Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability

Cindy I. Canale*, Pierre-Yves Henry

**UMR 7179 CNRS-MNHN, Département Ecologie et Gestion de la Biodiversité, Muséum National d'Histoire Naturelle,
1 avenue du Petit Château, 91800 Brunoy, France**

ABSTRACT: As ecosystems undergo global changes, there is increasing interest in understanding how organisms respond to changing environments. Recent evidence drawn from available vertebrate studies suggests that most of the phenotypic responses to climate change would be due to plasticity. We hypothesize that organisms that have evolved in unpredictable environments inform us about the mechanisms of phenotypic plasticity which provide an adaptive response to climate instability. As climate changes increase climatic hazards, these resilience mechanisms are expected to spread within species, populations and communities. We review studies that have demonstrated the importance of phenotypic plasticity in different life-history traits in overcoming climate uncertainty. We focus on organisms from unstable, recurrently energetically restrictive environments which possess a variety of morphological, physiological and/or behavioural adaptations to climate-driven selective pressures. First, we treat plastic morphological changes in response to fluctuating food availability. Adjustment of morphometric traits and/or organ size to energy supply would be essential in harsh environments. Second, we review the role of flexible energy-saving mechanisms, such as daily torpor, hibernation and energy storage, in overcoming climate-driven energetic shortages. Lastly, we address the role of plastic modulation of reproduction in fine-tuning the energy allocation to offspring production according to environmental conditions, with an emphasis on opportunistic breeding. Overall, we predict that species (or genotypes) possessing these efficient physiological mechanisms of resilience to unpredictable water and food fluctuations will be selectively advantaged in the face of increasing climatic instability.

KEY WORDS: Physiological flexibility · Global change · Environmental variability · Extreme climatic events · Morphology · Energy saving · Reproduction

1. INTRODUCTION

Climate strongly influences ecological and evolutionary dynamics through its influence on life-history traits, the temporal organization of life cycles and interactions among organisms (e.g. trophic interactions, competition). Complex interactions between atmospheric and oceanic circulation orchestrate interannual variability of climatic conditions over large regions. The resulting climatic cycles, such as El Niño Southern Oscillation (ENSO), impose climate-driven selective pressures on organisms of unstable frequency and intensity. El Niño events are poorly predictable in time, occurring every 2 to 7 yr in tropical regions, due to interactions between the ocean and the atmosphere (Allan et al. 1996). ENSO is composed of 2 phases: El Niño (warming phase) and La Niña (cooling phase; see Fig. 1). This dominant cycle of climatic anomalies imposes important constraints on organisms, particularly over the tropical and subtropical Pacific zones, through the occurrence of droughts and fire in tropical regions or wet conditions such as floods in arid regions (reviewed in Holmgren et al. 2001, Wang & Fiedler 2006). ENSO directly impacts primary production, with cascading effects on animal

communities (Holmgren et al. 2001, Stenseth et al. 2003, Wang & Schimel 2003).

In recent decades, climate change has disrupted ocean circulation, increasing the frequency of El Niño events (Yeh et al. 2009) and disturbing thermohaline circulation (Broecker 1997). These changes have begun to affect the frequency, length, geography and/ or severity of extreme climatic events. These climatic hazards include abnormal floods, droughts, tropical storm landfall and extreme temperatures (Easterling et al. 2000, Alley 2004, IPCC 2007, Chown et al. 2010, this Special). By disrupting the predictability of seasonal cycles, climate anomalies affect the timing of the life cycle of organisms (Parmesan et al. 2000). The increase in these extreme climatic events is likely to impose different selective constraints on organisms than gradual climate warming (Easterling et al. 2000, Parmesan et al. 2000, Mysterud et al. 2001, Stenseth et al. 2002, Pertoldi & Bach 2007, Chown et al. 2010). Climate warming imposes directional selection towards a hotter environment, whereas the increase in climate instability should select for multipurpose genotypes with a greater resilience to climatic fluctuations. The phenotypic response to more extreme events may not follow the same trajectory as for changes in average conditions (cf. non-linear relationships with climatic conditions). Furthermore, organisms mainly facing a change in climate stability are not expected to exhibit major range shifts, unless some neighbouring areas gain in climate stability. This is particularly true for island endemics (e.g. in the Galápagos, Madagascar and Australia) or highly fragmented ecosystems where populations are trapped in relict fragments of suitable habitat and accumulate genetic handicaps (e.g. low genetic variation, drift and inbreeding depression; Hannah et al. 2008, Hendry et al. 2008, Joubert & Bijlsma 2010, this Special). Actually, extreme climatic events are expected to become one of the major causes of species extinction during this century (Stenseth et al. 2002, Walther et al. 2002, Thomas et al. 2004, Foden et al. 2008, Chown et al. 2010).

Climate change can be counterbalanced by 3 adaptive mechanisms: microevolution, phenotypic plasticity and microevolution of phenotypic plasticity (Holt 1990, Pulido & Berthold 2004, Davis et al. 2005, Gienapp et al. 2008, Chown et al. 2010). Microevolution can result from the selection for local genotypes adapted to hotter conditions or earlier springs, i.e. the local adaptation to a changing climate. Alternatively, it can result from the selection for dispersing genotypes, which will be selectively advantaged by the extension of their ecoclimatic niche at higher latitudes and altitudes. Despite extensive research on thermal adaptation (e.g. this Climate Special), few field stud-

ies have demonstrated microevolutionary responses to climate change, probably because response to selection is too slow relative to the speed of climate change and is constrained by genetic correlations (Gienapp et al. 2007, Visser 2008). Only a few examples have been revealed in invertebrates or short-lived vertebrates (Bradshaw & Holzapfel 2006, Chown et al. 2010). Phenotypic plasticity should be the first mechanism to take place when the dominant selective pressure is increasing unpredictability of the environment. This should be the case particularly in long-lived organisms, which cannot sustain high selective loads, are largely temperature-independent and are exposed to interannual climatic fluctuations (Réale et al. 2003, Brommer et al. 2008, Charmantier et al. 2008, Teplitsky et al. 2008, Reed et al. 2009). Phenotypic plasticity is the ability of a single genotype to express different phenotypes in different environmental conditions. It is adaptive when it maintains fitness despite environmental changes (Price et al. 2003, reviewed in Nussey et al. 2007, but see Visser 2008). Phenotypic plasticity is characterized by the reaction norm of the phenotypic trait to the environmental condition. Individual-level plasticity has also been named phenotypic flexibility (Piersma & Drent 2003), and is defined as reversible, non-seasonal, within-individual variation. It is largely expressed in long-lived organisms, such as vertebrates, that need to adjust their phenotype to unstable environmental conditions. Contrary to developmental plasticity (Chown et al. 2010, de Jong et al. 2010, this Special), phenotypic flexibility allows organisms to adjust their phenotype throughout their life to non-predictable environmental changes. In highly unstable environments, unpredictable duration and intensity of favourable and unfavourable conditions select for the evolution of such trait flexibility (Sultan & Spencer 2002). Microevolution of phenotypic plasticity is expected to take place when the reaction norm has a genetic determinism, and thus can respond to changes in environmental heterogeneity by natural selection (de Jong 1995). Although genotype-by-environment interactions are well known in experimental genetics, we still have very little evidence of the evolution of reaction norms in response to climate changes (Nussey et al. 2005, Brommer et al. 2008, Chown et al. 2010).

The main limit to the efficiency of phenotypic plastic response to climate change is that present reaction norms may not be adaptive anymore under the new climatic conditions (reviewed in Visser 2008). Current reaction norms may not be adaptive for out-of-range, extreme climatic events. However, reaction norms of organisms dwelling in the most unpredictable environments on Earth, such as those under strong ENSO influence, are likely to have been selected to be adap-

tive over very large climatic gradients, much larger than for organisms from stable, temperate systems. The flexibility of behaviour, morphology and physiology allows these organisms to match the timing of crucial life stages, such as reproduction and growth, to fluctuations in environmental conditions. This way, organisms from unpredictable environments cope with a large spectrum of perturbations. They thus provide clues to which are the flexible life-history traits that are adaptive under unstable climatic conditions, and that are likely to spread within species, and species assemblages, exposed to increasing climate instability.

The present review concentrates on research results that have shown the importance of phenotypic plasticity in different life-history traits to overcome climate uncertainty. How do flexible control systems allow species to withstand climate anomalies? Which life-history traits show flexibility that could be adaptive in the context of ongoing climate change? We focussed on organisms from unstable, recurrently resource-limited environments (Fig. 1, Table 1), which most likely possess adaptations to climate-driven selective pressures. First, we treat adaptive modulations of external and internal morphology. Second, we review the role of plasticity of energy-saving mechanisms and the phenotypic adjustment of reproduction in time and space to overcome climate-driven energetic shortages. We conclude with suggestions for future research for a better mechanistic understanding of adaptive plastic responses, and their limits, linking current climate-driven environmental changes to ecological processes and patterns.

2. ADAPTIVE MODULATIONS OF EXTERNAL AND INTERNAL MORPHOLOGY

Geographic or temporal variations in body and organ size related to environment quality have been extensively studied (Cooper 1998, Smith et al. 2004, Yom-Tov & Geffen 2006, reviewed in Millien et al. 2006). However, actual anatomical flexibility, i.e. reversible, within-individual variation, has been less documented, although it could become an important topic of investigation in the context of resilience to climate change.

Not all animals reach a fixed external or internal morphology at sexual maturity. Several organisms undergo plastic morphological changes in response to varying food availability, strongly correlated to precipitation. Adjustment of morphometric traits and/or organ size to energy supply is essential in harsh environments. Morphological plasticity of whole body size is more widespread in reptiles than in mammals, which show only flexibility of some body parts (gut size, kidney, heart; reviewed in West-Eberhard 2003).

2.1. External morphology

During years of food shortage, reptiles shrink, thus limiting the allocation of energy to their unceasing growth. Hence, variability of resources would determine body size independently of interspecific competition, social status and predation. For example, in the Galápagos Islands, marine iguanas *Amblyrhynchus cristatus* adjust their body length to rainfall, which allows them to overcome harsh climatic events (Wikelski & Thom 2000). During El Niño years, the food with the highest nutritional quality disappears. This energetic stress is associated with body length shrinkage of up to 20%. However, La Niña events increase food availability and allow a larger body size. Shrinkage is sex-specific: females shrink more than males, allocating most surplus resources to egg production, rather than to growth (Wikelski et al. 1997). Shrinkage of marine iguanas appears as an adaptive response because individuals that have the largest body-size flexibility also have a higher survivorship. The physiological mechanisms of body-length regulation would be resorption of both soft tissues and bones.

In the arid area of the Succulent Karoo in northwestern South Africa, the rainfall period determines foraging opportunities for consumers. The duration of the growth season of the speckled tortoise *Homopus signatus*, the smallest tortoise in the world, is concomitant with the dry season. The dorso-ventral flexibility of their straight carapace length (SCL), shell height and volume allows them to allocate resources either to growth or survival. For instance, the SCL shrank in 57% of adult tortoises when resources were scarce, such as in 2002–2003, with the most flexible individual having the best survival rate. In contrast, important rainfalls were followed by high growth rates. Flexible growth was sex-specific, with females allocating more to egg production than to growth in dry years (Loehr et al. 2007).

2.2. Internal morphology

Morphological adjustment can also occur at the organ level. Phenotypic flexibility of size and constitution of kidney, heart and liver has been found in several species living in unstable environments. Changes of organ mass occur in response to fluctuating diet and temperature. It reduces the cost of organ maintenance and lowers the basal metabolic rate during periods of nutritional stress (Carey 2005, Naya & Bozinovic 2006). Digestive efficiency plays a crucial role in the energetic balance since it determines actual energy availability for all vital functions. In this way, it is not surprising to find that the gut structure is
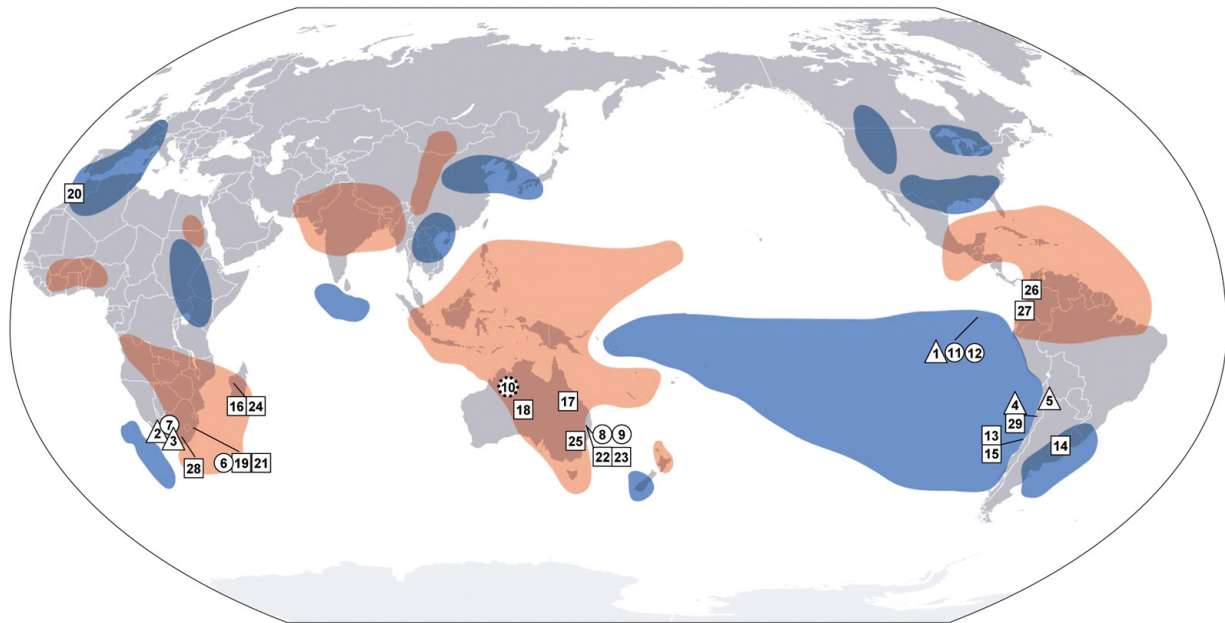
Fig. 1. Climatic anomalies during El Niño events resulting in extreme precipitation (blue) or drought (orange) distribution of organisms studied for their high phenotypic plasticity. Organisms are ordered by classes: reptiles (triangles, species 1–5), birds (circles, species 6–12) and mammals (squares, species 13–29). Dotted circle indicates a large repartition area all over the continent. Modified with permission from Allan et al. (1996). For species names and data sources, see Table 1

Table 1. Organisms studied for their phenotypic plasticity for which distributions are given in Fig. 1, and data sources

No. in Fig. 1	Taxon	Common name	Source
1	*Amblyrhynchus cristatus*	Galápagos marine iguana	Wikelski et al. (2000)
2	*Homopus signatus*	Speckled tortoise	Loehr et al. (2007)
3	*Xenopus laevis*	African clawed frog	Sabat et al. (2005)
4	*Liolaemus nitidus*	Shining tree iguana	Naya & Bozinovic (2006)
5	*Bufo spinulosus*	Andean toad	Naya et al. (2005)
6	*Colius striatus*	Speckled mousebird	McKechnie & Lovegrove (2001)
7	*Amadina erythrocephala*	Red-headed finch	McKechnie & Lovegrove (2003)
8	*Artamus cyanopterus*	Dusky woodswallow	Maddocks & Geiser (2007)
9	*Podargus strigoides*	Tawny frogmouth	Körtner et al. (2000)
10	*Taeniopygia guttata*	Australian zebra finch	Perfito et al. (2008)
11	*Geospiza fortis*	Medium ground finch	Grant et al. (2000)
12	*Geospiza scandens*	Cactus finch	Grant et al. (2000)
13	*Phyllotis darwini*	Leaf-eared mice	Bozinovic & Nespolo (1997)
14	*Akodon azarae*	Pampean grassland mouse	del Valle et al. (2006)
15	*Thylamys elegans*	Chilean mouse opossum	Bozinovic et al. (2007)
16	*Microcebus murinus*	Grey mouse lemur	Schmid & Speakman (2000)
17	*Sminthopsis macroura*	Stripe-faced dunnart	Körtner & Geiser (2009)
18	*Dasycercus blythi*	Brush-tailed mulgara	Pavey et al. (2009)
19	*Elephantulus myurus*	Eastern rock elephant-shrew	Lovegrove (2001)
20	*Elephantulus rozeti*	North African elephant-shrew	Lovegrove (2001)
21	*Saccostomus campestris*	Pouched mouse	Lovegrove & Raman (1998)
22	*Nyctophilus geoffroyi*	Lesser long-eared bat	Geiser & Brigham (2000)
23	*Nyctophilus gouldi*	Gould's long-eared bat	Geiser & Brigham (2000)
24	*Cheirogaleus medius*	Fat-tailed dwarf-lemur	Dausmann et al. (2009)
25	*Cercartetus nanus*	Eastern pygmy possum	Geiser (2007)
26	*Sciurus granatensi*	Red-tailed squirrel	Glanz et al. (1982)
27	*Myoprocta pratti*	Green acouchi	Morris (1962)
28	*Rhabdomys pumilio*	Four-striped field mouse	Jackson & Bernard (2005)
29	*Octodon degus*	Degus	Meserve et al. (1995)

modified according to changes in food quality and quantity. Digestive flexibility has been well documented since the 1950s. It is a widespread mechanism of physiological flexibility in small endotherms (rodents, birds) and ectotherms (lizards, frogs; Piersma & Lindstrom 1997, Starck 1999, Naya & Bozinovic 2006). These animals are able to adjust the length and anatomy of their digestive tracts to food quality (leaf-eared mouse *Phyllotis darwini*: Bozinovic & Nespolo 1997, African clawed frog *Xenopus laevis*: Sabat et al. 2005, Pampean grassland mouse *Akodon azarae*: del Valle et al. 2006) and quantity (shining tree iguana *Liolaemus nitidus*: Naya & Bozinovic 2006, Andean toad *Bufo spinulosus*: Naya et al. 2005, Chilean mouse opossum *Thylamys elegans*: Bozinovic et al. 2007). For instance, in the case of food shortage, the Chilean mouse opossum decreases the size of its small intestine and caecum (dry mass), i.e. the most expensive organs, to maintain energy and protein metabolism (Bozinovic et al. 2007).

3. ENERGY-SAVING MECHANISMS

One of the adaptations to environmental variability in energy supply is the ability to modulate the balance between energy acquisition and energy expenditure. To optimize this balance, energy is allocated to survival when food availability is limiting, and to growth or reproduction when surplus energy is available. Physiological mechanisms that allow this fine-tuning of the energy balance are hypometabolism, heterothermy and energy storage. Hypometabolism consists of a depression of metabolic rate with a reduction of oxygen consumption, reducing organ metabolic demands. In endotherms, hypometabolism usually anticipates heterothermy, i.e. a drop in body temperature for a variable amount of time, from some hours (daily torpor) to several months (hibernation; Geiser 2004). Avoiding thermoregulation leads to a major energetic gain. Actually, Geiser & Turbill (2009) found that 93.5% of recent extinct mammals were homeothermic, assuming that heterothermy is expressed in either 20 or 40% of mammals. It suggests that plastic modulation of energy expenditure could enhance the resilience of organisms to changing environmental conditions. When hypometabolism is not sufficient to match energy requirements with energy availability, another adaptive response is to store energy, either internally, e.g. in the form of adipose tissue, or externally, by food hoarding. If these energy-saving mechanisms are sufficiently flexible to compensate for climatic hazards, they could be a major component of the plastic phenotypic response to climate changes.

3.1. Daily heterothermy

Daily heterothermy has predominantly evolved in Afrotropical and Australasian regions highly influenced by ENSO (Fig. 1). These regions have the highest number of species exhibiting daily torpor, what allows animals to reduce their energy expenditure during the dry season (Lovegrove 2000, Geiser & Körtner 2010). The grey mouse lemur *Microcebus murinus* is one of the small tropical mammals intensively studied for its use of heterothermy during the lean season. This small Malagasy primate is able to adjust the depth and duration of torpor bouts, and thus its energy expenditure, in response to fluctuating food supply. Field studies have revealed that daily torpor appears spontaneously during the dry season, which corresponds to the period of food and water shortage (Schmid & Speakman 2000, Schmid 2001, Radespiel 2006). However, experiments have demonstrated that individuals exposed to food restriction could decrease their minimal body temperature, and increase the duration and depth of their daily hypothermia, within days to weeks (Génin & Perret 2003, Séguy & Perret 2005, Giroud et al. 2008, C. I. Canale et al. unpubl. data). These studies suggest that heterothermy is flexible, and can be adjusted rapidly in response to sudden environmental constraints, with an acclimation effect of former exposure to food shortage.

The flexible, aseasonal use of daily torpor to adjust the energetic balance to rapid environmental changes has been documented in several other mammals, including marsupials (Australia: reviewed in Geiser 1994, stripe-faced dunnart *Sminthopsis macroura*: Körtner & Geiser 2009, brush-tailed mulgara *Dasycercus blythi*: Pavey et al. 2009; South America: Chilean mouse opossum *Thylamys elegans*: Bozinovic et al. 2007), small terrestrial mammals (Africa: elephant-shrews *Elephantulus myurus* and *E. rozeti*: Lovegrove et al. 2001, pouched mouse *Saccostomus campestris*: Lovegrove & Raman 1998) and bats (Australia: reviewed in Geiser 2006, Australian long-eared bats *Nyctophilus geoffroyi* and *Nyctophilus gouldi*: Geiser & Brigham 2000). The spatial and temporal unpredictability of food availability is also an important determinant of avian hypothermia (McKechnie & Lovegrove 2002, Schleucher 2004). Food deprivation is actually the proximate determinant of heterothemy in many birds (South Africa: speckled mousebird *Colius striatus*: McKechnie & Lovegrove 2001, red-headed finch *Amadina erythrocephala*: McKechnie & Lovegrove 2003; Australia: dusky woodswallow *Artamus cyanopterus*: Maddocks & Geiser 2007, tawny frogmouth *Podargus strigoides*: Körtner et al. 2000).

Overall, facultative daily heterothermy would be an efficient, flexible adaptive response to overcome the

effects of unpredictable environment changes. The high physiological plasticity of heterotherms could be a major determinant of their success in overcoming the energetic challenges imposed by climate changes (Geiser & Turbill 2009, Liow et al. 2009).

3.2. Hibernation

Hibernation is usually associated with the avoidance of cold temperatures at high latitudes or altitudes. However, many animals also hibernate in the tropics to avoid the energy shortfall of the dry season (Dausmann et al. 2009). For instance, the fat-tailed dwarf-lemur *Cheirogaleus medius*, a Malagasy primate, remains in a hypometabolic state for 7 mo of the year. Thermoregulation avoidance allows this primate to overcome the winter food shortfall, even if ambient temperature rises to over 30°C (Dausmann et al. 2005, 2009). Even though, in that case, hibernation may not be flexible, the adjustment of body temperature to the insulation of hibernaculatum tree holes indicates plastic adjustments of energy savings to weather changes are possible. Opportunistic, non-seasonal hibernation has been shown in the eastern pygmy possum *Cercartetus nanus* from southeastern Australia (Geiser 2007). This marsupial is able to hibernate and to survive on body fat stores for up to 1 yr. These examples illustrate the opportunistic use of hibernation. Actually, even if hypometabolism can be sustained for several days in a row, hibernators have to awake regularly, for brief arousals. These arousals can be opportunistic, stimulated by the warm-up of external temperatures. For instance, Australian tree-roosting bats interrupt hibernation during the warmest nights, when insect activity is high. The adjustment of hibernation to ambient thermal fluctuations presumably optimizes food acquisition during the winter period (Turbill & Geiser 2008, Stawski et al. 2009). Hence when food and thermal constraints fluctuate, regular arousals during hibernation may allow animals to keep track of changes in the duration and severity of seasonally unfavourable conditions.

3.3. Energy storage

When the food shortage is too intense to be compensated for by energy conservation, supplementary energy has to be stored in anticipation. Storage can be internal, usually as fat in different organs, or external, with hoarding of food in caches accessible during the energetic bottleneck. The fattening of marsupial pygmy possum *Cercartetus nanus* (Geiser 2007) and the cheirogaleid primates *Microcebus murinus* and *Cheirogaleus medius* in response to weather unpredictability are examples of seasonal fattening to overcome the harsh season in Australia and Madagascar. The fat-tailed dwarf lemur *Cheirogaleus medius* can double its weight before the onset of hibernation (Schmid 2000).

Food caching has rarely been demonstrated in unpredictable habitats. Over periods of massive food supply, some rodents store seeds and nuts. Then, during the lean period, they rely on these stored resources (red-tailed squirrel *Sciurus granatensis*: Glanz et al. 1982, green acouchi *Myoprocta pratti*: Morris 1962). Food hoarding may be underexpressed in tropical regions because of high temperatures and humidity which spoil hidden food.

Since energy storage is largely anticipated relative to the period of maximum energetic demand, it may not be possible to flexibly adjust it according to the foreseen intensity and timing of the coming winter or dry season. Studies are needed to understand the relative role of photoperiodic cues versus proximal cues of food availability in regulating these forms of regulation of energy expenditure and/or acquisition.

4. PLASTIC MODULATION OF REPRODUCTION

A large number of species rely on photoperiod to time the life stages that are the most energy-demanding, such as reproduction. However, as seasons and prey phenology are disturbed by climatic changes, photoperiod is becoming a poor predictor of the timing of energy supply. This affects the regulation of trophic chains and interspecific interactions (Durant et al. 2007). Hence there is selection for a change in the sensitivity to environmental cues to time the breeding period. With a directional change in climate, microevolution of the photoperiodic threshold could help organisms to keep track of changing seasonality (Pulido 2007). In the case of increased climate instability, photoperiod can be used to time the basal endocrine preparation of the organism to reproduction (Hahn et al. 2008), but not to trigger the allocation of resources to reproduction. In unpredictable environments, organisms have evolved under high selective pressures to time their reproduction according to environmental cues more closely related to energy supply than photoperiod. Direct cues, such as food availability, and/or indirect cues related to rainfall, such as humidity or barometric pressure, are used to launch the actual investment in reproduction (Hau 2001, Scheuerlein & Gwinner 2002, Hau et al. 2004). All phases of reproduction can be modulated according to weather conditions: functional maturation and activity of gonads, expression of sexual behaviour and mor-

phological characters, pregnancy and rearing of offspring (Sikdar et al. 1992, Cynx 2001, Hau 2001, Wingfield 2008).

For instance, Australian zebra finches *Taeniopygia guttata* can breed during any month of the year. Experiments evidenced the use of non-photic cues to time the development of reproductive organs. Individuals exposed to long day photoperiods increased testis volume and luteinizing hormone secretion only when food was provided ad libitum (Perfito et al. 2008). In an extended view of the phenotype, we can also consider the nomadic displacement of breeding location as a phenotypic adjustment of reproduction in response to unpredictable resource fluctuations. In Southern Africa, nomadic bird species, which follow the rains throughout large parts of the continent, and breed just after the rain front, are expected to be 'pre-adapted' to increased rainfall variability (Simmons et al. 2004). Such opportunistic breeding in nomadic species is associated with a high flexibility of the neuroendocrine regulation of reproduction (Pereyra et al. 2005). Field studies on mammals have also related reproductive functions to environmental cues. Female four-striped field mice *Rhabdomys pumilio*, living in South Africa, inhibit their reproductive activity during harsh winters (Jackson & Bernard 2005). They reproduce opportunistically whenever conditions are suitable, using environmental cues such as rainfall (Christian 1979) and food availability (Jackson & Bernard 2005). Thanks to these plastic modulations of the timing and of the allocation to reproduction, organisms can maximize their reproductive output despite the poor predictability of favourable environmental conditions.

The flexible adjustments of reproduction to ENSO events have also been the focus of some long-term research. In the Galápagos Islands, the reproduction of Darwin finches has been documented for over 22 yr, including 4 El Niño events (medium ground finch *Geospiza fortis* and cactus finch *G. scandens*, Grant et al. 2000). This has revealed the fantastic plasticity of their reproduction activity, adjusted according to rainfall-driven fluctuations in food supply. The timing, duration and allocation (number of broods) to reproduction were flexibly adjusted to actual food availability, doubling during the strongest El Niño event. Clutch size and the number of fledglings were correlated to rainfall, and were up to 4 times higher during an El Niño event than in other years. In semiarid coastal Chile, rodents match their energetic requirements to unpredictable food fluctuations, also governed by El Niño events. Flexible traits allow them to increase their reproductive rate during ENSO years: leaf-eared mice *Phyllotis darwini* increases its period of reproductive activity, whereas degus *Octodon degus* initiates reproduction earlier, allowing for a longer pregnancy and larger, more numerous litters (Meserve et al. 1995, Previtali et al. 2010).

The major constraint that limits the evolution of plastic timing of reproduction according to short-term cues of resource availability lies in the important delay between the start of gonadal maturation and the time when the energetic demand for successful reproduction is the highest. This delay is determined by the duration of gonadal maturation and embryonic–offspring development (Dawson 2008). The longer the delay, the less reliable are short-term cues of resource availability, such as food availability or rainfall. An evolutionary response could be to gain in flexibility at all stages of reproduction, so that the timing of reproduction can be accelerated or slowed down depending on environmental variations. We can expect that increasing climate instability will select for more flexible timing of reproduction or even opportunistic breeding (Nussey et al. 2005).

5. FUTURE RESEARCH AND CONCLUSIONS

The high flexibility of the aforementioned morphological, behavioural and physiological traits would have evolved in response to unpredictable climate-driven selective pressures. We hypothesize that these flexible traits may predispose organisms to overcome climate changes, particularly where climate instability increases. In view of the predicted increase of extreme climatic events, understanding the mechanisms by which organisms can cope with abrupt environmental changes should be a major target in evolutionary physiological ecology (Pertoldi & Bach 2007).

Organisms living in seasonal environments are often highly sensitive to photoperiod, and rely on this environmental cue to time their life stages throughout the year. This photoperiod dependency likely evolved because of the strong correlation between photoperiod and seasonal fluctuations in food abundance (Coppack & Pulido 2004, Dawson 2008). However, as climate change decreases the predictability of seasonal food availability, sensitivity to environmental cues other than photoperiod should be selected for. Strong photoperiod dependency is put forward in several studies to explain the decline of temperate organisms that suffer from a mismatch between phenology of their prey and stationary environmental cues (Durant et al. 2007, Visser 2008). Organisms that evolved under unstable climates may give us an idea of the non-photoperiodic environmental cues (rainfall, food availability, temperature; Hau 2001, Dawson 2008) that may be used more and more to time phenotypic adjustments as climate instability increases.

Reaction norms of traits and of fitness components to expected environmental modifications provide us with a standard method for measuring the range and limits of adaptive phenotypic plasticity (e.g. de Jong 1995, Ghalambor et al. 2007, Joubert & Bijlsma 2010). Most of the information available on reaction norms to climate, and on the role of phenotypic plasticity in the response to climate change, comes from temperate organisms (Réale et al. 2003, Yeh & Price 2004, Charmantier et al. 2008, Teplitsky et al. 2008, Zhao & Wang 2009). These organisms evolved in relatively stable and predictable ecosystems, at least when compared with organisms from ENSO-driven tropical ecosystems with rainfall-dependent primary production. Hence reaction norms of temperate organisms are not expected to be adaptive over a broad range of climatic conditions. This raises the question of whether current reaction norms will provide an adaptive response to ongoing climate changes, since climate may go beyond the climatic range under which organisms evolved (e.g. Charmantier et al. 2008, Visser 2008). Thus we hypothesize that organisms from poorly predictable environments should exhibit more phenotypic flexibility than organisms from highly predictable environments (Hau 2001, Piersma & Drent 2003, Dawson 2008). However, this hypothesis has never been formally validated. To illustrate the plausibility of this prediction, we assembled examples of extreme phenotypic plasticity that are expressed in environments with extreme fluctuations. However, we still have very few formal demonstrations of adaptive, high phenotypic plasticity in unpredictable environments. For such a formal demonstration, it must be shown that individuals (or species) with the greatest phenotypic plasticity have the highest fitness during, or after, extreme events. In most studies presented here, this demonstration is lacking. Studies on ENSO-driven fitness and phenotypic changes in Darwin's finches and marine iguanas are the most complete demonstrations of adaptive, phenotypic adjustments to unpredictable, unfavourable conditions. The other studies mainly evidenced drastic, plastic changes of phenotypes, which are interpreted as adaptive responses to regimes of unpredictable environmental variations (Piersma & Drent 2003). Although the authors were likely right in making these interpretations, they did not provide formal demonstrations. One ideal experimental design to demonstrate increased phenotypic plasticity in unpredictable environments is to compare the reaction norms of organisms that evolved in highly fluctuating versus stable climates in common-garden experiments. A similar approach has been used (unsuccessfully) to test for a relationship between physiological flexibility and environmental aridity (Tieleman et al. 2003, Cavieres & Sabat 2008). An alternative approach is to perform comparative analyses of the phenotypic flexibility expressed in response to common climatic constraints of populations, or phylogenetically related species, that evolved in highly versus poorly seasonal environments. For both approaches, the key steps are the characterization of environmental predictability (as discussed by Cavieres & Sabat 2008 to explain unexpected results), the choice of the metrics of phenotypic plasticity to be used (e.g. Ghalambor et al. 2007, Tejedo et al. 2010, this Special) and the phenotypic traits to be measured.

Our poor knowledge of the range of reaction norms, their evolvability and their suitability for future ranges of climatic conditions limits our ability to assess whether phenotypic plasticity could provide an adaptive response to climate changes or not. Will current reaction norms provide adaptive phenotypic responses to future climates? Will the range of resilience to climate changes conferred by plastic phenotypic compensations be large enough? Microevolution of phenotypic plasticity could allow reaction norms to remain adapted to changing climatic conditions (Lande 2009, Shimada et al. 2010). Extensive experimental work has been done on genotype-by-environment interactions in invertebrate model systems, such as *Drosophila*, demonstrating that reaction norms have a genetic basis, and thus can evolve (Chown et al. 2010, Trotta et al. 2010, this Special). However, it remains virtually unknown to what extent phenotypic plasticity evolves in nature, particularly for long-lived organisms such as vertebrates, and if the evolution of reaction norms could provide an adaptive response to climate change. Few studies have evaluated the adaptive role of phenotypic plasticity of animals living in an unpredictable environment in response to climate change (Przybylo et al. 2000, Réale et al. 2003, Wingfield 2003, Dawson 2008). Quantitative genetic analyses of phenotype measurements, fitness measurements and pedigree data (Pigliucci 1996, Charmantier et al. 2008, Visser 2008) from organisms dwelling in unpredictable environments (e.g. Darwin's finches) would give us a first insight on the respective roles of microevolution and phenotypic plasticity in the adaptive response to climate instability.

Unfortunately, phenotypic plasticity is not a panacea. Its evolution and adaptiveness are constrained by several costs and limits (DeWitt et al. 1998, Ghalambor et al. 2007). First, phenotypic plasticity has evolutionary costs. Its fundamental cost is the common disadvantage of generalisation versus specialisation: the average performance across all environments is higher, but in each environment, specialists perform better (van Tienderen 1991, but see van Buskirk & Steiner 2009). Hence the temporal pace or spatial grain of environmental variations should be sufficiently

small so that the benefit of being able to change phenotype outweighs the cost of suboptimal fitness in each environment. Second, it imposes physiological costs, sometimes referred to as allostatic load (Wingfield 2003). Producing and maintaining the 'sensory and regulatory machinery' to constantly adjust the phenotype to current environment requires more energy than being specialized with fixed responses. General, direct costs of phenotypic plasticity include: maintenance and production of a plastic phenotype, acquisition of environmental cues, developmental instability and genetic costs (reviewed in DeWitt et al. 1998). The fitness costs of plasticity have rarely been addressed in the context of adaptation to unpredictable environments (but see Hahn et al. 2008). Third, the extent of phenotypic variation is not infinite. Genetic correlations or physiological trade-offs among functions impose limits to phenotypic changes, which may lead to maladaptive phenotypes. Costs and limits of phenotypic plasticity need more attention in future ecophysiological studies (Pigliucci 2005) before assuming that species from unstable environment may be the winners in the race against climate change.

To reach an integrated understanding of the adaptive responses to climate instability, we need to combine knowledge and methods across disciplines, particularly ecology, physiology, evolutionary biology and climatology. Field and laboratory biology bring us complementary information on the response of organisms to climate changes. Field data document mechanisms at large, relevant, spatio-temporal scales. Monitoring of natural populations is the only source of information on actual phenotypic changes related to climate changes. However, the causal relationships are hardly accessible with field data (Lepetz et al. 2009). In contrast, experiments under controlled conditions give us access to a very detailed understanding of the proximate mechanisms that link actual phenotypic changes to environmental changes. Manipulation of thermal conditions is the most widespread experimental treatment in the climate change literature. This is most likely because of the intuitive link between thermal adaptation and climate warming (de Jong et al. 2010, Fischer & Karl 2010, this Special, Joubert & Bijlsma 2010, Trotta et al. 2010). However, only basal levels or trophic chains, such as primary producers and ectotherms (primary consumers), strongly depend on thermal conditions. At higher levels in the trophic chain, the impact of climate changes is likely to be 2-fold: a direct impact via abiotic constraints (extreme temperatures or precipitations), but also as an indirect impact, resulting from the cascading effects through food webs of climate-driven modifications at low trophic levels. Hence it is legitimate to study the thermo-dependence of organisms low in the trophic chains to understand their potential adaptive response to climate changes. However, for organisms at upper trophic levels, food manipulation experiments may be more relevant. Under laboratory conditions, food manipulation experiments characterize the range and limits of physiological plasticity (reaction norms) to food availability (e.g. Dawson 2008). Under field conditions, they allow testing whether a phenotypic change is a fixed response, e.g. to seasonal changes (e.g. photoperiodic determinism of hibernation), or is flexible, and can be adjusted according to actual food availability (e.g. Humphries et al. 2003). Under laboratory conditions, it is hard to reproduce slight, directional environmental changes such as climate warming because the temporal scales are very different between the natural processes and what is achievable in the laboratory. But extreme climatic events may be easier to simulate, since they take place over much shorter time scales. With this evolutionary perspective, physiological ecology could play a major role in the understanding of the adaptive response to changing environmental extremes. The development of experimental physiological research on phenotypic plasticity, in an evolutionary framework, rooted in field observations of actual phenotypic changes, should improve our understanding of the adaptive responses of organisms to climate changes. Key research questions are: What are the major physiological mechanisms that allow coping with abrupt changes of the environment? To what extent are these physiological mechanisms flexible, and can they be rapidly adjusted to compensate for extreme climatic events? Are these flexible adjustments adaptive, i.e. do the most flexible individuals have the highest fitness?

Modelling of ecoclimatic niches could be a unifying framework to integrate the knowledge on phenotypic responses to climate-driven environmental changes between physiology, ecology and evolution (Kearney & Porter 2009, but see limitations in Chown et al. 2010). Experimental studies often aim to quantify the relationship between physiological traits and environmental conditions (e.g. temperature, food availability). Ecoclimatic niche models also link the occurrence of phenotypes to ecoclimatic variables, such as temperature, or indicators of primary production (Pettorelli et al. 2005, Araújo & New 2007). The usual phenotypes are species presence/absence, but they could be the expression of torpor, hibernation or opportunistic reproduction. Hence both approaches calibrate the statistical relationship between a phenotypic value and the value of an influencing environmental variable. This common denominator suggests that it should be possible to formally link reaction norms and ecoclimatic niches (Kearney & Porter 2009). The last step would be to integrate available scenarios of climate

change (IPCC 2007) so that the integrated model fore-casts the future distribution of species, given their physiological reaction norms, ecoclimatic niches and climatic changes. Such integrated 'evo-eco-climatic physiological models' would be valuable tools to explore the potential role of physiological plasticity in the resilience to climate changes.

In conclusion, extreme climatic events have profound and complex effects on entire ecosystems, at all trophic levels. One important conclusion is that they likely affect species differently according to the plasticity of their life-history traits. Species that evolved in unstable environments may be better prepared to cope with a more chaotic climate, given that climate variability remains in the range under which their reaction norm evolved. This review highlights the importance of evo-eco-physiological studies on these organisms to understand the potential of phenotypic plasticity, and particularly physiological flexibility, as an adaptive response to increased climate instability.

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