

Introduction

Impacts of climate change and environmental factors on reproduction and development in wildlife

Stuart R. Milligan^{1,*}, William V. Holt² and Rhiannon Lloyd²

¹*School of Biomedical and Health Sciences, King's College London, London Bridge Campus,
London SE1 1UL, UK*

²*Institute of Zoology, Regent's Park, London NW14RY, UK*

The robustness of the growth of the human population in the face of environmental impacts is in contrast to the sensitivity of wildlife. There is a danger that the success of reproduction of humans provides a false sense of security for the public, media and politicians with respect to wildlife survival, the maintenance of viable ecosystems and the capacity for recovery of damaged ecosystems and endangered species. In reality, the success of humans to populate the planet has been dependent on the combination of the ability to reproduce successfully and to minimize loss of offspring through controlling and manipulating their own micro-environment. In contrast, reproduction in wildlife is threatened by environmental changes operating at many different physiological levels.

Keywords: nutrition; stress; global warming; pollutants; epigenetics

1. INTRODUCTION

'It is impossible to foretell the future with certainty'—so opened the final address to the 3rd International Symposium on Comparative Reproduction in 1972 on 'The environment and reproduction in mammals and birds' (Mellanby 1973). Successful reproduction is fundamental to the survival and evolution of all species and the primary interest in that symposium was to understand the basic mechanisms underlying how the natural environment and its ambient fluctuations coordinated and modulated reproductive processes. While there were already increasing concerns about the inexorable increase in the human population and the impact of this on ecosystems and the future of wildlife populations, rapid climate change was not yet a recognized issue. In his address, Mellanby looked forward with some optimism that mankind would manage and cope with the future, but only on the assumptions that technological advances in energy supply, raw material usage, agriculture and pollution control would allow mankind the tools to undertake this task and that population growth would be brought under control.

How far have we come since 1972? The world's population then was about 3800 million; in October 2009 the world's population was about 6800 million and the forecast is that it will grow to reach at least 9100 million by 2050. At the same time, the life expectancy of individuals in developed countries continues to increase. It is sadly ironic that it is this very success of human reproduction and survival that is at the very

the root of the threats to the Earth's ecosystems. The size of the human population and the technological ability of humans to exploit and manipulate environmental resources are putting enormous pressures on the basic requirements of water, food, energy and space on which all life forms ultimately depend (Thomas *et al.* 2004). The effect of these pressures can often be most easily quantified for humans: for example, it has been estimated that by 2025, over 50 per cent of mankind will be living in conditions in countries experiencing water stress (i.e. shortages for all or part of the year). Agricultural yields have fallen in some areas of Africa by up to 50 per cent because of factors such as invasive pests, land degradation, erosion, drought and climate changes (United Nations Environmental Programme 2009). It is salutary to note that, even living a relatively modest lifestyle, the sustainable human population of the planet may be only about 3000 million (Optimum Population Trust 2009)—i.e. less than half of what it was in 2009 and less than one-third of the projected numbers for 2050.

In contrast to this growth of the human population, the rate of extinction of other species is accelerating. It is again ironic that while concerns over the management of human population size focus on limiting fertility and family sizes, concerns about wildlife populations increasingly focus on the conservation of breeding populations and the prevention of species extinction (table 1). This discrepancy is reflected in the observation that the current *hourly* growth rate of the human population in excess of 9000 dwarfs the *total* global populations of many threatened species. Some of the implications of such small population sizes for wildlife species in terms of coping with environmental changes are discussed in

* Author for correspondence (stuart.milligan@kcl.ac.uk).

One contribution of 11 to a Theme Issue 'Impacts of environmental change on reproduction and development in wildlife'.

Table 1. Number of threatened species (incorporating critically endangered, endangered and vulnerable to extinction) by major groups. Adapted from IUCN Red List of Threatened Species (2009).

	estimated number of described species	number of species evaluated by 2008	number threatened as % of species described	number threatened in 2008 as % species evaluated ^a
vertebrates				
mammals	5488	5488	21	21
birds	9990	9990	12	12
reptiles	8734	1385	5	31
amphibians	6347	6260	30	30
fish	30 700	3481	4	37
invertebrates				
insects	950 000	1259	0	50
molluscs	81 000	2212	1	44
crustaceans	40 000	1735	2	35
corals	2175	856	11	27
plants				
gymnosperms	980	910	33	35
dicotyledons	199 350	9624	4	74
monocotyledons	59 300	1155	1	68

^aApart from the mammals, birds, amphibians and gymnosperms (i.e. those groups completely or almost completely evaluated), the figures in the last column are gross overestimates of the percentage threatened owing to biases in the assessment process towards assessing species that are thought to be threatened, species for which data are readily available, and under-reporting of Least Concern species. The true value for the percentage threatened lies somewhere in the range indicated by the two right-hand columns. In most cases, this represents a very broad range. For example, the true percentage of threatened insects lies somewhere between 0.07 and 50 per cent.

Brown *et al.* (2009) in this volume ('Genetic variation, inbreeding and chemical exposure—combined effects in wildlife and critical considerations for ecotoxicology').

The threats of environmental changes to the fitness, survival and reproductive success of individuals, and ultimately to the survival of species and ecosystems come from many directions: habitat destruction, disruption of food chains, changes in disease and parasitic loads, increased pollution and direct and indirect effects of climate change. The physical environmental changes can be detected at almost any place on the planet: from pole to pole (Moline *et al.* 2008; Robinson 2009) and from ocean depths (Guinotte & Fabry 2008) to the stratosphere (Wilson *et al.* 2007). To what extent will these various changes and pressures affect the ability of individuals, species and ecosystems to survive in the long term? Unfortunately, our ability to answer such questions is limited by many factors, not least the difficulty of making forecasts from incomplete data, about biological systems in which there are many variables, and in a climate of ever changing baselines.

It is not just the magnitude of environmental pressures that poses a threat to the survival of species but also the rate of their change. The rate of change of the impact of human activities and its relation to the size of the global population is readily revealed by plotting the world's population over the last 10 000 years in relation to the change in some of the atmospheric greenhouse gases (figure 1). In the past, rapid changes in the Earth's climate have been associated with a number of mass extinctions (Twitchett 2006). Analyses of the fossil records indicate that while species can adapt to slow environmental changes, rapid changes are far more threatening, with previous periods of global warming being associated with increased rates of extinction and reduced biodiversity (Mayhew *et al.* 2008). While these previous rapid

climate changes have been of abiotic origin (e.g. volcanism), the environment of the planet today is changing largely owing to anthropogenic factors. The limited ability of many species to cope with such changes is reflected in the very high rates of species extinctions seen in recent years. It is important to recognize, however, that the extinction of one species can provide opportunities for the invasion or adaptation of other species, with the development of new species associations and biomes. This issue is discussed in the article by Carey (2009) in this volume ('The impacts of climate change on the annual cycles of birds').

2. INTERDISCIPLINARY UNDERSTANDING

The potential impact of current and forecasted future environmental changes on wildlife can, and needs to be, studied at many different levels. It requires reductionist approaches to unravel the basic mechanisms underlying specific responses, integrative whole organism approaches to understand the impact on and within an individual both acutely and over time, through to integrated studies of foodwebs, ecosystems and population dynamics. In the wider sense, it also requires analyses of the social, economic and political contexts that have driven us to the present situation and in which any solutions must be applied. The breadth of such work poses its own problems, not least because of the tendency for compartmentalization of individual studies into specialist journals and scientific societies devoted to relatively narrow subject areas. While understandable for practical purposes, this approach does not encourage the cross-fertilization of ideas and new challenges that cross-disciplinary approaches can provide.

At present, there is surprisingly little scientific overlap between researchers who study environmental

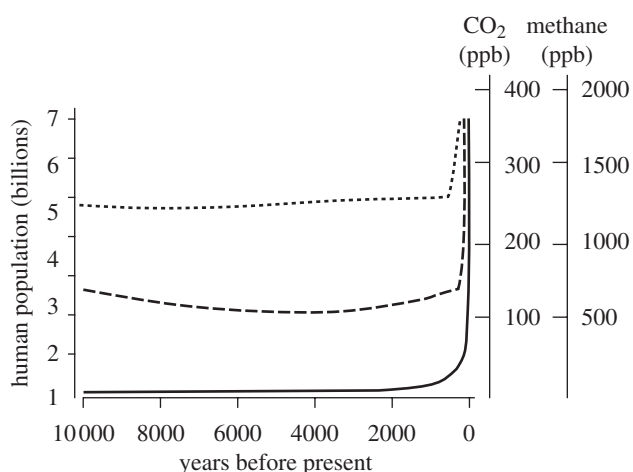


Figure 1. Relationship between growth of the human population (various sources) and the estimated concentrations of two 'greenhouse gases' (adapted from IPCC 2007) over the last 10 000 years. Dotted line, CO₂, dashed line, methane, solid line, human population.

change at large scales on populations and ecosystems and those who study detailed reproductive and developmental mechanisms in model species. The purpose of the current volume was to cross the discipline divide in relation to a fundamental principle associated with natural selection and the environmental challenges facing the planet's wildlife: i.e. whether individuals can survive, reproduce and successfully pass their genes onto the next generation. The contents of this volume reflect a 2-day meeting held at the Zoological Society of London in October 2009 entitled 'Impacts of environmental changes on reproduction and development in wildlife'. The wide breadth of the topics and species covered was deliberate to stimulate discussion and encourage the participants, audience and current readership to develop new insights into the variety of mechanisms underlying the effects of environmental change on reproductive success, health and fitness in wildlife.

3. PREDICTING THE UNPREDICTABLE

To predict how environmental changes will impact on reproductive success and survival of any individual or species, we need information on the nature, magnitude and dynamics of the environmental changes to be expected. We also need an understanding of how such changes affect biological systems. To what extent do we have these prerequisites?

At first sight, we might appear to have a good deal of such information. There has been considerable progress in developing complex models of climate change to accommodate increasing numbers of biotic and abiotic variables (e.g. IPCC 2007). These models provide forecasts of long-term trends of the major climate variables over wide geographical areas. Similarly, we have data (with greater or lesser amounts of detail) about the lifestyles and physiology of selected plant and animal species across a range of phyla. Together, these should allow forecasts of the potential impacts of climate changes on the physiology and viability of individual species and of the threats to generalized

ecosystems. Thus, Hansen (2009) in this volume ('Effects of heat stress on mammalian reproduction') addresses the impact of global warming on reproduction in mammals in relation to the known effects of heat stress on specific components of the male and female reproductive systems. Such effects have been well investigated because of the importance of heat stress in agricultural animals. Hansen emphasizes the advantage that endotherms may have in adapting to global warming owing to their well-developed thermoregulatory mechanisms. In contrast, ectotherms, which represent by far the most abundant animal species on the planet, may face much greater problems as all their systems (e.g. metabolism, locomotion, reproduction, development) are more directly influenced by environmental temperature. Deutsch *et al.* (2008) examined the impact of rising global temperatures on terrestrial insects and concluded that tropical species are likely to be most adversely affected and suffer the highest extinction risks, probably because many are currently living very close to their optimal temperatures; in contrast, species at higher latitudes have a higher thermal tolerance and are living in climates that are currently cooler than their physiological optima. Extending their observations to incorporate data from three groups of vertebrates (frogs, lizards and turtles), the authors concluded that the same situation would apply to ectotherms more generally. This theoretical analysis in animals showing that tropical species are most at risk is mirrored by the empirical data on the current IUCN threat of extinction for vascular plants (Vamosi & Vamosi 2008).

Such models and analyses are very useful, but we also need detailed insights into specific, local environmental conditions where additional pressures may come from such factors as local habitat destruction and pollution. Attempting to incorporate these variables into predictions raises the level of complexity. The general concept of 'global warming' obviously encompasses not only a global rise in temperature, but also increased frequencies of more extreme climatic events. While individual extreme climatic events may be themselves short-lived, their effects on ecosystems may be long-lasting (Barrett *et al.* 2008). Extreme climatic events may in turn trigger or amplify other threats (Robinson 2009). As an example, it is estimated that flooding accounts for 40 per cent of all natural disasters worldwide: these flooding events may not only cause habitat degradation *per se* but also increase human pressures on remaining habitats; in turn, these may have knock-on effects of food availability, changes in species distributions, disease etc. Such flooding events also increase the risk of release of man-made chemicals from storage, waste overflows and mobilization of those already in the environment (Euripidou & Murray 2004). Cascades and synergies (amplifying feedbacks) between such various environmental impacts may then operate (Brook *et al.* 2008; Wookey *et al.* 2009), and this issue is strongly highlighted by a number of authors in the current volume in connection with impacts on reproductive performance. A recent example of such effects is provided by the analysis of the declines in reindeer and caribou numbers (Vors & Boyce 2009).

Each of these many individual environmental variables comes with its own confounding levels of complexity. This is well illustrated by extending the discussion above about the release of pollutants into the environment. Specific and detailed information is available about the physical, chemical and toxicological profiles of many of the hundreds of thousands of man-made chemicals produced and used in the industrialized world. There is no doubt that detectable quantities of many of the potentially harmful contaminants can be found in samples of water, substrate, plants and animals from almost anywhere on the planet (Lyons 2006). Laboratory studies have clearly shown that some of these chemicals act as 'endocrine disruptors' and a variety of reproductive anomalies—ranging from imposex in molluscs, through intersex fish to impaired reproduction in a variety of mammals and the testicular dysgenesis syndrome in man—have been attributed to their effects (Diamanti-Kandarakis *et al.* 2009). Clear disruptions of development and reproduction have been seen in areas of high pollutant contamination (e.g. Jobling *et al.* 2002; Milnes *et al.* 2008). However, such information is not enough to decide what specific levels and durations of exposure really pose a threat to wildlife: confounding factors include the fact that these pollutants do not occur individually, but in myriad combinations, each with fluctuating exposure levels and potential for bioaccumulation, each chemical may induce a spectrum of responses in a variety of physiological systems and there may be variable sensitivities of different organisms at different stages of their life history.

The problems posed by environmental pollutants *per se*, and their possible synergistic interactions with other systems, including the immune system and disease susceptibility, are discussed by three articles in this volume (Rhind 2009: 'Anthropogenic pollutants—a threat to ecosystem sustainability', Acevedo-Whitehouse & Duffus 2009: 'Effects of environmental change on wildlife health', Brown *et al.* 2009: Genetic variation, inbreeding and chemical exposure—combined effects in wildlife and critical observations for ecotoxicology). From different perspectives, these authors all highlight the need to consider the cascades, synergies and interactions between environmental impacts. Thus, the effects of factors such as pollutants, undernutrition, water status and disease may all interact to exacerbate the effects of each other and increase stress levels; together with such threats as habitat degradation and other invasive species, these may all affect fitness and reduce survival and reproduction; on top of this, consequent reductions in population size or fragmentation of populations may raise the levels of inbreeding and reduce fitness further, providing another twist of the screw.

4. BIOLOGICAL KNOWN AND UNKNOWN

Just as our understanding of the specific nature and complexity of future environmental challenges lacks certainty, so also does our understanding of the biological systems with which they will interact. It is true that we have a good understanding of the physiological mechanisms controlling reproduction in a small

number of 'model' species, especially within the vertebrates. There is sporadic information about reproductive control mechanisms of selected species in some other phyla. For pragmatic reasons, such specific knowledge gained from a single, or a small number of, species is then often extrapolated and generalized to encompass related species, genera, orders and classes as required.

However, reproductive characteristics show immense species variability, and this poses real problems when considering how climate change may impact reproductive success. This point is well illustrated by considering the mechanisms underlying seasonal breeding. In the natural world, the selective advantage of coordinating reproduction with environmental conditions appropriate for maximizing the survival and fitness of the offspring is self-evident. For example, the timing of reproduction in both birds and mammals is often linked to cues about adult status (e.g. energy reserves) and cues about likely future environmental conditions (e.g. time of year). Selection pressures over millennia have fine-tuned this coordination. However, in the face of rapid climate change, the concern now is that this coordination may break down, owing to a mismatch between the 'expected' and the actual prevailing conditions (Thomas *et al.* 2004; Williams *et al.* 2007). Questions then arise as to how the reproductive success of individuals will be affected and how quickly the selection pressures acting on populations will force adjustments to the new conditions.

While these are relatively straightforward questions, the difficulties in providing answers are well described in this volume by Bronson (2009) ('Climate change and seasonal reproduction in mammals'), Lawrence & Soame (2009) ('The endocrine control of reproduction in nereidae: a new multi-hormonal model with implications for their functional role in a changing environment') and Carey (2009) (The impacts of climate change on the annual cycles of birds). In the case of mammals and birds, the readily apparent influence of seasons on breeding seasons provided early investigators with an extraordinarily useful experimental model to investigate how external cues can influence the hypothalamic–pituitary–gonadal system. The seasonality of breeding of mammalian species in temperate zones (e.g. sheep, voles, hamsters) was clearly shown to be primarily controlled by the length of the solar photoperiod and mediated, at least in part, by pineal-secreted melatonin; temperature effects appeared to be minimal or non-existent. Bronson emphasizes that while this general principle applies to many long-lived species in temperate zones, it is not appropriate to extrapolate it to the control of seasonal reproduction in the tropics where seasonal variations in daylength are minimal and where a variety of other cues and mechanisms may be involved. However, as our current understanding of those cues and mechanisms are slight, predictions of how individual species in the tropics will be affected by climate change must be speculative. The paucity of information on even basic invertebrate neuroendocrine mechanisms synchronizing reproduction with the environment is similarly highlighted by

Lawrence & Soame (2009). However, it is interesting to note that Bronson (2009, for mammals), Carey (2009, for birds) and Lawrence & Soame (2009, for Nereids) argue that global warming is likely to pose significant problems for reproduction in species that use photoperiod to cue breeding (and migration) in high latitudes because the phase relationship between environmental conditions and photoperiodic cues will tend to uncouple.

Considerations of seasonal breeding and the need to match breeding with food supplies highlight the importance of nutrition in controlling and modulating reproduction. The energetic costs of breeding are usually huge, ranging from the 'simple' production of large numbers of gametes in some species, through to full parental care of offspring in others, with sometimes additional costs owing to factors such as migration to suitable breeding areas on top (Carey 2009). More subtle effects of varying maternal nutrition are discussed by Ashworth *et al.* (2009) in this volume ('Nutritional effects on oocyte and embryo development in mammals: implications for reproductive efficiency and environmental sustainability').

5. INDIVIDUAL VARIABILITY TO ENVIRONMENTAL CHALLENGES: GENETIC AND EPIGENETIC RESPONSES

A common theme in this volume is that the threat to individuals comes from mismatches between the current phenotype determined by historical selection pressures and the new environmental pressures. The nature and pace of the environmental changes in climate, diet, predators, pathogens, pollutants or combinations of these pose intense and often novel selection pressures. The rate of extinctions in recent years reflects that, for many species, these pressures can overwhelm their ability to adapt and evolve appropriate responses.

Since individual variability provides the very substrate for natural selection, Brown *et al.* (2009; Genetic variation, inbreeding and chemical exposure—combined effects in wildlife and critical observations for ecotoxicology) raise the question of how useful or representative inbred or even outbred laboratory stocks are for experimentally assessing the likely long-term impacts of environmental conditions on wild populations exhibiting a much wider spectrum of genetic variation. Brown *et al.* raise this question with specific reference to ecotoxicology, while Bronson (2009) and Carey (2009) highlight the variability in individual responses in relation to seasonal breeding and migration in a number of mammalian and bird species in the temperate zone. Perhaps the observations of photoperiodic individuals living side-by-side with non-photoperiodic individuals of the same species suggest that the breadth of natural variation in large populations may provide a degree of optimism that some species will cope with even large environmental shifts. On the reverse side of the argument, small populations, inbred by default, may be particularly vulnerable.

Traditionally, thoughts on the adaptation of populations to environmental pressures have focused on selection acting on phenotypes that ultimately reflect

the genetic make-up of each individual, with consequent subsequent changes in the genetic profile of the population to better-adapted genotypes. However, the influence of non-genetic 'maternal factors' affecting foetal growth have been known ever since the pioneering studies of Walton & Hammond (1938) in their cross-breeding of Shire horses and Shetland ponies. Interest in this area has mushroomed lately owing to both the recognition of early-life and foetal 'programming' effects in humans (Barker 1995) and the discovery of the phenomenon of epigenetic regulation of gene expression (Russo *et al.* 1996).

Numerous epidemiological studies in humans and experimental studies in laboratory and farm animals have now shown that inadequate or unbalanced nutrition in early life may 'programme' development and produce marked effects on the health status, physiology, metabolism and longevity of the adult. This phenomenon is often referred to as the developmental (or foetal) origins of adult disease (McMillen *et al.* 2008). In humans, for example, small body size at birth and during infancy is associated with increased rates of chronic diseases in adulthood, including hypertension, cardiovascular disease and insulin resistance. As well as diet-related developmental programming, there is long-standing evidence for 'stress-related' programming. In this phenomenon, experiences during pre-natal or early post-natal life have been shown to exert permanent effects on behavioural and physiological responses in the offspring (Weinstock 2008). The specific effects of nutritional or other 'stresses' during development may depend on the timing and magnitude of the imposed stimulus. This is highlighted by Ashworth *et al.* (2009) in this volume. Even the very earliest stages of embryo development appear to be susceptible to diet-induced changes (Cross & Mickelson 2006). For example, feeding a low-protein diet to rats for just the first 4 days of pregnancy (i.e. pre-implantation) was associated with a gender-specific programming of imprinted gene expression in the blastocyst, changes in blastocyst cell number and hypertension in adulthood (Kwong *et al.* 2000, 2006).

While the main drive to understanding 'developmental programming' as described above came from its implications for human health, application of the concept to wildlife raises the possibility that any environmental (including nutritional, stress, pollutant exposure and disease) impact experienced by parents may induce epigenetic responses in the offspring. These could then contribute to the different characteristics, lifestyle pathways, fitness of animals born at different times of the year or phases of the population cycle. The evidence and implications of programming effects in mammals, including specific effects on fecundity, are discussed by Gardner *et al.* (2009) in this volume ('Early life programming of fecundity').

The essence of epigenetics is that environmental changes cause altered programmes of gene expression by modifying the chromatin platform on which the transcriptional machinery operates. These modifications may be long term and may even be transmitted from generation to generation. The molecular mechanisms underlying this are well described by

Turner (2009) in this volume ('Epigenetic effects of environmental change'). The fact that epigenetic effects can be transferred through the germ line in mammals has been known for some years and is evidenced by the phenomenon of imprinted genes. Until relatively recently, this was thought to be rather a special case, but Anway & Skinner (2006, 2008) have reported that exposures of mother rats to particular endocrine disruptors can induce epigenetic changes in the male germ line that are associated with changes in male fertility and reproductive behaviour up to four generations later. Turner (2009) raises the important issue of whether environmentally induced epigenetic characters may be incorporated into permanent changes in DNA sequences. If so, this opens up a new dimension in terms of the trying to understand the effects of environmental pressures on population genetics and evolutionary responses.

6. CONCLUSIONS

The current status of wildlife populations will undoubtedly change in response to the increasing pressures from the abiotic and biotic environments. The public and political concerns about the impact of climate and environmental change in humans tend to centre on such factors as food production and availability, water sources, the impact of extreme climatic events, sea levels, vegetation patterns etc and the economic, political and social consequences of all these factors, including immigration and emigration. Ecosystems feature mainly in relation to their ability to be sustainably exploited to meet human physical and cultural needs. Effects of environmental impacts on human reproduction do not normally feature at all, except for the particular case of pollutants and their potential for adverse effects on human reproductive and general health (Woodruff *et al.* 2008). The latter is a good example of a situation in which wildlife issues may readily reach the media headlines (e.g. 'Toxic waste causes hermaphrodite polar bears': *The Independent*, 10.01.2006), but tend not to go much further unless they coincide directly with, and reinforce, human issues.

The robustness of the growth of the human population in the face of environmental impacts is in contrast to the sensitivity of wildlife. There is a danger that the seeming success of reproduction of the human species provides a false sense of security for the public, media and politicians with respect to wildlife survival, the maintenance of viable ecosystems and the capacity for recovery of damaged ecosystems and endangered species. In reality, the success of humans to populate the planet has been dependent on the combination of their ability to reproduce successfully and then to minimize loss of offspring through controlling and manipulating their own micro-environment. Unfortunately, this local control has largely operated without consideration of the knock-on effects of resource use on the macro-environment. It is now clear that anthropogenic environmental changes may affect both the reproductive success and the survival of many wildlife species by multiple routes and in often unpredictable ways. Since man does not exist in isolation, these

wider impacts of anthropogenic macro-environmental changes need to be understood by society at all levels.

We are grateful to the Zoological Society of London for hosting the meeting at which these papers were presented.

REFERENCES

- Acevedo-Whitehouse, K. & Duffus, A. L. J. 2009 Effects of environmental change on wildlife health. *Phil. Trans. R. Soc. B* **364**, 3429–3438. (doi:10.1098/rstb.2009.0128)
- Anway, M. D. & Skinner, M. K. 2006 Epigenetic transgenerational actions of endocrine disruptors. *Endocrinology* **147**, S43–S49. (doi:10.1210/en.2005-1058)
- Anway, M. D. & Skinner, M. K. 2008 Epigenetic programming of the germ line: effects of endocrine disruptors on the development of transgenerational disease. *Reprod. Biomed. Online* **16**, 23–25.
- Ashworth, C. J., Toma, L. M. & Hunter, M. G. 2009 Nutritional effects on oocyte and embryo development in mammals: implications for reproductive efficiency and environmental sustainability. *Phil. Trans. R. Soc. B* **364**, 3351–3361. (doi:10.1098/rstb.2009.0184)
- Barker, D. J. P. 1995 Fetal origins of coronary heart disease. *BMJ* **311**, 171–174.
- Barrett, J. E., Virginia, R. A., Wall, D. H., Doran, P. T., Fountain, A. G., Welch, K. A. & Lyons, W. B. 2008 Persistent effects of a discrete warming event on a polar desert ecosystem. *Global Change Biol.* **14**, 2249–2261. (doi:10.1111/j.1365-2486.2008.01641.x)
- Bronson, F. H. 2009 Climate change and seasonal reproduction in mammals. *Phil. Trans. R. Soc. B* **364**, 3331–3340. (doi:10.1098/rstb.2009.0140)
- Brook, B. W., Sodhi, N. S. & Bradshaw, C. J. 2008 Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**, 453–460. (doi:10.1016/j.tree.2008.03.011)
- Brown, A. R., Hosken, D. J., Balloux, F., Bickley, L. K., LePage, G., Owen, S. F., Hetheridge, M. J. & Tyler, C. R. 2009 Genetic variation, inbreeding and chemical exposure—combined effects in wildlife and critical considerations for ecotoxicology. *Phil. Trans. R. Soc. B* **364**, 3377–3390. (doi:10.1098/rstb.2009.0126)
- Carey, C. 2009 The impacts of climate change on the annual cycles of birds. *Phil. Trans. R. Soc. B* **364**, 3321–3330. (doi:10.1098/rstb.2009.0182)
- Cross, J. C. & Mickelson, L. 2006 Nutritional influences on implantation and placental development. *Nutr. Rev.* **64**, S12–S18. (doi:10.1301/nr.may.S12-S18)
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. & Martin, P. R. 2008 Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672. (doi:10.1073/pnas.0709472105)
- Diamanti-Kandarakis, E., Bourguignon, J.-P., Giudice, L. C., Hauser, R., Prins, G. S., Soto, A. M., Zoeller, R. T. & Gore, A. C. 2009 Endocrine-disrupting chemicals: an endocrine society scientific statement. *Endocr. Rev.* **30**, 293–342. (doi:10.1210/er.2009-0002)
- Eurpidou, E. & Murray, V. 2004 Public health impacts of floods and chemical contamination. *J. Public Health (Oxf.)* **26**, 376–383. (doi:10.1093/pubmed/fdh163)
- Gardner, D. S., Ozanne, S. E. & Sinclair, K. D. 2009 Effect of the early-life nutritional environment on fecundity and fertility of mammals. *Phil. Trans. R. Soc. B* **364**, 3419–3427. (doi:10.1098/rstb.2009.0121)
- Guinotte, J. M. & Fabry, V. J. 2008 Ocean acidification and its potential effects on marine ecosystems. *Ann. NY Acad. Sci.* **1134**, 320–342. (doi:10.1196/annals.1439.013)

- Hansen, P. J. 2009 Effects of heat stress on mammalian reproduction. *Phil. Trans. R. Soc. B* **364**, 3341–3350. (doi:10.1098/rstb.2009.0131)
- IPCC 2007 Climate Change 2007. *Fourth Intergovernmental Panel on Climate Change Assessment Report*. See <http://www.ipcc.ch/ipccreports/assessments-reports.htm> date accessed 13/06/2009.
- IUCN Red List of Threatened Species 2009. See http://www.iucnredlist.org/documents/2008RL_stats_table_1_v1223294385.pdf (accessed 13 June 2009).
- Jobling, S., Beresford, N., Nolan, M., Rodgers-Gray, T., Brighty, G. C., Sumpter, J. P. & Tyler, C. R. 2002 Altered sexual maturation and gamete production in wild roach (*Rutilus rutilus*) living in rivers that receive treated sewage effluents. *Biol. Reprod.* **66**, 272–281. (doi:10.1095/biolreprod66.2.272)
- Kwong, W. Y., Wild, A. E., Roberts, P., Willis, A. C. & Fleming, T. P. 2000 Maternal undernutrition during the preimplantation period of rat development causes blastocyst abnormalities and programming of postnatal hypertension. *Development* **127**, 4195–4202.
- Kwong, W. Y., Miller, D. J., Ursell, E., Wild, A. E., Wilkins, A. P., Osmond, C., Anthony, F. W. & Fleming, T. P. 2006 Imprinted gene expression in the rat embryo-fetal axis is altered in response to periconceptual maternal low protein diet. *Reproduction* **132**, 265–277. (doi:10.1530/rep.1.01038)
- Lawrence, A. J. & Soame, J. M. 2009 The endocrine control of reproduction in Nereidae: a new multi-hormonal model with implications for their functional role in a changing environment. *Phil. Trans. R. Soc. B* **364**, 3363–3376. (doi:10.1098/rstb.2009.0127)
- Lyons, G. 2006 Viewpoint: policy requirements for protecting wildlife from endocrine disruptors. *Environ. Health Persp.* **114**, 142–146. (doi:10.1289/ehp.8070)
- Mayhew, P. J., Jenkins, G. B. & Benton, T. G. 2008 A long-term association between global temperature and biodiversity, origination and extinction in the fossil record. *Proc. R. Soc. B* **275**, 47–53. (doi:10.1098/rspb.2007.1302)
- McMillen, I. C., MacLaughlin, S. M., Muhlhauser, B. S., Gentili, S., Duffield, J. L. & Morrison, J. L. 2008 Developmental origins of adult health and disease: the role of periconceptual and foetal nutrition. *Basic Clin. Pharmacol. Toxicol.* **102**, 82–89.
- Mellanby, K. 1973 Can man come to term with his environment? *J. Reprod. Fert.* (Suppl. 19), 591–592.
- Milnes, M. R., Bryan, T. A., Katsu, Y., Kohno, S., Moore, B. C., Iguchi, T. & Guillette Jr, L. J. 2008 Increased posthatching mortality and loss of sexually dimorphic gene expression in alligators (*Alligator mississippiensis*) from a contaminated environment. *Biol. Reprod.* **78**, 932–938. (doi:10.1095/biolreprod.107.064915)
- Moline, M. A., Karnovsky, N. J., Brown, Z., Divoky, G. J., Frazer, T. K., Jacoby, C. A., Torres, J. J. & Fraser, W. R. 2008 High latitude changes in ice dynamics and their impact on polar marine ecosystems. *Ann. NY Acad. Sci.* **1134**, 267–319. (doi:10.1196/annals.1439.010)
- Optimum Population Trust 2009. Towards sustainable and optimum populations. [Online] available at <http://www.optimumpopulation.org/opt.optimum.html> (accessed 28 May 2009).
- Rhind, S. M. 2009 Anthropogenic pollutants: a threat to ecosystem sustainability. *Phil. Trans. R. Soc. B* **364**, 3391–3401. (doi:10.1098/rstb.2009.0122)
- Robinson, S. A. 2009 Introduction: climate change biology at the ends of the earth—international polar year special issue. *Global Change Biol.* **15**, 1615–1617. (doi:10.1111/j.1365-2486.2009.01977.x)
- Russo, V. E. A., Martienssen, R. A. & Riggs, A. D. 1996 *Epigenetic mechanisms of gene regulation*. Plainview, NY: Cold Spring Harbor Laboratory Press.
- Thomas, C. D. et al. 2004 Extinction risk from climate change. *Nature* **427**, 145–148. (doi:10.1038/nature02121)
- Turner, B. M. 2009 Epigenetic responses to environmental change and their evolutionary implications. *Phil. Trans. R. Soc. B* **364**, 3403–3418. (doi:10.1098/rstb.2009.0125)
- Twitchett, R. J. 2006 The palaeoclimatology, palaeoecology and palaeoenvironmental analysis of mass extinction events. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **232**, 190–213. (doi:10.1016/j.palaeo.2005.05.019)
- United Nations Environmental Programme 2009. The environmental food crisis. [Online] available at <http://www.grida.no/> (accessed 28 May 2009).
- Vamosi, J. C. & Vamosi, S. M. 2008 Extinction risk escalates in the tropics. *PLoS One* **3**, e3886. (doi:10.1371/journal.pone.0003886)
- Vors, L. S. & Boyce, M. S. 2009 Global declines of caribou and reindeer. *Global Change Biol.* (accepted article). (doi:10.1111/j.1365-2486.2009.01974.x)
- Walton, A. & Hammond, J. 1938 The maternal effects on growth and conformation in Shire horse–Shetland pony crosses. *Proc. R. Soc. Lond. B* **125**, 311–335. (doi:10.1098/rspb.1938.0029)
- Weinstock, M. 2008 The long-term behavioural consequences of prenatal stress. *Neurosci. Biobehav. Rev.* **32**, 1073–1086. (doi:10.1016/j.neubiorev.2008.03.002)
- Williams, J. W., Jackson, S. T. & Kutzbach, J. E. 2007 Projected distributions of novel and disappearing climates by 2100 AD. *Proc. Natl Acad. Sci. USA* **104**, 5738–5742. (doi:10.1073/pnas.0606292104)
- Wilson, S. R., Solomon, K. R. & Tang, X. 2007 Changes in tropospheric composition and air quality due to stratospheric ozone depletion and climate change. *Photochem. Photobiol. Sci.* **6**, 301–310. (doi:10.1039/b700022g)
- Woodruff, T. J., Carlson, A., Schwartz, J. M. & Giudice, L. C. 2008 Proceedings of the summit on environmental challenges to reproductive health and fertility: executive summary. *Fertil. Steril.* **89**, 281–300. (doi:10.1016/j.fertnstert.2007.10.002)
- Wookey, P. A. et al. 2009 Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biol.* **15**, 1153–1172. (doi:10.1111/j.1365-2486.2008.01801.x)