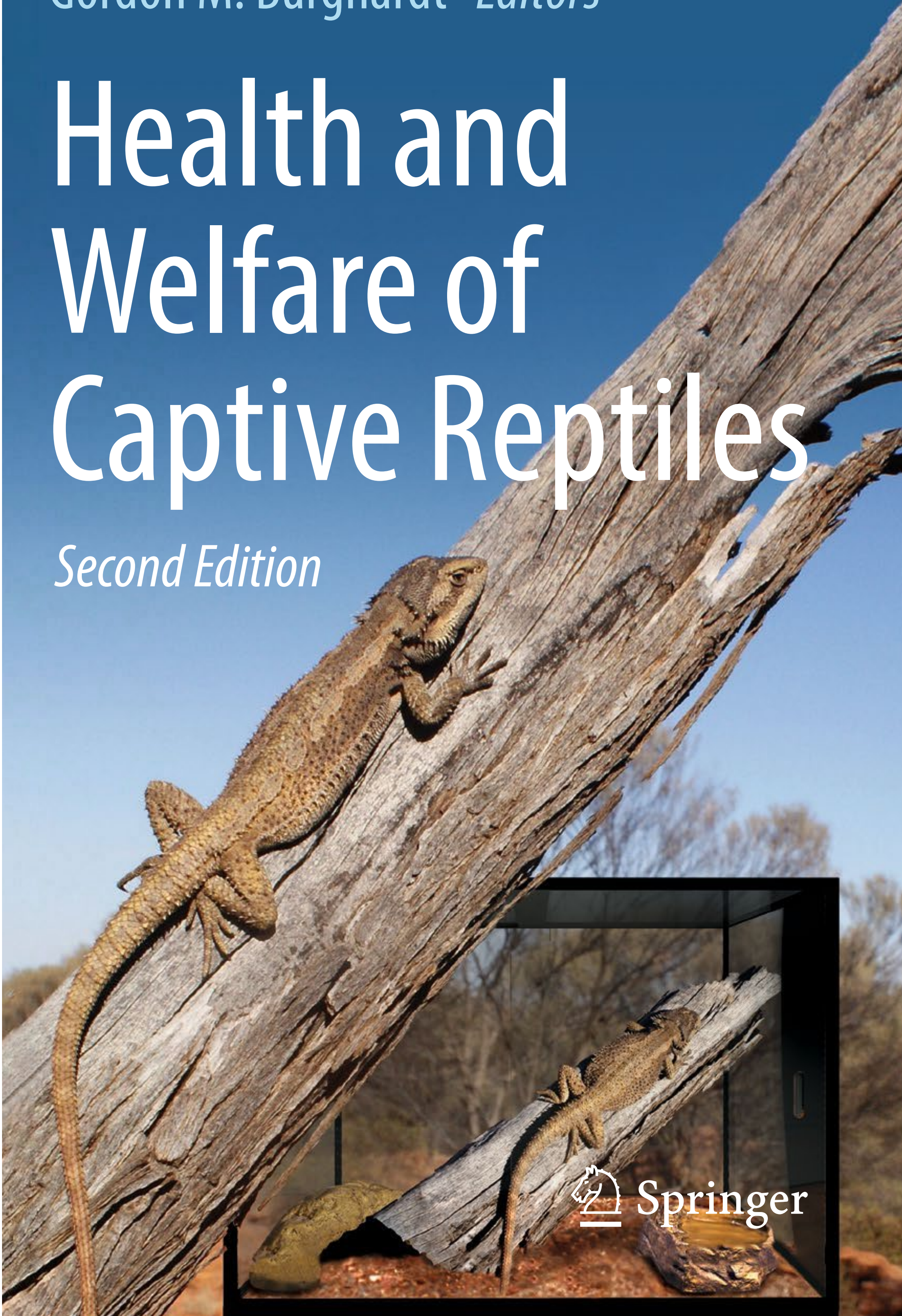
Clifford Warwick · Phillip C. Arena
Gordon M. Burghardt *Editors*

Health and Welfare of Captive Reptiles

Second Edition



Springer

Health and Welfare of Captive Reptiles

Clifford Warwick • Phillip C. Arena •
Gordon M. Burghardt
Editors

Health and Welfare of Captive Reptiles

Second Edition

Springer

Editors
Clifford Warwick
Emergent Disease Foundation
London, UK

Phillip C. Arena
College of Science, Health, Engineering and Education, Academic Operations, Environmental and Conservation Sciences
Murdoch University
Mandurah, WA, Australia

Gordon M. Burghardt
Departments of Psychology
and Ecology & Evolutionary Biology
University of Tennessee
Knoxville, TN, USA

ISBN 978-3-030-86011-0 ISBN 978-3-030-86012-7 (eBook)
https://doi.org/10.1007/978-3-030-86012-7

1st edition: © Springer Science+Business Media Dordrecht 1995
Originally published by Chapman & Hall in 1995
Prior edition to this work is ISBN 978-0-412-55080-5, "Health and Welfare of Captive Reptiles", edited by Clifford Warwick, Fredric L. Frye and James B. Murphy.

Cover image (original): Brett Bartek, University of South Florida
Design & adaptation: Phillip C. Arena, Gordon M. Burghardt, Clifford Warwick

This Springer imprint is published by the registered company Springer Nature Switzerland AG.
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Acknowledgements

The editors would like to express their deep appreciation to all authors for their contributions to this volume. All who have been involved in this project have so generously participated in the over-arching interests of reptile welfare, which is both gratifying and inspiring. A scientific book is defined not only by its content and authors but also by its reviewers. Accordingly, the editors also wish to convey their enduring gratitude to the following for their expertise, dedication, and guidance across the breadth of chapters and issues therein: Lydia Acaralp-Rehnberg, Stephanie Allard, Rocio Aguilar, Melissa Amarello, Kevin Arbuckle, Meredith J. Bashaw, George Bates, Dale DeNardo, Melanie Denomme, Bob Doneley, Matthew Evans, Marieke Gartner, Deon Gilbert, Steve Gorzula, Ray Huey, Tim Jessup, Robert Johnson, Michael Kreger, Angelo J. L. Lambiris, La'Toya V. Latney, Mathias Loertscher, Kevin Markwell, Georgia Mason, Robert T. Mason, Anne McBride, Meera Kumar Music, Ann-Elizabeth Nash, Emma Nicholas, Karen Overall, Jesús Rivas, Michael Salmon, Gordon Schuett, Kurt Schwenk, Sally Sherwen, Andrea M. Simmons, Marisa Spain, Levi Storks, Cliff Summers, Sasha J. Tetzlaff, Tim Tristan, Richard Vogt, Adrian Walton, Paul Weldon, Geoff While, Martin Whitehead, Alexandra Whittaker, Anna Wilkinson, and Alix Wilson. Scientific books, especially large and complex multi-author projects such as this, also require a dedicated publishing team, and with this in mind we thank in particular Annette Klaus, Bibhuti Bhusan Sharma, Lars Koerner, and all others involved at Springer, for their guidance and patience throughout. The editors are grateful to Dr Karen Mancera for reading and commenting on the complete final text. The editors also wish to express their gratitude to Michael Taber for his valuable assistance in the preparation of the species and genera index. The first edition of *Health and Welfare of Captive Reptiles* was, and remains, a historic and definitive milestone in the evolution of academic and applied scientific welfare, and we envisage that this new edition will continue to advance its messages long into the future. To all who are part of this journey, thank you!

Contents

Editors and Contributors

About the Editors

Clifford Warwick is an independent human medical scientist and reptile biologist. He holds several advanced professional qualifications specialising in reptile science, as well as a PhD in reptile welfare biology. He has produced approximately 150 peer-reviewed articles, book chapters, and books, mostly concerning the biology and welfare of reptiles, with a focus on anthropogenic impacts.

Phillip C. Arena is an awarded educator and functional morphologist specialising in reptile biology, health, and welfare. He has published material on the anaesthesia, anatomy, and physiology of reptiles and contributed to key investigations on the impact of farming and recreational practices on the lives of reptiles, including rattlesnakes, marine turtles, and crocodiles.

Gordon M. Burghardt is Alumni Distinguished Professor of Psychology and Ecology and Evolutionary Biology at the University of Tennessee. He has published widely on reptile behaviour, behavioural development and evolution, captive animal issues, animal play, and conceptual and historical aspects of animal ethology and comparative psychology.

Contributors

Phillip C. Arena College of Science, Health, Engineering and Education, Academic Operations, Environmental and Conservation Sciences, Murdoch University, Mandurah, WA, Australia

Lauren Augustine Saint Louis Zoo, Saint Louis, MO, USA
Smithsonian Institute National Zoological Park, Washington, DC, USA

Meredith J. Bashaw Life Sciences and Philosophy Building, Franklin and Marshall College, Lancaster, PA, USA

Judith Block Registrar Emerita, Zoo Registrars Association, Washington, DC, USA

Gordon M. Burghardt Departments of Psychology and Ecology & Evolutionary Biology, University of Tennessee, Knoxville, TN, USA

David L. Clark Department of Biology, Alma College, Alma, MI, USA

Jenna M. Crowe-Riddell Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA

J. Sean Doody University of South Florida, St. Petersburg, FL, USA

Enrique Font Ethology Lab, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Valencia, Spain

Fredric L. Frye Fund for Clinical Research, La Primavera Organic Farm, Cloverdale, CA, USA

Eric J. Gangloff Department of Zoology, Ohio Wesleyan University, Delaware, OH, USA

James C. Gillingham Department of Biology, Central Michigan University, Mt. Pleasant, MI, USA

Rachel Grant Department of Applied Science, London South Bank University, London, UK

Neil Greenberg Department of Ecology and Evolutionary Biology, The University of Tennessee, Knoxville, TN, USA

Barbara Ann Henry Cincinnati Zoo & Botanical Garden, Cincinnati, OH, USA

Tiffani Howell School of Psychology and Public Health, La Trobe University, Bendigo, VIC, Australia

Mike Jessop Veterinary Expert Services, Swansea, UK

Donna G. Layne-Colon Texas Biomedical Research Institute, San Antonio, TX, USA

Manuel Leal Division of Biological Sciences, University of Missouri, Columbia, MO, USA

Harvey B. Lillywhite Department of Biology, University of Florida, Gainesville, FL, USA

Karen F. Mancera Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Albert Martínez-Silvestre Catalonian Reptiles and Amphibians Rescue Centre, Barcelona, Spain

Michael Thomas Maslanka Department of Nutrition Science, Smithsonian National Zoological Park and Conservation Biology Institute, Washington, DC, USA

Robert W. Mendyk Department of Herpetology, Audubon Zoo, New Orleans, LA, USA
Department of Herpetology, Smithsonian National Zoological Park, Washington, DC, USA

Clive J. C. Phillips Curtin University Sustainable Policy (CUSP) Institute, Bentley, WA, Australia

Anthony Pilny Arizona Exotic Animal Hospital, Phoenix, AZ, USA

Catrina Steedman Emergent Disease Foundation, London, UK

Clifford Warwick Emergent Disease Foundation, London, UK

Martin Whitehead Chipping Norton Veterinary Hospital, Oxon, UK

Introduction

1

Clifford Warwick, Phillip C. Arena, and Gordon M. Burghardt

Abstract

Like the first edition of *Health and Welfare of Captive Reptiles*, this book ('*HWCR2')* invited all authors to bring the best science and novel thinking to their contributions, whilst thematically centralising reptile welfare. Arguably, the herpetological world still lags behind much of the stance of the original book, yet this second edition will continue to forge ahead and set the landscape for reptile welfare long into the future. *Health and Welfare of Captive Reptiles, 2nd edition* offers concepts, principles, and applied information that relates to the well-being of reptiles. Therefore, *HWCR2* is essentially a manual on health and welfare in a similar vein to volumes addressing the sciences of anatomy, behaviour, or psychology; thus, the book is about the biology of reptile welfare and meeting biological needs. In nature, animals conduct their lives and manage their own well-being. Whatever challenges may be faced in the natural world, animals have evolved to occupy this place. However, once an individual arrives in captivity, by whatever means, its life and well-being become our responsibility. In theory, the knowledge base within *HWCR2* ought to inform, inspire, and guide reptile caretakers to apply the latest findings and ideas for enhancing the welfare of the animals whose lives are substantially within their hands.

C. Warwick (✉)
Emergent Disease Foundation, London, UK

P. C. Arena
College of Science, Health, Engineering and Education, Academic Operations, Environmental and Conservation Sciences, Murdoch University, Mandurah, WA, Australia
e-mail: phil@ecoarena.com.au

G. M. Burghardt
Departments of Psychology and Ecology & Evolutionary Biology, University of Tennessee, Knoxville, TN, USA
e-mail: gburghar@utk.edu

C. Warwick et al. (eds.), *Health and Welfare of Captive Reptiles*,
https://doi.org/10.1007/978-3-030-86012-7_1

Keywords

Captivity · Nature · Welfare

1.1 Authors

The first edition of *Health and Welfare of Captive Reptiles* (*HWCR)* included authors who were not only biologists, veterinarians, and scientists within the reptile field, but also pioneers in the history of herpetology: a theme that we can again boast for this second edition—*HWCR2*. A tremendously heartening feature of both editions has been the generosity and enthusiasm of so many to bring the best science and novel thinking to their work. All authors were asked to thematically centralise reptile welfare within their contributions, with an obligation to align themselves as constant allies 'for reptile welfare'—above and beyond any other interest. Accordingly, all chapters follow the principle that wherever doubt or debate may have arisen concerning any welfare issue, reptiles were to receive the benefit of such doubt.

Across both editions, authors were invited to exercise their thinking on relevant issues that may advance reptile welfare. The thoughts and ideas founded in *HWCR* spawned global research and invaluable data, yet almost all of the concepts, principles, and research suggestions from the first edition remain current or still advanced. Whilst some original messages were intentionally speculative, various suggestions have inspired the navigational process of modern academic and applied reptile- (and other animal-) related sciences—including Springer's own momentous and current *Animal Welfare* series. Unsurprisingly, contributors for the new edition have again been asked to push the frontiers of our understanding towards reptile welfare; and where evidence does not yet underpin these frontiers, it will likely follow. Arguably, the herpetological world still lags behind much of the stance of the original book, yet this second edition will continue to forge ahead and set the landscape for reptile welfare long into the future.

Sadly, not all of our original compatriot authors are with us today—David Chiszar, Louis J. Guillette Jr., Hobart M. Smith, and Robert E. Gatten Jr. have passed away. Also, for others, life has gotten in the way of their availability to participate this time, in this book. However, to all of those, lost or amongst us, who were unable to take part in this new venture, their contributions remain a guiding influence throughout this entire edition as well as for the future of reptile biology and welfare by continuing to bring warmth to the 'cold-blooded'.

1.2 Peer Review and Quality Control

The quality control and developmental process for *HWCR2* is probably second to none. Contributions for this volume have undergone extensive and robust scientific peer review by the three primary editors, three external examiners, and Springer's own series editor and expert technical editing team. The fact that one of the world's leading and most established scientific publishers, Springer, has overseen *HWCR2's* production has been greatly welcomed, and will not be lost on the discerning reader.

1.3 Audience

Although this volume is primarily aimed at academic professionals, authors have adopted a user-friendly writing style where feasible to accommodate a broad readership. *Health and Welfare of Captive Reptiles, 2nd edition* offers concepts, principles, and applied information that relates to the well-being of reptiles. As such, it is fundamentally a biology book that can also inform captive reptile husbandry. Therefore, *HWCR2* is essentially a manual on health and welfare in a similar vein to volumes addressing the sciences of anatomy, behaviour, or psychology; thus, the book is about the biology of reptile welfare and meeting biological needs.

Advances in biology and improvements in animal husbandry can offer a better quality of life to individual animals under artificial conditions, but these advances should not be taken to serve as justifications for keeping reptiles in captivity. *Health and Welfare of Captive Reptiles, 2nd edition,* like its predecessor, is designed to improve the lifestyle and well-being of captive reptiles, but takes no position on whether reptiles should be kept in captivity; this is not its purpose. *Health and Welfare of Captive Reptiles (2nd ed.)* sets itself apart from the plethora of variable quality 'how to keep reptiles' type handbooks, many of which emerge from the stable of vested interest writers, who target profit and aspire to aid or proliferate convenience-led rather than evidence-based husbandry.

The complexity and often overlapping foci of the contributions inevitably influence the structuring and ordering of such diverse yet related chapters. For *HWCR2* we have adopted a structure that loosely follows the organisation of *animal* (e.g. nature, physiology, anatomy, stress, normal behaviour, cognition); *environment* (e.g. captivity, abnormal psychological and behavioural states, ontogenetic processes, deprivation and enrichment, noise and light disturbance); *management* (e.g. informed design and practice, spatial and thermal factors, nutrition, naturalistic versus unnaturalistic environments, thresholds for species suitability in captivity, record keeping); and *miscellaneous* (e.g. occupancy and post-occupancy evaluation, euthanasia, human–animal interactions, ethics).

All these, and other subjects, permeate or relate to every section of every chapter to provide an integrated and holistic text. However, whilst the book should be read as an entire resource, readers will find that individual chapters often cross-reference others, mainly to indicate where a particular continuum of information or theme exists and is most relevant.

1.4 Introducing Chapters

In the quarter of a century since *HWCR* was first published, herpetological and allied sciences have made exponential-like progress across many fields relevant to reptile well-being. As postulated in the original edition, with increased investigation and understanding of reptile biology comes greater appreciation of their true needs and the challenges required to meet them—biological revelations continue to outpace our ability to fulfil holistic husbandry. The inherent requirements of animals remain relatively constant, whereas husbandry approaches do not. Although scientific and technical improvements in care edge forward, the science of reptile welfare has long been beyond most ordinary folk who keep these animals captive, and this distance arguably is increasing. Thus, for all but a small number of reptiles in extraordinary and unique captive settings and within the custodianship of exceptional scientists, life in captivity is almost certainly one of deprivation by degrees.

Health and Welfare of Captive Reptiles championed the general priority of reptilian welfare as well as behavioural complexity, dietary subtlety, pain, stress, perception, psychology, cognition, sentience, neuroscience, sociality, and individualism, amongst other (then) 'esoteric' areas, at a time when little attention or regard was considered justified. Today, all these subjects are viewed in a new light and their illuminating effects will continue to breach the shadows that have for so long restrained welfare progress and maintained ignorance. Also, as hinted at in the first edition, and firmly emphasised in this revision, whether casually or systematically observing and assessing reptile behavioural, mental, or physical characteristics, it is important to remember that assumptions and tests alike need to focus on investigations that are biologically relevant to the species. In other words, to be meaningful and contextual, how we test animals must suit their evolved biologies. Were humans to be judged by many reptilian mental and physical abilities, we would actually be inferior. On these and related subjects *HWCR2* readers are, in particular, directed to the following chapters: *'Physiology and Functional Anatomy', 'Sensory Systems', 'Brains, Behaviour, and Cognition: Multiple Misconceptions', 'Biology of Stress', 'Normal Behaviour', and 'Social Behaviour as a Challenge for Welfare'.*

The front cover of the original edition depicted a natural lush swamp habitat in which discretely rested a basking turtle. To some, the relevance of that image to captive husbandry was as obscure as the turtle itself, yet the inference was intentional and the messages of this book again emphasise that what happens in nature should not stay in nature—the natural world must inform the artificial one. What was then an arguably provocative and less supported paradigm has today been almost normalised, although far from universally appreciated. Amongst the myriad of problems implicit to artificial conditions, one may simply be the absence of nature. Providing naturalistic environments to occupants that are imperceptible from the natural world is a major challenge, and rarely, if ever, achieved. On these and related subjects *HWCR2* readers are in particular directed to the following chapters: *'Psychological and Behavioural Principles and Problems', 'Controlled Deprivation and Enrichment', 'Effects of Ontogeny, Rearing Conditions, and Individual Differences on Behaviour: Welfare, Conservation, and Invasive Species Implications', 'Effects* *of Captivity-Imposed Noise and Light Disturbance on Welfare'*, and *'Naturalistic Versus Unnaturalistic Environments'*.

Much of both past and current reptile husbandry practices emerged from trial and error, or untried and untested, handed-down information about reptile biology and care. Which techniques worked and those that did not, often evaded objective scientific scrutiny, with commonly catastrophic welfare consequences. This haphazard approach is now known as 'folklore husbandry'. Although the more proactive herpetologist (and their institution) guards and educates against such laxity, the normalisation of many long-standing bad practices remains pervasive in the general hobby and private pet sectors, and also commercial production as with turtles and crocodylians. Concomitant with unreliable husbandry are issues of informed decision-making regarding species suitability for captivity, and whether there are appropriate resources and caretaker expertise to provide comprehensive care. Such questions are unavoidable queries for anyone practising responsible custodianship of another species. On these and related subjects *HWCR2* readers are in particular directed to the following chapters: *'Ethologically Informed Design and DEEP Ethology in Theory and Practice', 'Spatial and Thermal Factors', 'Nutritional Considerations', 'Evidential Thresholds for Species Suitability in Captivity', 'Record Keeping as an Aid to Captive Care', and 'Arbitrary Husbandry Practices and Misconceptions'*.

Inevitably, in a project of this size, topics arise that may appear singular or slightly disjointed from each other; they may also be inspired creative suggestions that warrant examination in their own right and further complement other sections. Such suggestions, at the very least, emphasise that—in terms of the welfare of captive reptiles—there is still so much to learn. On these and related subjects *HWCR2* readers are in particular directed to the following chapter: *'Miscellaneous Factors'*.

1.5 Conclusion

Building on the success and influence of *HWCR* as a definitive scientific reference volume addressing reptile welfare, the concepts and principles for *HWCR2* are unchanged from its origins, marking the enduring quality of its authors' many messages. Whether one adopts the descriptive term of welfare, well-being, or wellness in their goals for animals, achievement of such a positive state may signal the coming together of most or all of the 'right' things.

In nature, animals conduct their lives and manage their own well-being. Whatever challenges may be faced in the natural world, animals have evolved to occupy this place. However, once an individual arrives in captivity, by whatever means, its life and well-being become our responsibility. In theory, the knowledge base within *HWCR2* ought to inform, inspire, and guide reptile caretakers to apply the latest findings and ideas for enhancing the welfare of the animals whose lives are substantially within their hands.

Who amongst the present alumni of authors will be available to oversee further editions of this book cannot be presumed. However, any future revision that does not hold reptile welfare above the needs or deeds of those who may keep captive these astonishing creatures will not speak in legacy of the *Health and Welfare of Captive Reptiles*.

Physiology and Functional Anatomy

2

Harvey B. Lillywhite

***In memoriam: This chapter is dedicated to the career and memory of Robert E. Gatten, who co-authored the equivalent chapter in the first edition of this book. Bob was a special friend and colleague, and an outstanding and dedicated individual. He passed away on 23 February 2018 in Greensboro, North Carolina.**

Abstract

Physiology and morphology are interactive determinants of behaviours that are especially sensitive to environmental influences and are important to the health and welfare of captive reptiles. Although many reptiles appear to be easily managed in captive circumstances, others have special requirements to remain in health and vigour. This chapter focuses on understanding the functional attributes of reptiles as they relate to behaviour and the health of captive individuals. Comparative studies of reptilian physiology and ecology illustrate how guidelines for optimal care will vary not only among higher order taxa but also between closely related species. Ambient temperature, light, and humidity strongly influence the health of reptiles. Important aspects of physiology include ectothermy, generally low energy requirements, diet, periodic inactivity, reproductive mode and cycling, health of skin, adequate hydration, cardiovascular and respiratory health, and infectious disease. Conditions of poor husbandry may include obesity, inappropriate temperature, humidity, and lighting conditions, lack of access to seclusion, and suppression of the immune system that can interact synergistically with other forms of stress related to captivity. Further research is needed to understand stressful states and how they can be ameliorated

H. B. Lillywhite (✉)
Department of Biology, University of Florida, Gainesville, FL, USA
e-mail: hblill@ufl.edu

C. Warwick et al. (eds.), *Health and Welfare of Captive Reptiles*,
https://doi.org/10.1007/978-3-030-86012-7_2

in captive animals. In view of the diversity and complex evolutionary histories of reptiles, variation among species must be appreciated in order for these animals to live, thrive, and reproduce in captive settings.

Keywords

Ectothermy · Energy · Skin · Osmoregulation · Digestion · Respiration · Blood Circulation · Stress

2.1 Introduction

Consideration of physiology and morphology is important to the health and welfare of captive reptiles, particularly in view of their diversity and complex evolutionary histories. Evolutionary history endows reptiles with characteristics that can be very different from those of domesticated or laboratory mammals. Although many reptiles seem to be successfully managed in captive circumstances, others will have special requirements and can diminish in health or vigour even whilst appropriate care appears to be provided. Such problems of health and well-being are often related to some aspect of physiology that is either inadvertently neglected, or more usually, not well understood.

Structure-function relationships are essential to understanding the normal behaviours that are characteristic of a species. Physiology is an important underpinning of behaviour, and the behaviours of reptiles are especially sensitive to environmental influences on physiology. Current technologies enable investigators to map patterns of nerve activity onto behaviour and reveal which neurons constitute circuits for specific behaviours (O'Leary and Marder 2014). These same neurons can be genetically tagged. Hence, the interrelationships of structure, function, and behaviour can be understood at very sophisticated levels, and such insights enable understanding of both differences and similarities between reptiles and, say, mammals. However, in the context of this chapter, what is more important than the sophistication of current ethological studies is the understanding of functional attributes of reptiles as they relate to the normal behaviours and health of captive individuals.

2.2 Body Temperature, Energetics, and Ectothermy

Non-avian reptiles are characteristically regarded as ectothermic because they are highly dependent on external sources of heat to determine body temperature, in contrast to endothermic birds and mammals that regulate body temperature largely by means of internal metabolic heat production. There is ongoing debate regarding whether extinct reptiles, and especially dinosaurs, were endothermic (Dunham et al. 1989; Padian et al. 2001; Seymour 2013; Grady et al. 2014). Some of the stronger evidence for endothermy of dinosaurs comes from data for rapid growth rates of bone (Erickson et al. 2001; Padian et al. 2001; Lee and Werning 2008). However, when the effects of size and temperature are considered, the metabolic rates of dinosaurs were shown to be intermediate to those of endotherms and ectotherms, suggesting that the controversial dichotomy of endothermic versus ectothermic is overly simplistic (Grady et al. 2014). Putting the controversy aside, smaller reptiles are generally ectothermic and are not capable of sustaining a body temperature above ambient by means of endogenous heat production. However, there are a few notable exceptions, including swimming sea turtles, incubating pythons, digesting rattlesnakes, yolk metabolism of hatchling snakes, and seasonal reproductive endothermy of tegu lizards (Tu et al. 2002; Lillywhite 2014; Pough et al. 2016; Tattersall et al. 2016). These examples are of much scientific interest, and they demonstrate the capacity for limited, facultative endothermy and physiological control of muscular heat production (in several species of pythons during incubation). However, in general, the majority of captive reptiles depend on external sources of heat to determine body temperature, and transient variations of metabolic heat production (independent of external environment) are usually of little significance in captive settings.

The term 'cold-blooded' is not appropriate for most reptiles, inasmuch as body temperatures can be considerably higher than surrounding ambient air or other features of the environment. Many species behaviourally regulate their body temperature during deliberate basking behaviour, characteristically elevating the core temperature significantly and near the upper part of the range of tolerable temperatures. The desert iguana (*Dipsosaurus dorsalis*), for example, prefers body temperatures around 38–41 °C, which exceeds the core temperature of many so-called 'warm-bodied' mammals (see Pough and Gans 1982 for terminology).

The body temperature of ectothermic reptiles is dependent on the net balance of heat exchanges between the animal and its environment, and this condition can be defined by an equation for energy balance that, in simplest form, states that gains of heat energy equal the losses of heat energy. A more complex form of this statement, expressed as an equation, includes a term for each of the major routes of heat gains and losses for an animal (Fig. 2.1). Such biophysical modelling of reptiles is beyond the scope of this chapter, but the reader should appreciate that considerations of the complexity of heat exchanges have improved our understanding of how reptiles regulate their body temperature, and, coupled with information about the environment, has been used to interpret or predict where various reptiles can live and what behavioural options are required for survival in extreme or changing environments. A sampling of examples can be found in Porter et al. (1973), Tracy (1982), O'Connor and Spotila (1992), Kearney and Porter (2009), and Fei et al. (2012). The design of enclosures for captive reptiles makes use of the same principles with respect to placement of heat lamps or other devices that modify the temperatures that are available to a captive animal (see Arena and Warwick 2023).

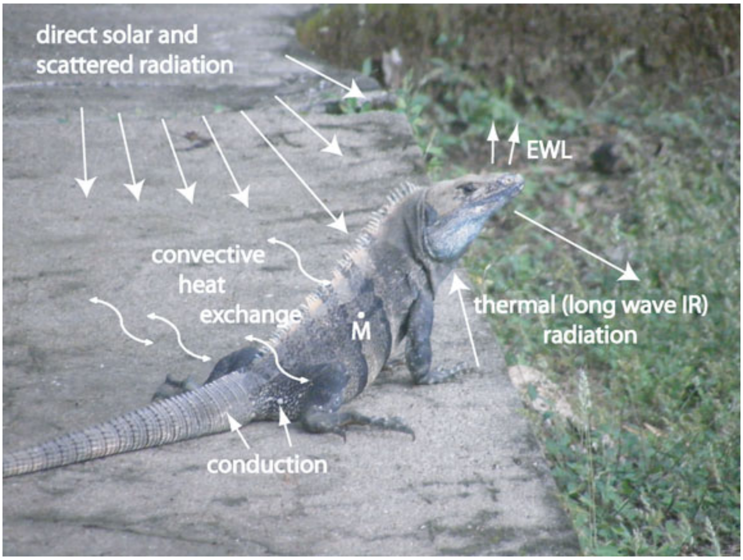


Fig. 2.1 Pathways of heat exchange featuring an iguana on a roadside in Guanacaste, Costa Rica. The hypothetical body temperature of this lizard is determined principally by direct solar radiation that is absorbed by the dorsal skin surfaces and conduction of heat from the heated surface of the road that is assumed to be warmer than the body of the animal. Convective heat transfer to or from the lizard will depend on the relative temperatures of the body and the surrounding air. Metabolic heat production ($\dot{M}$) and thermal radiation contribute relatively modest amounts of heat to determine the body temperature. Thermal radiation is in bidirectional flux with respect to the lizard which is assumed to be cooler than the road surface but warmer than the grass at the edge of the road. Evaporation of water (EWL) from the respiratory passages removes heat from the nasopulmonary surfaces. Photograph by the author

2.2.1 Temperature and Energy Expenditure

The significance of ectothermy in context of coupled biological advantages has been discussed by Pough (1980). Two important consequences of ectothermy are very relevant to the husbandry of reptiles. First, the rate of energy expenditure derived from food or fat stores is comparatively low because metabolic heat is not required to maintain body temperature. Therefore, to maintain a steady state with respect to energy balance, relatively few calories from food are required as input to match the low rate of energy use. The requirement for food is further lowered by behaviours that might include relatively long periods of inactivity and nocturnal seclusion. Thus, night-time cooling and long periods of inactivity contribute to a low rate of energy expenditure of many reptiles, roughly 2–5% of that of a bird or rodent of equivalent size (Nagy 1983). Energy requirements are minimal for fasting and inactive reptiles at low body temperature, and they increase to substantially higher levels in animals that are active at elevated body temperature. As an example, a red-eared turtle (*Trachemys scripta*) has a rate of aerobic metabolism during vigorous movement at 40 °C that is 270 times as great as during rest at 10 °C (Gatten 1974). The coupling of food requirements to both temperature and activity varies with species and the circumstances of captivity. One should be vigilant of animals that might experience weight loss due to excessive energy expenditure related to 'escape' or exploratory activity whilst in new or inadequate enclosures, conspecific aggression or related stress, and disease or parasitism (see Warwick 2023). The reproductive status of females should also be taken into account and monitored carefully.

Much research has been conducted in relation to quantifying the metabolic energy expenditure of both ectothermic reptiles and endothermic avian reptiles and mammals (McNab 2002). Perhaps the broadest generalisation to emerge is that body size and temperature account for most of the known variation in the rates of energy expenditure of organisms. Rates of energy expenditure are typically measured in the laboratory whilst animals are at rest, and these rates generally underestimate the rates of metabolic energy expenditure when animals are free-ranging in the field. Thus, numerous data are now available for field metabolic rates measured in free-ranging animals using dual-isotope techniques. This is done by administering a dose of doubly labelled water (deuterium and oxygen-18), then measuring the rates of elimination of the heavy isotopes in the animal over time. Conventionally, this involves regular sampling of heavy isotope concentrations in body water by sampling blood, urine, or saliva (see Speakman 1997). Studies of field metabolic rates have shown that in some cases, the energy requirements of animals in nature (e.g. moving, digesting) are roughly threefold greater than those measured under standard conditions in the laboratory, and that rates of energy expenditure can be roughly 25- to 40-fold greater in mammals and birds than in a lizard (Bennett and Nagy 1977). These differences reflect the greater activity of the endothermic mammals and birds and the lower nocturnal body temperatures of the lizard. More generally, variation in field metabolic rates of 229 species of terrestrial vertebrates studied by Nagy (2005) is largely attributable to body size, and much of the remaining variation is attributable to differences in physiology related to temperature with rates of energy expenditure in endothermic mammals and birds being about 12 and 20 times greater, respectively, than that of ectothermic reptiles of similar size (Fig. 2.2).

Growth and reproduction of course also influence the energetic state of reptiles. Both of these factors may also be confounded by changes in body temperature in various states and various species (McNab 2002). Reproductive costs are different between oviparous and viviparous species. As an example, in the bimodal lizard (*Zootoca vivipara*), oxygen consumption of females increases progressively during the course of reproduction, peaking just prior to giving birth when it was 46% (oviparous form) and 82% (viviparous form) higher than it was at the pre-reproductive stage (Foucart et al. 2014). The total increase in post-ovulation oxygen consumption was threefold higher in the viviparous than oviparous females, whereas the pre-reproductive oxygen consumption of both reproductive modes was similar. Substantial energy costs are likely incurred by prolonged embryonic retention in viviparous species. However, reproduction in gravid females may incur an energetic cost that is greater than what is required to meet the energetic demands of developing embryos (Beuchat and Vleck 1990). When the rate of metabolism in

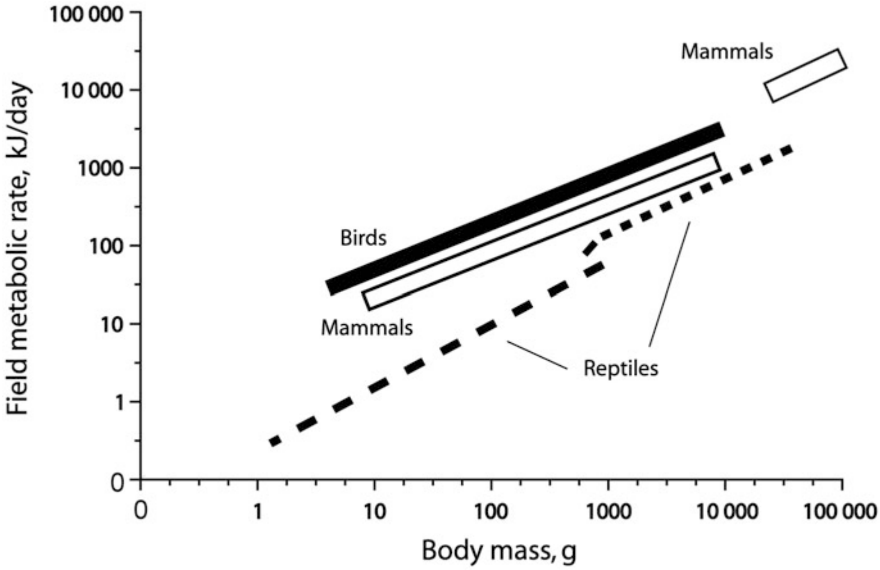


Fig. 2.2 Field metabolic rates shown as a function of body mass in 229 species of non-avian reptiles, birds, and mammals. The bars represent the central densities of collective data points for the various taxa, estimated by eye. The relationships are adopted from data in Nagy (2005)

female lizards (*Sceloporus undulatus*) was adjusted for that of embryos, the energy expenditure of females when gravid was elevated by 122% compared with that when non-gravid (Angilletta and Sears 2000). Energy expenditure of reptiles also can be correlated with growth rates, which generally are 10- to 30-times higher in mammals and birds (McNab 2002). Growth rates may vary seasonally and are increased with the selection of higher body temperatures, which can be dictated by the amount of food energy available. Maximal growth rates of ectotherms may be associated with preferred body temperatures that are maintained in the laboratory or the field (Lillywhite et al. 1973).

With respect to husbandry, persons unfamiliar with reptiles may not fully appreciate the comparatively low rates of feeding (either frequency or quantity) required to sustain individuals in a healthy state. Daily or frequent feeding is often not necessary, and voluntary periods of fasting are not harmful, especially for intermittent feeders such as snakes. In fact, many reptiles such as snakes and crocodylians that are kept for public display are abnormally obese compared with conspecific individuals that are living in nature. Our current understanding of the health risks of obesity in reptiles is minimal, but optimal care most likely involves balancing energy availability and energy expenditure. Allowing animals to fatten excessively represents poor husbandry. The low requirement of energy by reptiles is often misunderstood or not appreciated. The amount of food that is fed or offered to captive reptiles should be based on direct observations of the condition of animals and at least a basic understanding of seasonal behaviour and dietary requirement of each species rather than a uniform protocol that is intended for application to all species. For further review of the energetics and feeding of ectotherms, see McNab (2002), McCue (2012), and Andrade et al. (2016). There is also veterinary literature on topics potentially related to obesity; examples include hepatic lipidosis (Divers and Cooper 2000; Gumpenberg et al. 2011), cardiovascular disease (Schmidt and Reavill 2010; Stephens and Rosenwax 2018), and intestinal obstruction (Corbit et al. 2014).

2.2.2 Regulation of Body Temperature

The second important consequence of ectothermy is the variation of body temperature that is possible (or obligatory) in relation to the physical surroundings of an animal. However, reptiles are not strictly poikilothermic, and most are capable of impressively precise thermoregulation by behaviour (DeWitt 1967; Huey 1982; Hertz 1992; Goller et al. 2014). Nonetheless, a prolonged constancy of temperature for periods of weeks or months is not a physiological requirement in most cases and, in fact, can be deleterious to the health of many species. Variability of body temperature has importance with respect to species variation (phylogeny), seasonal acclimatisation, feeding and nutrition, activity, reproduction and physiological state, including immunity and disease (Goessling et al. 2017).

'Regulation' of body temperature implies that the activity of an animal maintains a particular level or narrow range of temperature relative to the variation of temperature in the surrounding environment. Such a feature of homeostasis requires an active neuronal system in which sensory input from central and peripheral thermoreceptors is compared with single or dual 'set points' (Heath 1970; Firth and Turner 1982). Deviations of body temperature from such set points are 'corrected' (controlled) principally by behaviour in most species of reptiles. In context of the controlling system, 'body temperature' might be represented by the brain, core, or peripheral tissue temperatures, or some combination of these. However, such considerations are beyond our focus here. For many purposes, 'body temperature' can be considered as the temperature of the central 'core' of body tissue, including the central nervous system (brain and spinal cord). Although heterogeneity and gradients of temperature may exist between different body parts, it is the 'core' temperature that is principally defended against undue variation. Regional differences of temperature are greater in larger animals and may be attributed to physiology, physical differences between different parts of the body, or behavioural mechanisms (Peterson et al. 1993). For purposes of husbandry, measurement of body temperature at a single location (for example, cloaca or mouth; trunk or head if utilising an infrared device) usually suffices for evaluation of thermal behaviour and requirements.

Thermoregulatory behaviours commonly employed by reptiles include shuttling movements between a heat source (such as sunlight or warm substrate) and a heat sink (such as shade, water, or burrow), as well as precise adjustments of body volume, shape, orientation, and posture. Postural adjustments can be subtle and are capable of providing remarkably precise control over body temperature (DeWitt 1967). All thermoregulatory behaviours require some heterogeneity of environment in terms of the physical factors affecting heat exchange (Tracy 1982). Indeed, both mean environmental temperatures and spatial heterogeneity potentially influence thermoregulation, movement, and energetics of reptiles (Sears and Angilletta 2015).

Physiological responses that produce some control over body temperature include metabolic heat production in muscle tissues of a few species, colour change in squamates (especially lizards), circulatory adjustments, and ventilatory changes to increase evaporative water loss from mucous membranes (Bartholomew 1982). Some reptiles may respond to higher temperatures by gaping or panting. Such responses are associated with heat stress, and captive animals should not be kept in conditions where they are exposed to high temperatures without the possibility of behavioural avoidance. On the other hand, at lower temperatures below the regulated range, reptiles become inactive or torpid and digestion ceases (Stevenson et al. 1985; Ultsch 1989). If animals are provided with a meal at lower temperatures and subsequently denied access to higher temperatures requisite for digestion, the ingested, potentially incompletely digested food can putrefy and kill the animal, although characteristically it is regurgitated before this can happen.

Conscientious care of reptiles requires knowledge of a species' thermal requirements, including mean selected (= 'preferred') or activity temperatures (Pough and Gans 1982), thermoregulatory behaviours, and characteristics of the physical environment normally utilised by a species. Thus, many temperate diurnal species may need a radiant heat source, whereas nocturnally-active species may avoid a photothermal resource and prefer to exploit a thermally variable substrate or hiding area. However, in most cases, a daily thermal cycle or behavioural access to thermal variation is desirable. The availability of infrared heat lamps and heating tapes now makes it feasible to arrange basic and inexpensive thermal gradients for reptiles held in enclosures. An alternative to thermal gradients is a thermal mosaic in which shelter devices or other elements of the enclosure provide an array of discrete temperatures (Gibson et al. 1989). In any case, heat availability can be either coupled to, or independent from, light cycles.

2.2.3 Variation of Body Temperature

Many reptiles experience variation of body temperature during a season and even during a single day. Tropical or aquatic species may experience comparatively little temperature variation and can be sensitive to temperature changes readily tolerated by temperate, terrestrial, and amphibious species (Inger 1959; Ruibal 1961; Hertz 1992). Indeed, non-basking species constitute a major component of the diversity of lizards in the neotropics (Huey et al. 2009). The marine file snake (*Acrochordus granulatus*), for example, thrives at water temperatures near 30 °C, but does not tolerate prolonged exposure to temperatures below about 25 °C (Lillywhite 1996). Tuataras (*Sphenodon punctatus*) are active at body temperatures well below those of most other reptiles and have a temperature for peak aerobic activity much lower than that of turtles, lizards, and snakes (see Avery 1982, for review). On the other hand, some terrestrial species inhabiting the tropics actually experience and may require greater microclimatic variation of temperature than might be presumed solely from macrogeographic considerations (Hertz 1992).

Many factors determine or modify selected body temperatures; the need for a particular temperature can change with time and is dependent on the physiological state of an animal. Important parameters affecting thermoregulation include feeding or digestive state, lean mass or body condition, reproductive status, acclimation, disease, parasitism, trauma, dehydration, hypoxia, acid-base status, ecdysis, and seasonal rhythms. The magnitude of change in thermal behaviour as a result of such factors can be substantial. Snakes, for example, increase body temperature voluntarily from a few to more than 8 °C following feeding (Lutterschmidt and Reinert 1990). In some cases, the selected body temperature may not change, but factors such as feeding or reproductive state can influence the amount of time an animal spends at the higher temperature. Body temperature can also modify the pattern of postprandial increase in metabolic rate (Crocker-Buta and Secor 2014), and the converse is probably true. Such patterns of behaviour should be part of considerations in the development of schemes for improving the care of reptiles. Further, because of the numerous phylogenetic as well as physiological parameters producing variation of body temperature, and the paucity of relevant information for many species, thermal regimens represent one area where oversight or management authorities should not attempt to formulate rigidly specific requirements intended for broad or universal application.

Data from both laboratory-housed and free-ranging reptiles, as well as theoretical models, suggest that shifts in thermal preferences have physiological and ecological importance (reviews in Huey 1982; Lillywhite 1987a, 2013; Peterson et al. 1993; Angilletta 2009). However, further investigations are required to establish the nature and magnitude of harmful consequences should captive reptiles be denied access to appropriate thermal variation. Clearly, the inability to cool below activity temperatures for prolonged periods can affect appetite and reproduction as well as produce deleterious physiological changes (Licht 1965). Inappropriate thermal exposure can suppress the immune systems of reptiles and can operate synergistically with other forms of stress that are imposed by captivity (Regal 1980; Lance 1992; DeNardo 2006; Zimmerman et al. 2010; Zimmerman 2016).

Bacterial infections can induce reptiles to select a body temperature that is several degrees above normal levels, termed 'behavioural fever' (Kluger et al. 1975). This phenomenon has been reported in a wide range of ectothermic vertebrates, including many reptiles (Hutchison and Dupre 1992; Rakus et al. 2017). Studies of lizards have shown that the elevated body temperature, acting in concert with reduced levels of blood iron, enhances survival of animals infected with potentially lethal pathogens (Kluger 1979) (Fig. 2.3). Thus, in circumstances where reptiles are provided with thermoregulatory options, prolonged basking behaviour and the associated elevated body temperature presumably have adaptive value and, among other things, may be an indicator of infection.

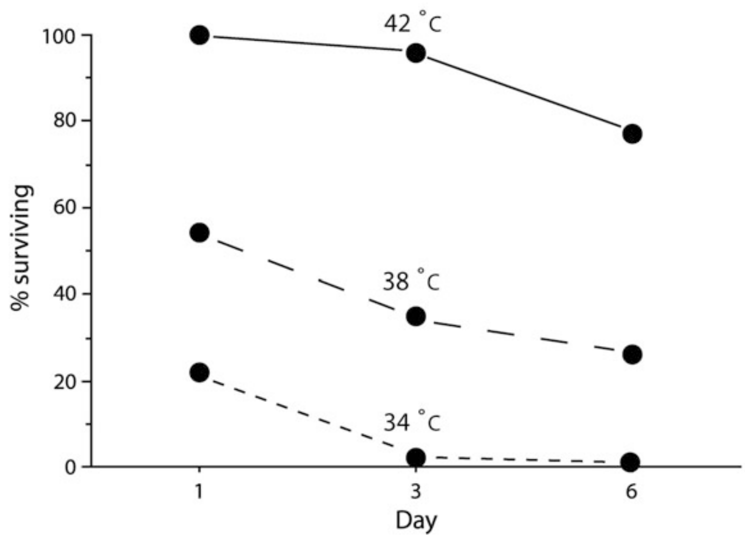


Fig. 2.3 Percentage survival of desert iguanas, *Dipsosaurus dorsalis*, injected with bacteria, *Aeromonas hydrophila*, and maintained at temperatures of 34 to 42 °C. The number of lizards in each group is 12 at 34 °C, 36 at 38 °C, and 24 at 42 °C. Adopted from data published in Kluger et al. (1975)

2.2.4 Functional Significance of Body Temperature Variation

Variation of body temperature has important functional consequences. Changes of body temperature affect biological processes and thus are important to growth, reproduction, and general health.

The thermal dependencies of biological processes are well known and have been quantified in a number of reptilian species (Huey 1982; Hochachka and Somero 2002; Angilletta 2009). In the context of husbandry, it is important to consider whole-animal functions rather than those at the cellular or molecular level. Typically, processes such as digestive rate, growth, speed of locomotion, capture of prey, and frequency of heart beat exhibit a linear or exponential increase over a broad range of temperatures, peak at one temperature or a narrow range of temperatures (plateau), and then decline, often precipitously, at higher temperatures (Fig. 2.4). Such thermal dependency curves are subject to changes in shape and position owing to thermal acclimation or acclimatisation. Therefore, the conditions in which reptiles are maintained in captivity significantly affect their metabolic functions and behavioural performance. Learning abilities of lizards are also affected significantly by temperature (Brattstrom 1978), and gestation time as well as the condition of developing or newborn offspring are influenced by gestation temperature and its variation (Peterson et al. 1993).

Temperature is very important in context of its significance to reproduction (Krohmer and Lutterschmidt 2011). Consequently, persons who keep various

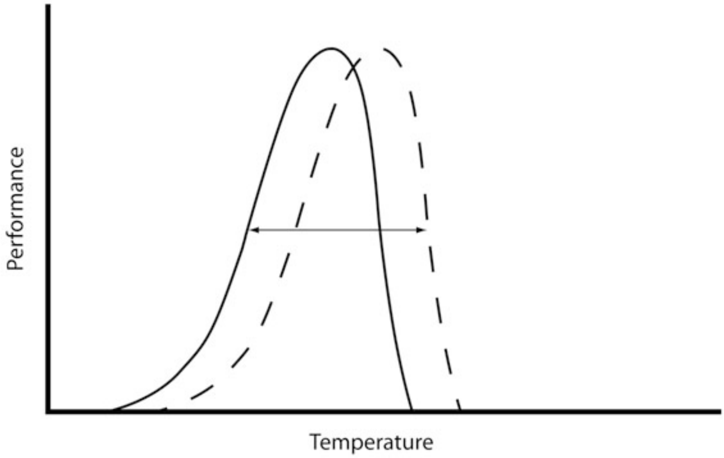


Fig. 2.4 Hypothetical 'performance curve' depicting how a rate variable (such as running speed, digestion) changes with temperature. The shift in the curve illustrates hypothetical changes that might be attributable to acclimation. The shift in performance could occur in either direction depending on the acclimation temperature; the horizontal dashed line represents the total change or range of possible performance breadth attributable to 'phenotypic plasticity.' Drawing by Rachel Keeffe

reptiles with intentions of breeding them need to be aware of thermal requirements that are compatible with reproductive cycles, including production of gametes, courtship and mating, birth or ovulation, and post-reproductive maintenance. Regimens of temperature requirements before and during reproduction can vary among species, and people who breed reptiles learn what regimens are best for a given species based on successful breeding in captivity. Such details and considerations of variation by taxa are beyond the scope of this chapter, but some publications are available to persons seeking recommendations for given species (e.g. Whittier et al. 1987; Schwarzkopf and Shine 1991; Lance 2003; Barker and Barker 2006; Krohmer and Lutterschmidt 2011; Shine 2012). There is an abundance of manuals and books that cover the breeding of the most popular pet reptiles. One of the better series is the *Proceedings of the International Herpetological Symposium*, which started in 1976 and includes many articles on captive breeding and husbandry of many reptiles (see: https://www.internationalherpetologicalsymposium.com/proceedings). It has proven to be relatively easy to breed many species under conditions that are not natural for the species (E.R. Jacobson, pers. com.). Those kept outdoors in areas where they are found probably do the best. Nutrition has improved dramatically, and better artificial lights for those requiring UVB have contributed to this success (see Maslanka et al. 2023).

2.3 Light and Photoreception

Both qualitative and quantitative characteristics of light have important consequences for the physiology and health of captive reptiles (Baines et al. 2016). The eyes are the principal receptors for light, whereas the pineal complex and possibly skin have secondary importance (Zimmerman and Heatwole 1990; Krohmer and Lutterschmidt 2011; Crowe-Riddell et al. 2019). The pineal organ is a neuroendocrine transducer of changes in photoperiod, and it has a functional role in many aspects of reptilian biology (Tosini 1997). Circadian oscillators may also be part of the pineal complex and are thought to be involved in the circadian organisation related to reproduction and other aspects of biology. Many functions attributable to the pineal complex are mediated by the hormone melatonin, and exogenous administration of melatonin may affect a reptile's physiology and behaviour (Tosini 1997; Krohmer and Lutterschmidt 2011).

Light reception interacts with physiology largely through centres of integration within the central nervous system (e.g. Butler 1978; Goris 2011). The periodicity of light reception is an important variable to control for captive reptiles, especially where breeding programmes are involved. Photoperiod can be a critical factor influencing reproductive cycles, although temperature is generally more important (Licht 1972; Jones 1978; Krohmer and Lutterschmidt 2011). The influence of photoperiod and its interaction with temperature or other seasonal phenomena on reproduction is known for relatively few reptilian species. Annual cycles of day length may affect appetite and metabolism, in addition to reproductive cycles.

The effects of variation in the intensity or spectral composition of light are poorly understood. Some reptiles require ultraviolet light for mineral metabolism and normal behaviour (Moehn 1974; Regal 1980; Townsend and Cole 1985; Adkins et al. 2003). Like birds and mammals, some species of reptile require UV light for cutaneous synthesis of previtamin D_3 and the maintenance of levels of the active vitamin in the blood (Pough 1991; Holick et al. 1995). Indeed, there is evidence that some lizards might adjust basking and UV exposure in relation to requirements for vitamin D_3 (Ferguson et al. 2003). On the other hand, some reptiles have been raised or maintained successfully, sometimes for multiple generations, without UV light, but with dietary supplementation of vitamin D_3 (Gehrmann et al. 1991; Pough 1991). Some reptiles may have multiple types of previtamin D_3 in their skin (Holick 1989). Neither the biochemistry of vitamin D synthesis nor the spectral qualities of UV light involved in the process are well studied in reptiles.

There is relatively little information concerning the range of irradiance that is appropriate for a given species of reptile. Ferguson et al. (2010) quantified the UV exposure of 15 species of reptiles in the field and suggested that knowledge of basking behaviour and daytime exposure to light can provide a reasonable estimate of likely UV exposure experienced or required for a species. Based on this information, species can be grouped into four zones (termed 'Ferguson zones') according to thermoregulatory behaviour and preferences for microhabitats, and each such zone can be used potentially for guidelines for UVB based on the quantitative measurements reported from the field work. The Ferguson zones extend from crepuscular or shade-dwelling to basking in the midday sun. Further discussion of such irradiance criteria can be found in Ferguson et al. (2010, 2014), Carmel and Johnson (2014), and Baines et al. (2016).

Information about the spectral properties of commercially available light bulbs has been discussed by Gehrmann (1987), Pough (1991), Baines et al. (2016) and others. The reader is referred to these sources for suggestions regarding the use of specific bulbs for captive animals. Species of reptiles differ substantially in their requirement for, and sensitivity to, UV exposure, so a conservative approach to the use of bulbs with intense UV emission is advised. Open-habitat species have protective melanin deposits in their skin and peritoneum which limit UV light penetration, whereas species from forests may be more sensitive to UV exposure (Porter 1967). Middle wavelength UV light (bulbs designated UVB) can be injurious to the eyes of animals and their caretakers, so broad-spectrum bulbs may be advisable for the initial husbandry of species with unknown UV requirements. Care should always be taken regarding not only the duration of exposure but also the placement of lamps and irradiance intensity at varying distances from the lamps. To ensure adequate UV irradiance, a regular schedule for changing bulbs is necessary (Townsend and Cole 1985; Baines et al. 2016).

2.4 Water Exchange and Humidity

Adequate availability of water and microclimatic humidity are two of the more fundamentally important requirements of captive reptiles. Contrary to the misconception of some, reptiles (including desert species) are not waterproof, and their small body size can promote rapid dehydration in the absence of adequate environmental humidity. In natural environments, many smaller reptiles spend much time in burrows, beneath rocks or leaf litter, or secluded in other refugia where humidity is higher and air convection lower than might be suggested by the casual perceptions of climate by humans. These considerations led Pough (1991) to recommend that ambient relative humidity be maintained at levels above 70% for nearly all species of reptile. Some species, such as chamaeleons, require very humid conditions in addition to periodic misting or access to water for soaking. Fossorial species from mesic habitats (e.g. Florida worm lizard, *Rhineura floridana*) will desiccate rapidly if their ambient moisture in soil or sand is inadequate. On the other hand, too frequent soaking or excess humidity causes skin blemishes or lesions (Hatt 2010), even in species that are amphibious (for example, *Thamnophis* or *Nerodia* spp.). Most reptiles require access to free water, but it may be advisable in some circumstances to remove water bowls from cages occasionally, so that continuous soaking is prevented.

2.4.1 Water Exchange

Water balance compatible with normal body function is achieved through equality of input and output (Fig. 2.5). Reptiles gain water from food—both preformed water and metabolic water produced from the oxidative metabolism of assimilated products from digestion—and drinking, as well as condensation in nasal passages and absorption across the skin. Lesser amounts of water can be acquired by absorption across buccal or cloacal membranes in some circumstances involving aquatic species. Drinking is typically voluntary, but some water can also be taken in as a minor consequence of ingestion of food in marine and aquatic species, called 'incidental drinking' (Dunson 1985; Dunson and Mazzotti 1989). Food and free water are the more important sources of input for most captive reptiles and the more readily controlled. Metabolic water can provide significant quantities of water for arid-adapted species that have comparatively water-impermeable skin (roughly 12% of the total water intake for a desert iguana (*Dipsosaurus* sp.): Minnich 1982). Normally, metabolic water is produced at rates that roughly balance—but do not exceed—output by evaporation (Minnich 1982) and is probably significant only during periods of drought when animals cease feeding (Nagy 1972). Except for freshwater aquatic species, uptake of water across the integument or via condensation on nasal membranes provide only minor contributions to the total water budget.

Reptiles lose water by evaporation across skin and respiratory membranes, in urine and in faeces and digestive excretions. Evaporative losses may account for more than half of the total water loss and are very significant in mesic-habitat species

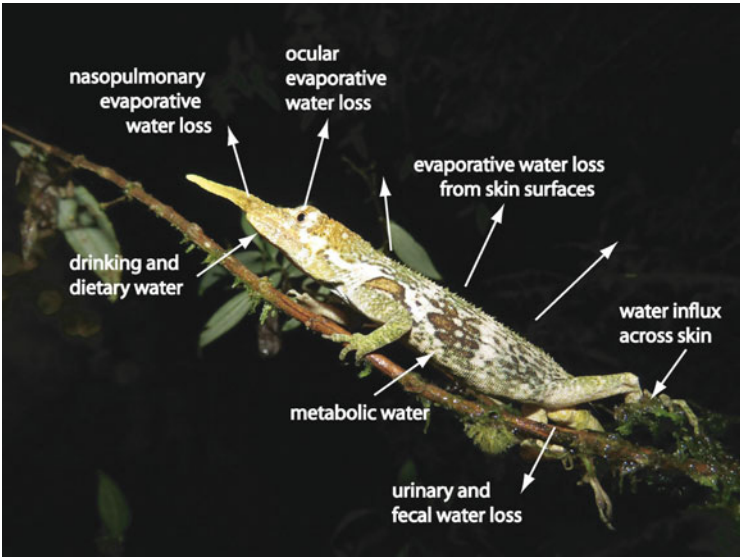


Fig. 2.5 Pathways of water exchange featuring a Pinocchio lizard, *Anolis proboscis*, climbing on a tree branch in the lower montane Andes of western Ecuador. Photograph by Michael Miyamoto