-268). Thus, new information can add to, alter or eliminate, genetically inherited information.

Several authors have argued that innateness should be viewed as a concept, rather than a specific mechanism, and that inborn traits can be placed along a continuum of dependence on the environment (269-271). It is also suggested that evolutionary forces develop innateness to stabilise an organism with its environment (272-274). Nevertheless, innateness infers that pre-set (regardless of whether at some stage it may change or be augmented) information arrives inborn to an organism, and that the information is fundamental to organising its life within its normal environment (265-268).

As Griffiths (268) summarises, innateness is not so much about how an organism acquires the information that complements its inborn suite, rather it is a matter of from where the information comes; nevertheless, the exact mechanism for how novel information gets to become innate is unclear. Importantly, there is agreement that once innate, such information acts to anticipate an organism's environment and its interactions within.

Innateness is a fundamental characteristic of reptilian biology (12, 64, 68, 113, 176, 227, 229, 275). Essentially, although reptiles possess various phenotypic traits of adaptive plasticity (12, 176, 276-278), genotypic drive states and precocity determine fundamental life-long behavioural and psychological condition (64, 68, 113, 227, 275, 279). For example, in nature, reptilian innateness manifests diversely in that although parental care is minimally present in a few species (e.g. crocodilians, certain Pythonid snakes and tuatara) (82, 280, 281), and mostly consists of nest guarding, in the majority of species parental care is absent. All reptilian newborns of all species emerge imbued with a comprehensive intact suite of physical, mental and behavioural features facilitating immediate environmental recognition, locomotion, predator avoidance, defence, shelter selection, maintenance and other normal activity (82, 280-283). Ontogenetic changes in respect of reproductive behaviour, dietary preferences and habitat selection occur over time (275, 284), but these developments build on extant hard-wired psychological and behavioural states evolved for specific lifestyles under natural conditions. Inborn precocity also manifests as great ethological similarity between juvenile and adult reptiles (176, 181, 285) thus, reptiles behaviourally and psychologically, change little throughout their lives.

Although it may be argued that novel inherited traits could develop in captive reptiles - 'trial and error'– learning (265, 267, 268), no scientific reports of such behaviours have emerged, despite centuries of multigenerational artificial selection in captivity. This lack of change could hypothetically relate to the functionless-ness of captive conditions – *ergo* captive conditions do not meet the possible requirement of being 'in the right evolutionary-biological direction' for cue adaptation (37, 171, 172).

Innateness involves both inherited hard-wired behaviours and learning parameters, and both attributes are components of an organism's adaptive flexibility. However, in this thesis it is argued that in reptiles, innateness is such a dominant feature of their evolved biology, that adaptive flexibility is constrained to situations that fall within the 'right' biological context (37, 171, 172). As evidenced by extensive historical argument (reviewed by Griffiths (268)), innateness is neither a singular nor uncomplicated phenomenon, in which all current ideas for precise mechanisms regarding innate character acquisition, modification, and heritability remain debateable. However, the fact that all studied reptiles across all orders and species throughout recorded history are born with intact physiological, morphological, behavioural, and psychological characteristics to sustain an entirely independent life within evolved niche environments, implies that (howsoever becoming innate) inborn information among reptiles sets its expectations for life. Given the widely accepted non-variance of behaviour between free-ranging and captive reptiles, this 'expectation' is for a life in the wild – whatever debate may be ventured regarding mechanisms and limitations of innateness, innate dominance suits 'the reptile model'.

Furthermore, examination of behaviour in certain other animal classes may offer a usefully comparative example for reptiles and the issue of hard-wired, inflexible, problematic behaviours in captive conditions. Thigmotaxic boundary exploration is observed in many animals (286-290). However, interaction with transparent boundary behaviour (ITB) is by definition distinct in that its presence involves focal attention on transparent areas rather than general boundaries. Below is a summary of ITB behaviour across four animal classes:

Invertebrates, fishes and amphibians constitute large and diverse classes of animals involving highly diverse physiological (291), morphological (292), and behavioural (293, 294) features, as well as clearly described cognitive capacity and adaptive learning (295-297). Environmental preferences are well-described among these classes with many cues being attributable to innate behaviour and cognition (295, 296, 298-300).

A commonly observed aspect of invertebrate behaviour is 'the wasp at the window', which in effect is an interaction with transparent boundaries, and this behaviour is thought to be attributable to confounded positive phototaxy - i.e. behavioural preference to access to a visual light cue stimulus being blocked by an invisible boundary (295). A commonly observed aspect of fish behaviour is 'glass surfing', which again is in effect an ITB at the front of their enclosure, in many fish species (301-303), and although this behaviour is commonly described by amateur observers, its scientific and / or hypothetical aetiology appears not to have been described. Nevertheless, it is anecdotally widely reported e.g. (302-304). A commonly observed aspect of amphibian behaviour is 'wall walking', which again is in effect an interaction with transparent boundaries at the front of their enclosure in many amphibians species (305), and once more although this behaviour is commonly described by amateur observers, its scientific and / or hypothetical aetiology appears not to have been described in this animal class. Nevertheless, it is anecdotally widely reported.

Despite the great diversity in species and natural histories of invertebrates, fishes, amphibians, and reptiles, ITB is thus commonly observed across these four distinct animal classes when held under captive conditions in which their normal controlling interactions with the environment are at least spatially highly limited. A common biological feature of all these animals is innate dominancy (invertebrates (295, 296, 298-300), fishes (306-308), amphibians (37, 309, 310)).

As presented previously, and at least theoretically, while reptiles - like other animals - cannot be said to lack the cognitive abilities to adapt to challenges such as transparent boundaries, the material outcome is that they do not adapt to transparent boundaries, and this is a feature commonly shared with other innately-dominated animals.

Racine (263), using a human evolutionary psychological context, suggests that mismatches between ancestral (innate) traits and modern environments (that demand novel traits) may explain cognitive maladaptation. Reptilian innateness strongly associates with ancestral traits, and thus the perspective has possible importance for issues of adaptive plasticity, as well as governing reptilian habits and biological expectations (64, 68, 128) – one can take the animal out of nature, but not nature out of the animal. Therefore, failure to accommodate innate trait factors may be largely responsible for maladaptation, stress, morbidity and premature mortality among captive reptiles.

Ectothermy

All organisms are to some degree dependent on environmental (ecological, solar) temperature for their internal thermal stability, but ectothermy is a defining feature of reptilian biology (63, 82, 168, 311, 312). Thus, reptiles, with few exceptions, are ectothermic, producing minimal internal heat by physiological means and thus highly dependent on environmental factors for thermal stability (63, 82, 168, 311, 312). Almost all normal reptilian activities are dependent or significantly influenced by interlock between ectothermy and biological maintenance, including thermoregulation (63, 82, 168, 311, 312), sex-determination (313-315), foraging (82), digestion (63, 168), sociality (82, 316), reproduction (49), and locomotor activity (64). Inadequate captive thermal regimes that fail to accommodate diverse temperature gradients manifest numerous well-recognised negative consequences, including thermoregulatory compromise (115), that may lead to a variety of physical problems, including: thermal burns due to low ambient temperatures and efforts to gain close proximity to focal heat sources (63, 113, 214), reduced immunocompetence (49, 63, 64, 214), opportunistic disease (63, 214), heat stress (63, 64, 113), compromised recovery from disease (63, 214), and behavioural problems, including: excessive basking behaviour or 'hyperbasking' due to inability to heat the entire body (260), hypoactivity (64, 113, 224, 236, 260, 317, 318), and compromised recovery from emotional fever (319-321). Accordingly, a raft of factors and associated welfare considerations are integral to reptilian ectothermy and thermoregulation.

Metabolism and energy

Reptilian metabolic and energetic rates are typically low compared with that of mammals and birds (63, 115, 168). For example, resting metabolic rate for many reptiles is approximately 2 – 5% of that for an equivalently-sized rodent or bird (169). In nature, low metabolic rate and its association with ectothermic low physiological energy consumption produce inherent advantages in habitats of low availability of nutrition and better enable, where required, long fasting periods during hibernation, brumation or aestivation (168). Low metabolic rate and immune response are linked in reptiles, thus while development of systematic infection is slow compared with mammals and birds, reactivity to disease, as well as its physical manifestation, is also slower, due to natural adaptations to poikilothermy (body temperature variation changing according to environmental temperature) (63). By way of converse example, high metabolic rate among birds exposed to pathogenic microbes frequently results in early infection and onset of disease (322, 323) and other rapid responses such as to shock (324), or noxious chemicals – *ergo* the historical use of canaries as early warners of environmental contamination (325, 326). Therefore, low metabolic rate involves some factors that under artificial conditions in captivity may lead to specific welfare problems, including: diagnostic impedance due to symptomatic latency and delayed onset of disease (63, 69, 168, 214), where infections, organ compromise, and other issues remain unrecognised until advanced states; long survival time and exposure to negative affective states resulting from abnormal stressors and disease (49, 64, 260); long survival time and exposure to pain associated with thermal extremes (327), and severe injuries, post-decapitation consciousness and sensitivity (328-333). Accordingly, reptilian adaptations for low metabolic activity may act to compromise welfare in conditions of atypical environmental and physical insult.

Nocturnalism

Nocturnalism is a common feature of reptile biology and behaviour (49, 64, 82, 168, 185, 208, 236, 334). Nocturnalism allows reptiles and other animals to avoid certain challenges such as diurnal temperatures, predators and inter-species resource competition as well as predatorily capitalise on other nocturnal species (49, 168, 335-338). At least two welfare considerations are related to nocturnality and captive reptiles, and these are: disturbance of rest and sleep; and observational deficits. Disturbance of rest and sleep for reptiles may be an important issue because human diurnal behaviour may result in disruption of reptilian sleep patterns where, for example, reptile keepers impose handling or cause general noise (64). Some evidence suggests that reptilian sleep patterns may differ from birds and mammals (339), although sleep in reptiles essentially parallels that in other animals (including humans) in function (340-343). Accordingly, reduced sleep quality is thought to negatively impact on welfare, notably via stress and physiological disruption and immunological compromise (49, 64). Observational deficits also arise due to the human-diurnalism *versus* reptilian-nocturnalism paradox: observations for changes in behaviour or physical condition are compromised both in terms of opportunities for direct observation, and because sedentarism of sleeping animals may be non-indicative of health state (236, 334). Accordingly, conflicting sleep and activity patterns between certain reptiles and humans imply reduced opportunities to ascertain health and welfare.

1.5 **Endpoints or consequences of captivity and typical husbandry practices for reptiles**

1.5.1 ***Controlled deprivation***

Controlled deprivation refers to the phenomenon that regardless of captive environmental sophistication, enrichment and resource provisions, reptiles nevertheless experience inferior conditions compared with their evolved scope for diversity and stimulation (37, 231, 344, 345). Controlled deprivation both outlines a concept in animal husbandry as well as indicates summary endpoint conditions or consequences of captivity and typical husbandry practices associated with inadequate environmental enrichment. Although originating from reptile-based husbandry philosophy the concept and implications of controlled deprivation may be extended to all organisms within human husbandry domains. Controlled deprivation arguably expands on the concept that captive reptile husbandry equates to a 'life-support system' (64) in the sense that artificial conditions with attendant 'vivarium paraphenalia', serve only immediate and identifiable rather than long-term holistic biological needs.

1.5.2 ***Morbidity and mortality***

In a review of negative affective states and their effects of morbidity, mortality and longevity, Mason et al (346) report that negative effects correlate with higher mortality and reduced longevity in human and non-human animals. Those conclusions are consistent with many other studies finding identifying physiological and psychological stressors and stress with shared mechanisms of disease across animal classes (including reptiles) and humans e.g. (66, 72, 347, 348). Thus, negative affective states can be predictors of morbidity and mortality in populations. Mason et al (346) also acknowledge that the presence of stereotypical behaviours may act as measures of welfare. Reptiles appear not to have malfunctional stereotypical behaviours, but they do perform a range of behaviours accepted to indicate stress (see 1.4.4. '*Abnormal, maladaptive and stress-related behaviours in reptiles*' and '*Stereotypies and reptiles*'). Therefore, conventional links between stress and morbidity, mortality and reduced longevity are also reasonably applied. Overall, Mason et al (346) postulate that both typical drivers of morbidity and mortality (such as historical unpleasant experiences including injury and malnutrition), as well as negative affective states (such as fear, anxiety and loneliness) may have directly causal implications in disease and death.

At least 550 reptile species are involved in captive sectors (111). However, data for mortality (or survival/longevity) rates in nature across this species range are highly incomplete or unavailable. Some limited population mortality/survival data exist, for example, regarding freshwater turtles in the United States, which manifest 15-75 year survival depending on ecological niche (e.g. level of predators present) (349). Another study of freshwater turtles in the US found that an average of 23% of animals survive 17 years (350). Some of these mortalities are anthropogenic, for example, road kills (351) and fishing by-catch (352).

Based on limited records for individual reptiles, a range of species-associated potential longevities of 8 (for small species) - 120 (large species and chelonians) years are reported (305), thus reptiles have long potential lifespans. However, as reported in Table 9, mortality rate for reptiles during only 10 days associated with a wholesale distributor was found to be 41% (69). In addition, a six-year study of annual mortality rates for reptiles found that 75% of animals did not survive one year in the home ((353), Table 9). Furthermore, the causes of captive reptile mortality are typically diagnostically associated with stress, disease and injury linked to captive conditions (63, 66, 69, 247).

Comparing mortality or survival rates among free-living and captive animals requires careful interpretation. For example, in nature, a high population mortality among reptiles attributable to predation or starvation may be argued to constitute an acceptable rate of attrition in an ecological context. However, the same rate cannot be used as a justification for acceptable mortality for reptiles in captivity, because these mortalities are typically attributable to artificial stressors (63, 69, 247).

Regardless, in the hypothetical event that it was proven that, for example, a 75% mortality in captivity corresponded with a 75% mortality across the board for wild reptiles, and relatedly one chose to regard such mortality as consequently acceptable, an arguably overriding conclusion can be posited that society does not accept such theoretical comparisons as supporting high captive mortality rates. For example, depending on reporting parameters, wild wolves (*Canis lupus*) experience annual mortality rates of approximately 47% (354). Most domesticated dogs succeed in surviving to their potential longevities of over 11 years (355). Although comparison of annual mortality rates *versus* domestic longevity rates are not synchronised, they nevertheless convey that most dogs (wolves) in the wild do not achieve potential lifespan, whereas most domesticated dogs do achieve potential lifespan. Similarly, humans in Africa show life average expectancy of 62 years compared with humans in Europe and North America that show average life expectancy of 78 years (356). Significant causes of the higher mortality rate in humans in Africa are malnutrition, infection and associated disease (357), which are avoidable conditions in Western countries. Thus, in Western countries most domesticated dogs and people achieve natural longevity and, importantly, in Western countries annual mortality rates among dogs of 47% and longevity for humans of 62 years would be considered unacceptably poor and avoidable. Accordingly, possible higher mortality rates in some conditions (e.g. among deprived African people and free-living wild animals) cannot be considered markers to justify high mortality rates in captivity (195). If 75% of dogs or 75% humans did not survive one year, then this would be considered a failure of husbandry or lifestyle respectively (195) and thus an indicator of poor welfare, and similarly annual mortality rates of 75% observed in captive reptiles can be considered indicators of poor welfare.

Table 9. Example morbidity and mortality rates among captive reptiles in trade and transportation.

Common name	Scientific name	Context	Mortality rate	Resources
Chameleons	*Chemeleo* sp.	Premature mortality	10-50%;	(358)
Soft-shelled turtles	*Apalone* sp..	Premature mortality	36%	(358)
Skincid lizards	*Emoia* sp.	Premature mortality	36%	(358)
Map turtles	*Graptemys* sp.	Premature mortality	32%	(358)
Agamid lizards	*Agama* sp.	Premature mortality	23%	(358)
Anolid lizards	*Anolis* sp.)	Premature mortality	16.%;	(358)
Geckonid lizards	*Hemidactylus* sp.	Premature mortality	11%	(358)
Various species	*Reptilia*	First year	90%	(359)
Various species	*Reptilia*	Premature mortality	65%	(360)
Various species	*Reptilia*	10 days	testudines = 37%; lacertilians = 48%; and serpentes = 29%; cumulative = 42%	(69)
Various species	*Reptilia*	Annual	trade and private keeping = 81%; private keeping 75%	(353)

Several studies examine reptile trade (69, 361-363), and private ownership (246, 247, 353, 364-371) habits and associated husbandry practices for reptiles, and raise concerns regarding frequent suboptimal conditions and welfare. However, studies pertaining to specific husbandry conditions linked to morbidity and mortality do not appear to be available. Nevertheless, very many studies report captivity-associated clinical consequences among captive reptiles including wide-ranging injury (e.g. (63, 214)) and disease (e.g. (63, 214, 246, 247, 364-367, 369, 370)). Among these findings, many clinical conditions are reported to be associated with stress-related injurious behaviours (e.g. friction-lesions and damages limbs as results of escape attempts) and stress-related (adrenocorticoid complex and immunosuppression) opportunistic infections being cited as major causalities (63, 69, 214, 246, 247, 360, 364-367, 369, 370, 372-374).

As introduced earlier, animal welfare investigators suggest that morbidity and premature mortality indicate that animals may have experienced stress and poor welfare, and thus morbidity and mortality are important indicators of poor husbandry (6, 19, 20, 43). There are no clear reasons for not adopting this general approach where reptiles are concerned, thus it appears reasonable to hypothesise that many of the commonly reported instances of morbidity and premature mortality in reptiles are probably indicative of captivity-stress and poor coping mechanisms, and low adaptive plasticity to unnatural lifestyles in vivarium conditions.

1.6 **Author contribution to reptile biological science**

From the above Introduction, numerous issues are identifiable and that occupy common roles within reptilian biology and welfare. Of these issues, two convergent threads will be selected as focal subjects for the Aims of this thesis, and these have at their roots evolved innateness and adaptive plasticity, and human approaches and practices inherent to captive husbandry. Relatedly, in the forthcoming section (Aims), two questions will be investigated: Question 1. Are reptiles adaptable to captivity? and Question 2. Are typical husbandry practices consistent with reptile welfare?

As part of the investigation this thesis refers to six selected published peer-reviewed articles for which in all examples the present author was the primary contributor and compiler of content. Collectively, these articles form a cogent contributing relationship within welfare biology, and specifically address the research questions by providing both theory and empirical evidence regarding adaptational paradigms as well as signs of stress and their probable aetiologies.

Prior to my contributions to reptilian welfare biology, academic literature characteristically adopted applied husbandry information aimed at promoting survival and reproduction among animals via refinements of essential environmental features such as dietary, thermal and humidity regimes. During that period, very little published work existed that had as its primary focus reptile welfare for the benefit of the individual animals. For example, an *ad hoc* literature search using the first five pages of Google Scholar (accessed 24.6.19) and including the term ‘reptile welfare’ for the period 1960 - 1989 revealed only five publications in which the words ‘reptile’ and ‘welfare’ relevantly appeared. In comparison, for the period 1990 – 2019 there were 28 relevant publications, of which 10 were produced either by myself or by myself and co-authors. Notably, inclusion of issues pertaining to animal-centric psychological and behavioural health states have become increasing objects of study and theoretical and applied reptile welfare, with these subjects appearing in at least 16 of the 28 above items.

Appendix 1a and 1b provide information regarding the author's key welfare-associated publications and the primary subject contributions within each paper. This information is included because a number of concepts, principles and methodologies directly and indirectly relevant to reptile welfare and to the Aims of this thesis were either initiated or further developed by the author, and including the fuller materials provides both additional context and transparency to this work.

Sustained contribution

The following data set out the author's published scientific contributions to reptile welfare biology since 1984: years are followed by number of annual publications in parentheses: 1984 (1); 1985 (4); 1986 (4); 1987 (2); 1988 (2); 1989 (3); 1990 (7); 1991 (4); 1992 (2); 1994 (1); 1995 (4); 1996 (3); 1997 (1); 1998 (1); 1999 (2); 2000 (1); 2001 (2); 2002 (2); 2005 (2); 2006 (2); 2009 (1); 2010 (2); 2011 (5); 2012 (3); 2013 (4); 2014 (7); 2015 (2); 2016 (2); 2017 (2); 2018 (7); 2019 (7); 2020 (12) including in preparation/in press).

Collectively, and by example the six submitted publications, these works have advanced both theoretical and applied reptile biological science and welfare, and have become some of (if not the) most frequently cited and utilised foundational explanations for reptilian welfare biology and assessment. Broadly, the selected six papers provide a cogent theme of welfare biology and continuity concerning recognition and development of reptile specific humane approaches. The specific contributions of these works will be further indicated under Results and Discussion.

2. AIMS

This thesis has two overarching aims, and these are: to investigate the scope of reptilian adaptability or nonadaptability to artificial environments - that is, whether reptiles are adaptable to captivity; and to investigate welfare-relevant endpoints or ‘consequences’ of captivity for reptiles - that is, whether typical captive husbandry practices are consistent with reptile welfare. These aims are important because they are fundamentally relevant to reptile welfare biology, and whether, and under what conditions, problem recognition, prevention or amelioration may be feasible. In order to address these aims, the thesis will present data from studies into the adaptability and nonadaptability of reptiles to captivity and some frequent problematic results of captivity.

Research shows that reptiles possess a behaviourally adaptive reach that lends itself to some extraordinary novel and problem-solving scenarios comparable to those of traditionally viewed ‘higher’ animal classes (birds and mammals) (176, 177, 278, 279, 375). However, adaptational limitations appear set to innately pre-determined coping strategies bound to environmental and lifestyle challenges that are in the ‘right evolutionary and biological direction’, that is, context (which excludes captive conditions) (195, 276, 277). Superficially, the findings that ‘extraordinary novel and problem-solving abilities’ exist for studied reptiles and that ‘adaptational limitations appear set to innately pre-determined coping strategies’ might appear entangled and incongruous because the former suggests good adaptability, whereas the latter suggests poor adaptability. However, what these apparently competing scenarios imply is that reptilian adaptability is nuanced to challenges for which they already possess innate degrees of flexibility, such as navigational abilities in nature (180, 376,

377) relating to successful adaptation to maze tests in laboratories (180, 378, 379), and conversely innate transient drive states in nature relating to unsuccessful adaptation to restrictive spatial conditions in captivity (236, 238).

There appear to be no studies comparatively scaling reptilian innateness with other animal classes, although innate dominance varies across class boundaries. For example, endothermic animals (birds and mammals) displaying high-level to vital dependence on parental nurturing for early survival (380, 381) *versus* endothermic animals (invertebrates, fishes, amphibians and reptiles) displaying zero to moderate-level dependence on parental nurturing for early survival (82, 382), thus they alternatively rely on developmental precocity and intact innate characteristics ('Innateness').

Welfare is affected by diverse individual and interrelated convergent factors (37, 63, 231, 246, 247, 383); therefore, various meritorious questions pertinent to the prescribed literature may be investigated with possibly resultant useful or important outcomes. The study questions investigated herein reflect the author's choice – they are not the only options.

Question 1. Are Reptiles Adaptable to Captivity? Reptiles possess a suite of relevant adaptive responses (176, 177, 278, 279, 375), and are known to be capable of seemingly atypical or 'unnatural' tasks by, for example, navigating artificial mazes (376, 377) and selecting artificial indicators providing food (378, 379). Identifying natural potential for adaptation to artificial environments (captivity) is fundamental to establishing both prospects for positive or negative welfare states and the possible remedies for problematic issues. In particular, what is the role of genetic hard-wiring and precocity in cognitive and ethological adaptive modalities?, as presented in submitted papers 1,2,3,6.

Question 2. Are Typical Husbandry Practices Consistent with Reptile Welfare? Husbandry practices vary across reptile-use sectors, which include zoological facilities, research laboratories, private homes, wholesalers, retailers and commercial production, for example, for 'pets'(361), skin (384), meat (385), and scientific or zoological captive-breeding programmes (225). Despite these differing situations, husbandry approaches generally rely on shared principles (for example, spatial restriction, artificial climate control, and human presumption of biological/welfare needs. Determining the generalisability of these approaches to successful husbandry and resultant welfare is important to verifying their validity as a paradigm. In particular, what is the role of typical husbandry practices in maladaptation, nonadaptation, and causally-related stress, morbidity and mortality?, as presented in submitted papers 3,4,5,6.

2.1 **List of submitted publications**

Paper 1. Warwick, C. (1995) Psychological and behavioural principles and problems. In: **Warwick**, C., Frye, F.L. & Murphy (Eds.) *Health and Welfare of Captive Reptiles*. Chapman & Hall/Kluwer, London and New York, pp205-235. (I conceived this project, conducted all of the literature research and review, conducted all of the original field research, and prepared the manuscript.) (Relates to Q 1)

Background: Rationale for this paper was investigation of abnormal behaviour and associated aetiologies in captive reptiles. These considerations are central to the aims of this thesis because abnormal behaviour is reflective of coping mechanisms, adaptational plasticity and associated limitations, as well as welfare consequences. *Methods:* Based on observations of over 4,000 scan- and focal-sampled reptiles at United Kingdom and other European zoological and private reptile collections. *Main findings:* Approximately 30 problematic psychological and behavioural issues were identified, and proposed as causally-related to conflicts between biological needs and overly-restrictive conditions of captivity. *Conclusions:* The paper relates to the aims of the thesis by hypothesising how conflicts between reptilian adaptability and artificial environments may originate and compromise welfare.

Paper 2. Warwick, C. & Steedman, C. (1995) Naturalistic versus clinical environments in husbandry and research. In: **Warwick**, C., Frye, F.L. & Murphy (Eds.) *Health and Welfare of Captive Reptiles*, Springer, London and New York, pp113-129. (Although this was a dual-authored text, I conceived the project, conducted most of the research, and prepared the initial and final draft manuscripts.) (Relates to Q 1)

Background: Rationale for this paper was investigation of naturalistic *versus* unnaturalistic (clinical) husbandry practices and reptile welfare. These considerations are central to the aims of this thesis because they involve comparative opposing husbandry approaches and their effects on reptile behaviour and welfare. *Methods:* Based on observations of 345 focal-sampled reptiles at 22 European zoological research facilities. *Main findings:* Naturalistic environments are more consistent with reptile welfare, including in highly experimental conditions. *Conclusions:* The paper relates to the aims of the thesis by reporting differences in factors that may affect reptile welfare under naturalistic and unnaturalistic conditions, and hypothesises on possible associations with limited coping mechanisms and adaptive plasticity.

Paper 3. Arena, P.C., **Warwick**, C. & Steedman, C. (2014) Welfare and environmental implications of farmed sea turtles. *Journal of Agricultural and Environmental Ethics*, 27:(2); 309-330. https://doi.org/10.1007/s10806-013-9465-8
(Although this was a multi-authored text, I conceived the project, conducted most of the literature research and review, conducted all of the field research, and prepared the initial and final draft manuscripts.) (Relates to Qs 1, 2)
Background: Rationale for this paper was investigation of physical and behavioural indicators of welfare in farmed sea turtles. These considerations are central to the aims of this thesis because physical health state and abnormal behaviour can be reflective of husbandry practices, as well as limited coping mechanisms and adaptive plasticity, and welfare consequences. *Methods:* Based on observations of 338 scan-sampled turtles in both naturalistic and unnaturalistic conditions, with supplementary video-based observations. *Main findings:* Identified three distinct signs of physical injury and disease, six signs of abnormal and problematic behaviour, and three signs of normal quiescence- and comfort-related behaviour, that overall indicated significant welfare compromise associated with the farmed turtles. *Conclusions:* The paper relates to the aims of the thesis by reporting differences in reptile welfare under naturalistic and unnaturalistic conditions, consequences of typical husbandry practices, and hypothesises on possible associations with limited coping mechanisms and adaptive plasticity.

Paper 4. Ashley, S., Brown, S., Ledford, J., Martin, J., Nash, A. E., Terry, A., Tristan, T. & **Warwick**, C. (2014) Morbidity and mortality of invertebrates, amphibians, reptiles, and mammals at a major exotic companion animal wholesaler. *Journal of Applied Animal Welfare Science*, 17:(4);308-321. https://doi.org/10.1080/10888705.2014.918511 (Although this was a multi-authored text, I conceived the paper, conducted most of the literature research and review, some of the field research, and prepared the initial and final draft manuscripts. Contributors were listed alphabetically.) (Relates to Q 2)

Background: Rationale for this paper was investigation of husbandry conditions and welfare for >26,000 animals, of which approximately >16,000 were reptiles. These considerations are central to the aims of this thesis because husbandry practices, morbidity and mortality may be reflective of limited coping mechanisms and adaptational limitations, and welfare consequences. *Methods:* Based on collaborative observations of >16,000 focal-examined reptiles in unnaturalistic conditions. *Main findings:* Identified 80% morbidity and 42% mortality rates during 10 days primarily due to malhusbandry, problematic behaviour and stress, indicating significant welfare compromise. *Conclusions:* The paper relates to the aims of the thesis by reporting consequences of typical husbandry practices and hypothesises on associations with limited coping mechanisms and adaptive plasticity.

Paper 5. Warwick, C., Arena, P. & Steedman, C. (2019) Spatial considerations for captive snakes. *Journal of Veterinary Behaviour: Clinical Applications and Research*, 30:37-48. https://doi.org/10.1016/j.jveb.2018.12.006 (Although this was a multi-authored text, I conceived this project, conducted most of the literature research and review, conducted most of the field research, and prepared the manuscript.) (Relates to Q 2)

Background: Rationale for this paper was investigation of typical husbandry practices and prevalence of normal rectilinear (straight-line) behaviour in captive snakes. These considerations are central to the aims of this thesis because normal behaviour is reflective of typical husbandry and welfare consequences. *Methods:* Based on observations of 65 scan-sampled snakes at eight zoological facilities in Canada and the United Kingdom. *Main findings:* Identified 37% prevalence for rectilinear or near-rectilinear behaviour when snakes were physically able to adopt straight-line postures, and that this normal behaviour is frequently not provided for in typical captive conditions. *Conclusions:* The paper relates to the aims of the thesis by reporting typical husbandry practices and hypothesising on restriction of normal behaviour relevant to welfare.

Paper 6. Warwick, C. (2014) The Morality of the Reptile "Pet" Trade. *Journal of Animal Ethics,* 4:(1);74–94. (This was an invited article by the Oxford Centre for Animal Ethics. I conceived this project, conducted all of the literature research and review, and prepared the manuscript.) (Relates to Qs 1,2)

Background: Rationale for this paper was investigation of diverse issues regarding the reptile pet trade in a moral context. These considerations are central to the aims of this thesis because ethical examination is transcendent of common practice, law and science. *Methods:* Based on self-directed literature research, experiential context and welfare-centric argument. *Main findings:* Multifaceted problematic welfare issues permeate the reptile pet trade, with serious negative moral implications. *Conclusions:* Reptiles commonly experience poor welfare resulting from limited coping mechanisms and adaptability to captivity, public misperceptions regarding their biological needs, and endure conditions that would be considered unacceptable for dogs and cats.

3. RESULTS AND DISCUSSION

Paper 1. Psychological and behavioural principles and problems. Together with Warwick (68) and Warwick, et al. (113) this paper constitutes one of a trilogy of globally foundational publications presenting information and discussion regarding concepts and principles relating to reptilian biology, adaptability, and nonadaptability in artificial environments, as well as psychological and behavioural consequences of maladaptation on welfare. The paper has been cited over 20 times in the literature, although as a book chapter in a substantial volume its circulation is relatively restricted to academic institutional rather than semi academic audiences. However, combined with the original article on which the chapter is based (68) as well as a more recent abbreviated open access derivation (113) this work has been cited at least 130 times. Essentially, the paper constitutes an investigation, modernisation and expansion on an original article on captive reptile psychological and ethological problems (68). The paper follows the hypothesis that hard-wired traits, innate drive states and resultant strong (in particular) psychological and behavioural precosity result in low adaptive plasticity among reptiles, thus implying that their coping mechanisms in suboptimal captive conditions are insufficient to create homeostasis. It is argued that several behaviours indicate hard-wired psychological and behavioural inflexibility in captive reptiles.

Interaction with transparent boundaries (ITB) involves reptiles engaging in typically prolonged attempts at climbing glass or other transparent borders, which are common features of reptile vivariums. It is hypothesised that ITB involves conflict between exploratory behaviour (whether normal or abnormal), innate environmental cues (i.e. what reptiles inherently expect from their environment, which does not include invisible impenetrable barriers), and highly limited adaptive capacity. In addition to probable psychological and behavioural compromise, negative physical signs of ITB also manifest, including common localised snout friction lesions, associated infection, tissue necrosis, occasional systemic infection, and death. Therefore, ITB is strongly linked to coping abilities, adaptive capacity, and captive reptile welfare. As a result of my investigations, ITB is nowadays widely accepted as representing an abnormal and stress-related state, and has become integrally utilised in research as an indicator of captivity-stress in reptiles.

It is also postulated that reptiles appear to have two primary strategies for avoiding unfavourable environmental conditions: exploratory and escape behaviour or sedentarism and biological shutdown behaviour (64, 68, 113, 260). As reviewed earlier in this thesis, these two strategies also appear common to other (non-reptilian) animals. Exploratory and escape behaviour typically manifests among reptile species that roam to avoid unfavourable environmental conditions, such as drought or food shortage (64, 68, 113, 128, 260), or in some species where searching for more favourable environments, such as novel genetic populations for reproductive purposes (82). In managed captive conditions where food, water and other biological needs are artificially met, alternative environmental conditions ought not to be drivers of exploratory and search activities, thus significant locomotor behaviour constitutes hyperactivity.

Captive environments lacking space are commonly associated with exploratory, search or hyperactive behaviours in reptiles. Spatial factors, including extensive home ranges in which reptiles actively occupy large areas (82) and reproductive transience behaviour in which sedentary species sporadically leave resident populations to search for novel ones (82) may demonstrate hard-wired spatial needs. Restricted movement attributable to spatial limitations has been regarded as one of the primary contributors to captivity-stress (8, 9) in many animals, and thus may also be relevant in reptiles. Sedentarism and biological shutdown behaviour typically manifests among reptile species that habitually aestivate, hibernate or brumate to avoid unfavourable conditions (64, 68, 113, 260). In captivity, this state is frequently observed as hypoactivity, and probably reflects avoidance strategy within suboptimal environments. In captivity, sedentarism and biological shutdown behaviour or hypoactivity strategy is thwarted because unfavourable conditions do not seasonally desist and therefore these states may equate as the reptilian equivalent of 'learned helplessness'. Again, as reviewed elsewhere in this thesis, sedentarism or hypoactivity has been associated with captivity-stress and failed coping mechanisms.

This paper relates to the Aims and, in particular, to study question 1 of the thesis because it includes original concepts pioneered by the present author and investigates reptilian adaptability or nonadaptability to artificial environments, typical captive husbandry practices, and reptile welfare biology. The paper relates to study question 1 by providing possible answers for abnormal and problematic behaviour among captive reptiles, in particular regarding apparent failures to adapt to captivity, which may be associated with hard-wired innate behavioural and psychological states evolved for ancestral spatio-environmentally habitats. Captive reptile husbandry practices typically frustrate certain key psychological and behavioural expressions, which combined with insufficient coping mechanisms, low adaptive plasticity, and maladaptation, result in contextually abnormal states and stress.

Paper 2. Naturalistic versus clinical environments in husbandry and research.

This paper includes research and empirical material and focuses on reptile husbandry in research environments, although its concepts and principles are not limited to this context and may be applied broadly to other captive reptile situations. The paper has been cited at least eight times in the literature, although as a book chapter in a substantial volume its circulation is relatively restricted to academic institutional rather than semi academic audiences, and has limited scope of appeal. Essentially, the paper considers welfare issues in several contexts including from a research directed approach, where compromised welfare may impact purity of results, and proposes that welfare is intrinsically important. It is argued that conditions in nature, while challenging, continue to incorporate as fundamental phenomena a diversity of factors that – no matter how difficult – remain contextualised and offer animals environments where much continues to operate normally. Natural normality is proposed as a major stabilising influence in holistic (or positive) physiological, psychological and behavioural states. In contrast, captive conditions, in particular unnaturalistic and clinical forms, can incorporate destablising influences promoting negative physiological, psychological and behavioural states.

This paper relates to the Aims and to study question 1 of the thesis by providing a series of postulates that essentially juxtapose and critically compare conditions in nature with conditions in captivity that have relevance to reptile husbandry welfare, and conclude that natural conditions are more favourable. The paper relates to the study question by indicating that the presence of captivity stress-related conditions, which are more prevalent in small and unnaturalistic environments, imply that reptiles are not adaptable to captivity.

Paper 3. Welfare and environmental implications of farmed sea turtles. This paper provided a detailed research-based study of welfare implications for sea turtles at a major captive breeding facility. The paper has attracted over 2,700 views and downloads, and has been cited at least 12 times in the literature. Essentially, the paper provides evidence identifying 10 signs of physical injury or disease conditions, six signs of abnormal behaviour and stress-related behaviour, and three signs of normal quiescent- or comfort-related behaviour.

The paper relates to the Aims and to study questions 1 and 2 of the thesis by including issues of both adaptability and husbandry. The paper relates to study question 1 by suggesting that limitations of adaptive plasticity in these reptiles is causally-related to abnormal behaviour, injury and disease. Accordingly, accepted primary signs of adaptability (such as normal behaviour, and low prevalence of morbidity and mortality) are significantly compromised indicating that these reptiles do not adapt to their conditions of captivity. The paper relates to study question 2 by providing data to indicate that behavioural and physical welfare are strongly compromised by captive conditions. Accordingly, typical husbandry practices are not consistent with reptile welfare.

Paper 4. Morbidity and mortality of invertebrates, amphibians, reptiles, and mammals at a major exotic companion animal wholesalers. This paper provided a detailed research-based account of morbidity and mortality, and associated causes, among animals held commercially for exotic pets. The paper has been cited at least 25 times in the literature. Susceptibility or resilience to disease is an indicator of coping mechanisms in suboptimal environments (63, 247). Causes of disease are indicators of coping mechanisms (63). High morbidity and mortality are strong indicators of whether or not environmental conditions are consistent with good welfare (6, 14, 19, 20, 43).

The paper relates to the Aims and to study question 2 of the thesis by documenting that high morbidity and mortality, along with particular related causalities among reptiles, are endemic to intensive commercial conditions. Because reptiles are known for their slow metabolic rate, disease onset is slow from issues such as malnutrition and dehydration (63, 214). However, average turnaround time for reptiles at the studied facility was six weeks. This relatively short period indicates that other factors, including generalised captivity-stress, were significantly responsible for the high levels of morbidity and mortality. The paper relates to the study question by reporting that conditions constituting 'industry standard' can be multifactorially harmful to reptiles. Accordingly, typical husbandry practices are not consistent with reptile welfare.

Paper 5. Spatial considerations for captive snakes. This paper is probably the first of its kind to look at snake spatial habits and implied welfare needs in captivity. The paper has attracted over 20,000 views and downloads. Although minimally cited in the literature, the paper has only very recently been published. This paper relates to the Aims and to study question 2 of the thesis because it reviews normal rectilinear (straight-line) postural and locomotive behaviour in wild snakes, and provides observational research concerning rectilinear behaviour among captive snakes.

Snakes and many other reptiles, whether commonly sedentary or roaming by habit, frequently occupy extensive home ranges and regularly adopt rectilinear (straight-line) postures during locomotion or rest. In captivity, diminutive enclosures prevent this normal behaviour. Essentially, the paper clarifies that where available, snakes commonly occupy areas of captive enclosures with linear dimensions that allow them to adopt rectilinear or straight-line body postures. The paper concludes that rectilinear behaviour is probably necessary to the health and welfare of reptiles, and contrasts this biological need with the frequently spatially deficient captive enclosures for snakes that prevent normal rectilinear behaviour.

The paper relates to study question 2 by exemplifying that in terms of spatial provisions alone snakes, which are possibly the most commonly kept pet reptiles, are frequently deprived in captivity of the opportunities and abilities to express normal locomotor and rest associated postural behaviour, and the paper has implications for other spatial needs issues. Accordingly, typical husbandry practices are not consistent with reptile welfare.

Paper 6. The Morality of the Reptile "Pet" Trade. This paper probably constitutes the most in-depth existing academic essay regarding morality and ethics relevant to the trading and keeping of reptiles for pets. The paper has been cited at least 17 times in the literature. Essentially, the paper provides a background of fact-based information pertaining to the selling and keeping of reptile pets, as well as scale, operation, conservation, ecological alteration, welfare implications, morbidity, mortality and zoonoses. The paper presents a series of arguments and postulates that contextualise and critique numerous aspects of the trading and keeping of reptiles for pets. A large commercial supply industry co-exists with the private keeping of reptiles. Supply includes wild capture, open cycle 'ranching' (wild-sourced breeder stock producing captive offspring), and closed cycle captive breeding. Physical handling, transportation, storage and hygiene abuses result in many injuries and subsequent diseases, which although more common among wild-caught animals also occur in captive-bred situations. Stress is presumed to accompany the raft of physical insults.

This paper relates to the Aims and study questions 1 and 2 of the thesis by connecting all relevant primary issues and applying an overarching moral theme. The paper relates to study question 1 by exemplifying differences in adaptability between reptiles and domesticated animals, such as dogs, in a moral context. For example, normal life spans for dogs are expected to match natural potential longevity whereas premature mortality for reptiles is accepted. Accordingly, accepted primary signs of coping with environmental conditions and adaptability (including normal behaviour, longevity, and low prevalence of morbidity and premature mortality) are significantly compromised indicating that reptiles do not cope well with or adapt to their usual conditions of captivity. The paper relates to study question 2 by exemplifying commonness of endpoint husbandry failures, and the issue that many with genuine interests in reptiles are incidentally among their greatest abusers, and that attitudes to reptiles as well as their treatment are inferior to domesticated animals such as dogs. Accordingly, typical husbandry practices are not consistent with reptile welfare.

3.1 **Concluding summary**

Early examples of reptile keeping reveal nonchalant attitudes to their husbandry, and dismissive reactions to their welfare (208). Historically, morbidity and mortality were met with legal and moral impunity. Of concern, little has changed (386). Regulatory laws and welfare-oriented frameworks now exist that are theoretically capable of amelioratory application to reptiles (31, 32, 67, 109-111, 114, 334). However, conscientious implementation of such initiatives by regulatory authorities may continue to be undermined by issues such as human misperceptions regarding reptilian physiological sensitivities to adverse conditions (128, 196) and lack of ‘cuteness’(387). Accordingly, generalised resistance to act against incidental or deliberate reptile abuse may persist because mammal-comparable suffering (often perceived via human-mammalian affiliative similarities and vocalisation) among these animals is evidentially challenging to formally establish.

Regardless, it can be proposed that the above papers, along with others from the present author’s contributory stable establish key concepts and principles, as well as relevant data, to exemplify that not only are reptiles capable of feeling and suffering, but also that in some respects, notably because of their dominant ancestral innate biology, they may be subject to greater psycho-behavioural frustration and suffering than might affect a mammal under similar conditions. Moreover, the papers arguably present a raft of novel key approaches to welfare, and to the rationalisation of it, and firmly seek to provide both theoretical constructs for welfare-related biology as well as applied measures to identify and ameliorate problems.

Paper 1 discusses many diverse adaptational and related limiting factors pertinent to reptiles, and presents a range of behaviours relevant to captivity that can be used as indentifiers of positive or negative welfare, along with postulates regarding their aetiologies. Paper 2 discusses salient factors pertaining to life in nature compared with different types of captive situation, and postulates that nature should inform the unnatural conditions of captivity, and is consistent with the concepts and principles of Paper 1. Paper 3 provides research that demonstrates that reptiles may not cope well or adapt to their captive environments, that typical husbandry conditions are inconsistent with welfare, and that the generalised identifiers of positive and negative welfare, as proposed in Paper 1, are conventionally discoverable and consistent with the concepts and principles of Papers 1 and 2. Paper 4 provides research that demonstrates that typical husbandry conditions are inconsistent with welfare, and that insufficient coping mechanisms and low adaptive plasticity is probably a factor, and the paper is consistent with the concepts and principles of Papers 1, 2 and 3. Paper 5 provides a review and research exemplifying that typical husbandry conditions are inconsistent with welfare for snakes, and is consistent with the concepts and principles of Papers 1, 2, 3 and 4. Paper 6 provides an overarching biological and ethical essay summarising broadly relevant issues and presents moral questions and postulates, and is consistent with the concepts and principles of Papers 1, 2, 3, 4 and 5. Cumulatively, these six papers provide a cogent theme and complement a journey through the Aims and Study questions of the thesis, that hopefully suggest that reptile welfare has been better explained, better understood, and will be better respected as a result of these works.

4. CONCLUSIONS

A regular theme of my work proposes that under natural conditions diverse stimuli and influences manifest that one may reasonably speculate are relevant to individual animals, including: abiotic factors, such as climate, season, weather, habitat, habitat selection, normal chemical cues, normal sounds, and open space; and biotic factors such as seasonal or other particular dietary variation, specific prey search and acquisition, environmental immune stimulation, sociality, randomised social interactions, territoriality, reproductive transience, and incidental learning from natural phenomena. Even within isolated natural ecosystems, many of these factors may be relevant. Individually or collectively these phenomena and ancestral traits may be strongly 'pre-accounted for' in dominantly innate and precocious animals such as reptiles, as well as developmentally and holistically important to their health and welfare. Nature-based hardships occur against a background of normality. Whatever happens to an animal in nature happens where and how it should, and the animal ought to be evolutionarily prepared for it. Nature-based pleasures must also be presumed to be as present as hardships, or perhaps dominant, otherwise evolution would have normalised adversity – which would make adversity nonaversive!

Dominant ancestral innate traits in reptiles imply high-level precocity and independence, independence implies inborn anticipated control over interactions between an organism and its environment, lack of control over interactions between an organism and its environment in captivity imply captivity-associated inherent welfare compromise. Also, it seems reasonable to propose that under the standard scientific protocols for assessing or measuring welfare (The Five Freedoms, The '3Fs', and The

Five Welfare Needs), captive reptiles probably commonly experience poor welfare. On these premises, an explanatory foundation is laid for numerous elements of my work regarding limitations of reptilian coping mechanisms and adaptive plasticity, and psychological and behavioural problems in captivity, for which in particular my designed welfare criteria have proceeded to permeate applied research and practical assessments globally. Relatedly, my work studying husbandry practices and welfare outcomes provides detailed evaluations to demonstrate typical practices and consequences.

The Aims and the Study questions for this thesis, were to investigate:

- the scope of reptilian adaptability or nonadaptability to artificial environments - that is, whether reptiles are adaptable to captivity?;

- the welfare-relevant endpoints or 'consequences' of captivity for reptiles - that is, whether typical captive husbandry practices are consistent with reptile welfare?

The thesis has investigated its Aims and Study questions by outlining essential adaptational principles as well as exemplifying biological and stress-related issues that hypothesis on limitations of reptilian coping mechanisms and adaptive plasticity, to conclude that reptiles are not adaptable to captivity and by extension to the artificial conditions in which they are typically confined; and also that typical captive husbandry practices are inconsistent with reptile welfare.

5. FUTURE DIRECTIONS

Reptile biology and welfare, including formerly unpopular areas such as psychological and behavioural needs, are attracting increasing interest and research. Accordingly, the future of reptile welfare science appears promising. However, the expanding evidence-base is disproportionately deterministic of the position that greater understanding of these animals infers greater recognition of their unsuitability to the unnatural, minimalistic environments of captivity. Intuitively, this disproportionate academic race ought to be won by conjoined scientific and ethical rationale concluding that reptiles should not be held captive. Whether or not this rationale emerges as the race winner, a lag phase between the *status quo* of currently accepted reptile keeping and future abolition or bans appears set.

Moderating this *status quo* are numerous initiatives based around four general approaches: animal husbandry education to inform especially impulse acquirers of reptiles and hobbyists regarding more advanced animal care; species suitability algorithms to pre-inform prospective acquirers of the degree of challenge associated with particular species; pet labelling to provide impartial guidance about reptiles in line with the principle of food labelling; and positive lists to provide a register of species that can be legally kept subject to impartial objective evidence-based determination that their welfare can be routinely met in captivity. The present author recently published limited reviews of these approaches (111, 334). Furthermore, as contributions towards these approaches, the present author has also been strongly instrumental in designing and publishing targeted resources, including: general (across classes and species) animal husbandry education guidance based primarily on natural history principles; a general (across classes and species) animal suitability algorithm (109); a reptile specific suitability algorithm (114); and a pet labelling scheme (111). Accordingly, while science will continue to reveal greater biological complexities and welfare needs for reptiles, and objective impartial evidence-based information may provide amelioratory measures, ethical scrutiny and regulatory intervention probably harbours lasting resolution to the anthropogenic-reptilian welfare paradigm.

DECLARATION

Whilst registered as a candidate for the above degree, I have not been registered for any other research award. The results and conclusions embodied in this thesis are the work of the named candidate and have not been submitted for any other academic award.

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APPENDICIES

Appendix 1a,b

Appendix 1a. Key welfare-associated publications and subject contributions.				
Author(s)	*Year*	*Title*	*Journal*	*Subjects*
Warwick, C.	2019	Cruel world or humane nature?	*The Ecologist J.,* 20 May: 1-6.	Coping mechanisms, biological strategies, environmental deprivation, incidental compassion in nature.
Warwick, C., Arena, P. & Steedman, C.	2019	Spatial considerations for captive snakes.	*J. Vet. Behav.,* 30:37- 48.	Snake biology, roaming habits, spatial needs, evolutionary considerations, behavioural versus physiological assessments of captivity stress, injury, and disease.
Warwick, C., Bates, G., Arena, P. & Steedman, C.	2018	Reevaluating the use of hypothermia for anesthetizing and euthanizing amphibians and reptiles.	*J. Am. Vet. Med. Assoc.,* 253:12;1536-1539.	Use of hypothermia for sedation, anaesthetisation and euthanasia of reptiles.
Warwick, C., Jessop, M., Arena, P., Pilny, A. & Steedman, C.	2018	Guidelines for inspection of companion and commercial animal establishments.	*Frontiers in Vet. Sci.,* 5:(151);1-21.	Evidence-based facility inspection protocols, cross-species naturalistic husdandry principles.
Warwick, C., Steedman, C., Jessop, M., Arena, P., Pilny, A. & Nicholas, E.	2018	Exotic pet suitability: understanding some problems and utilizing a labeling system to aid animal welfare, environment, and consumer protection.	*J. Vet. Behav.,* 26:17-26.	Evidence-based labelling protocol for point of sale education on pet acquisition.
Warwick, C., Jessop, M., Arena, P., Pliny, A., Nicholas, E. & Lambiris, A.	2017	Future of keeping pet reptiles and amphibians: animal welfare and public health perspective.	*Veterinary Record*, 181(17), 454-455.	Debate article on welfare compromise among kept reptiles.
Ashley, S., Brown, S., Ledford, J., Martin, J., Nash, A. E., Terry, A., Tristan, T. & **Warwick, C.**	2014	Morbidity and mortality of invertebrates, amphibians, reptiles, and mammals at a major exotic companion animal wholesaler.	*J. Appl. Anim. Welf. Sci.*, 17:(4);308-21.	Multi-animal class morbidity and mortality statistics, presumptive causes of morbidity and mortality, distribution of traded animals.
Warwick, C.	2014	The morality of the reptile "pet" trade.	*J. Anim. Ethics,* 4:(1);74–94.	Pet trade, ethics, premature mortality, welfare, stress, disease, environment.
Arena, P.C., **Warwick, C**. & Steedman, C.	2014	Welfare and environmental implications of farmed sea turtles.	*J. Agric. and Env., Ethics*, 27:(2);309-30.	Welfare, captivity stress, disease injury, normal and abnormal behaviour.
Warwick, C., Steedman, C., Jessop, M., Toland, E. & Lindley, S.	2013	Assigning degrees of ease or difficulty for pet animal maintenance: the EMODE system concept.	*J. Agric. and Env. Ethics*, 27:(1);87-101.	Evidence-based protocol for assessment of species suitability for captivity.
Warwick, C., Steedman, C. & Nicholas, E.	2013	Veterinarian accountability and the exotic pet trade.	*AWSELVA J.*, 17:(1);3-6.	Ethical argument concerning the role of veterinarians in the pet trade, animal welfare.
Warwick, C., Arena, P.C., Lindley, S., Jessop, M. & Steedman, C.	2013	Assessing reptile welfare using behavioural criteria.	*In Practice*, 35:(3);123-131.	Normal and abnormal behaviour, spatial considerations, captivity-stress, overcrowding and crypto-overcrowding, behavioural fever and stress, voluntary hypothermia, protocol for c30 signs behavioural assessment tool.
Nicholas, E. & **Warwick, C.**	2011	Alleviation of a gastrointestinal tract impaction in a tortoise using an improvised vibrating massager.	*J. Herp. Med. & Surg.*, 21:(4);93-95.	Pica, captivity-stress, gastrointestinal impactions, relief protocol.

Appendix 1b. Key welfare-associated publications and subject contributions.				
Author(s)	*Year*	*Title*	*Journal*	*Subjects*
Scott, S. & **Warwick, C.**	2002	Behaviour problems in a monitor lizard (Case report: interaction with transparent boundaries).	*UK. Vet*, 7:73-75.	Maladaptation, captivity-stress, interaction with transparent boundaries, husbandry.
Close, B., Bannister, K., Baumans, V., Bernoth, E.M., Bromage, N., Bunyan, J., Erhardt, W., Flecknell, P., Gregory, N., Hackbarth, H., Morton, D. & **Warwick, C.**	1996	Recommendations for euthanasia of experimental animals. Part 2.	*Laboratory Animals*, 31: 1-32.	Investigation of and recommendations for physical and chemical killing of animals across all relevant species in laboratories.
Close, B., Bannister, K., Baumans, V., Bernoth, E.M., Bromage, N., Bunyan, J., Erhardt, W., Flecknell, P., Gregory, N., Hackbarth, H., Morton, D. & **Warwick, C.**	1996	Recommendations for euthanasia of experimental animals. Part 1.	*Laboratory Animals*, 30: 293-316.	Investigation of and recommendations for physical and chemical killing of animals across all relevant species in laboratories.
Arena, P.C. & **Warwick, C.**	1995	Miscellaneous factors affecting health and welfare.	*Health and Welfare of Captive Reptiles*. Chapman & Hall/Kluwer, 263-280.	Stress, pain and sensitivity, natural versus captivity-related stressors and stress, emotional stress, thermal factors and thermoregulation, thermal burns, photo-invasive environments, euthanasia and killing, decapitation and spinal cord severance.
Warwick, C. & Steedman, C.	1995	Naturalistic versus unnaturalistic clinical environments in husbandry and research.	*Health and Welfare of Captive Reptiles*. Chapman & Hall/Kluwer, 113-129.	Naturalistic *versus* unnaturalistic environments in husbandry and research.
Warwick, C.	1995	Psychological and behavioural principles and problems.	*Health and Welfare of* Captive Reptiles. Chapman & Hall/Kluwer, 205-235.	Maladaptation, signs of positive and negative psychological and behavioural states, exploratory, search and escape activities, interaction with transparent boundaries, hyperactivity, hypoactivity, social stress, aggression, feeding behaviour and problems, behaviour-related self-injury, body posture and position, biological and behavioural strategies, spatial considerations, disturbance of rest and sleep.
Warwick, C.	1991	Observations on disease-associated preferred body temperatures in reptiles.	*Appl. Anim. Behav. Sci.*, 28:(4);375-80.	Investigation into voluntary selection of low environmental temperatures during disease.
Warwick, C.	1990	Observations on collection, transport, storage and slaughter of western diamondback rattlesnakes (*Crotalus atrox*).	*Herpetopathologia*, 2:31-7.	Investigation into killing of snakes by decapitation, welfare.
Warwick, C.	1990	Important ethological considerations of the study and maintenance of reptiles in captivity.	*Appl. Anim. Behav. Sci.*, 27:(4);363-6.	Maladaptation, welfare in approaches to research.
Warwick, C.	1990	Crocodilian slaughter methods, with special reference to spinal cord severance.	*Texas J. Sci.*, 42;(2);191-8.	Farm killing of alligators by spinal cord severance, welfare.
Warwick, C.	1990	Reptilian ethology in captivity: observations of some problems and an evaluation of their aetiology.	*Appl. Anim. Behav. Sci.*, 26:(1);1-13.	Adaptability, spatial requirements and restrictions, interaction with transparent boundaries, hyperactivity, hypoactivity, disposition-related voluntary hypothermia, aggression.
Cooper, J.E., Ewbank, R., Platt, C. & **Warwick, C**.	1987	Euthanasia of amphibians and reptiles.	*UFAW/WSPA,* 37pp.	Recommendations for physical and chemical killing of reptiles.

Appendix 2

Submitted publications