Extreme climatic events in relation to global change and their impact on life histories

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Abstract Extreme weather conditions occur at an increasing rate as evidenced by higher frequency of hurricanes and more extreme precipitation and temperature anomalies. Such extreme environmental conditions will have important implications for all living organisms through greater frequency of reproductive failure and reduced adult survival. We review examples of reproductive failure and reduced survival related to extreme weather conditions. Phenotypic plasticity may not be sufficient to allow adaptation to extreme weather for many animals. Theory predicts reduced reproductive effort as a response to increased stochasticity. We predict that patterns of natural selection will change towards truncation selection as environmental conditions become more extreme. Such changes in patterns of selection may facilitate adaptation to extreme events. However, effects of selection on reproductive effort are difficult to detect. We present a number of predictions for the effects of extreme weather conditions in need of empirical tests. Finally, we suggest a number of empirical reviews that could improve our ability to judge the effects of extreme environmental conditions on life history [*Current Zoology* 57 (3): 375–389, 2011].

Keywords Bet hedging, Climate change, Extreme weather, Reproductive failure, Truncation selection

1 Introduction

Extreme climatic events, also named extreme weather events or extreme meteorological events in the climatological and meteorological literature, are rare occurrences happening 5% or less of the time as gauged from the expected distribution of the climate variable in question (e.g. http://www.emc.ncep.noaa.gov). Although the exact choice of the cut-off climatological probability value in the definition is somewhat arbitrary, this has not prevented climatologists from relating the frequency of such events to present global change. Thus, extreme climatic events are predicted to increase in frequency in most future climate scenarios (Rind et al., 1989; Liang et al., 1995; Easterling et al., 2000). Fires, floods, hurricanes, blizzards, droughts and marked temperature anomalies both in the atmosphere and in seawater may become a normal environmental feature for many animal populations (Peters and Lovejoy, 1992; Karl et al., 1995; Schneider and Root, 1996). For instance, hurricane frequencies and intensities are predicted to increase (Wendland, 1977; Emanuel, 1987; 1988). These trends may shift the distributions of meteorological variables towards more extreme values, which in turn

may affect the quantitative criteria for defining extremeness. Extreme environmental conditions may have severe consequences and impose strong abiotic selection pressures. The literature on adaptation to climate change primarily involves research into adaptation to climate trends, and not to extreme climatic events (Jentsch et al., 2007). Including responses to extreme events may give a more balanced view on the adaptive potential of species to all aspects of climate change. Such adaptation may involve changes in life histories.

Extreme environmental conditions may affect population dynamics and the composition of communities through effects on life history traits. Thus, extreme environmental conditions may have stronger effects on population dynamics than average climate (Knopf and Sedgwick, 1987; Franklin et al., 1992; Hellman, 2002) and control or limit distribution changes (Scriber and Gage, 1995). High flows and debris avalanches associated with heavy winter storms may strongly disrupt animal communities in stream and river ecosystems (Gregory et al., 1991). Common proximate causes of local extinctions of butterfly populations are extreme weather events like prolonged droughts, floods and late or early freezes (Ehrlich et al., 1972). Mechanical dama-

ge to coral reefs and massive blow-downs of trees in tropical forests are typical effects of such weather disturbances. Hurricanes can strip all living coral from long stretches of reef (Levinton, 1982). Hurricane Hugo destroyed 70% of the nesting trees of the largest population of the endangered red-cockaded woodpecker *Picoides borealis* (Peters, 1992). Population recovery after such extreme disruption may become impossible after repeated setbacks. Thus, reefs may take decades to recover following storms (Gardner et al., 2005). Rain forests may be critically affected by the frequency of severe storms (Boucher, 1990). These examples show that animal populations may suffer important set-backs after extreme climatic events for which recovery time may exceed intervals between such weather disruptions if their frequency increases in a scenario of global climate change. The emphasis in the literature is on negative repercussions of extreme climatic conditions on animal populations, although some prolonged heat waves may have positive effects on some species due to disturbance effects on competitors, herbivores, parasites or predators (e.g. Holmgren et al., 1996). Moreover, many invasive species are dependent on ephemeral habitats created by weather-induced environmental alterations and may strongly benefit from extreme climatic events. We will here focus on negative impacts on animal populations while acknowledging that many species depend on new habitats created by severe weather disturbances.

Our objective in this review is to present a first synopsis of the impacts of extreme weather events on life history traits. To that end, we will first review the general evidence for dramatic effects of recent extreme weather-related events on animal populations (section 2). These effects on populations may impinge on crucial life history traits such as fecundity and survival. Thus, we subsequently review specific impacts on breeding output (section 3) and adult survival (section 4) in natural populations. Responses to extreme climatic events may be facilitated by phenotypic flexibility or lead to genetic change. Thus, we next consider from a theoretical viewpoint the potential importance of phenotypic plasticity and microevolutionary change as mechanisms of adaptation to extreme climate (section 5). In the case of microevolutionary change, we could expect to find evidence of life history evolution in animal populations. The direction of potential evolutionary changes in life history traits is therefore considered next (section 6). In this context, we next review the scant evidence for recent changes in fecundity possibly related to extreme climate which could derive from predicted micro-evolutionary change (section 7). The absence of

systematic research programs on links between extreme climate and the potential for life history evolution reflected in this review calls for renewed efforts by ecologists. Thus, in a final section (section 8) we propose methods that allow detection of effects of increased weather-related breeding failure in long-term population studies. Here we also list a number of ways in which hypotheses about effects of extreme environmental conditions on life histories can be tested, as well as of reviews that can further our empirical knowledge about the consequences of extreme environmental conditions. We also suggest establishing some fixed standard meteorological distributions for conditions prior to global change in order to be able to estimate its effects at all.

2   General Evidence for Impacts of Extreme Climate

The recent literature covers many cases of dramatic impacts of recent extreme climatic events on animal populations. We will not consider paleo-climatological or paleontological evidence in this review. The literature on impacts of extreme events applies the terminology of meteorologists to weather conditions without clearly stating how rare they are in relation to the climatological probability distribution (5% level or less). Thus, some papers report as extremely high temperatures those above the 75th percentile (e.g. Mantzouni and MacKenzie, 2010). Here, consideration of climatic conditions as extreme has been derived from the authors' own interpretation by searching the Web of Science for papers including the term 'extreme' in relation to climate or weather and either fecundity or survival. We assume that the scientists most familiar with the study system in question are the best at making such a judgment. There may be a heavy bias to report negative rather than positive effects of extreme weather, which may be partly due to a social demand for predicting the consequences of future climate change scenarios. One case of negative effects is the extreme temperature anomaly in Europe in 2003, when summer temperatures in France and other countries exceeded 35ºC for several weeks. Many bird species decreased dramatically in abundance in response to this extreme situation, showing evidence of either reduced reproductive success and/or survival as a consequence of the extremely high temperatures (Jiguet et al., 2006). However, it has also been reported for numerous species of insects (dragonflies, butterflies, acridids) and birds that populations with a mostly southern distribution, for instance occurring in Mediterranean biomes, show a high reproductive

output in hot years at higher latitudes, boosting their demography and leading to colonization of northern areas beyond the traditional range (e.g. Kinzelbach et al., 1997). Interspecific differences in the sign and magnitude of the effects of the 2003 conditions highlight the fact that not all species were equally affected, and that some species were particularly resilient to extreme environments as reflected by their broad thermal geographic range. Unfortunately, we have no information on clutch size, laying date, nest desertion or survival before, during or after this extreme event. An understanding of such interspecific differences and the underlying mechanisms is crucial for research in this important area.

The diversity of potential effects covered by the literature is impressive. Thus, butterfly migration may be impeded by strong winds, leading to decreased survival (Hellman, 2002). Extreme alteration of seasonal cycles may also lead to mass mortality. Thus, exceptionally wet conditions prior to the flowering season in 1970 led to failed fruiting and massive famine and starvation for most mammals on Barro Colorado Island (Foster, 1982). Mass starvation of anchovy and other fishes (Harte et al., 1992) and significant damage on tropical coral reefs (Glynn, 1984; Goreau, 1990) frequently follow strong temperature anomalies in seawater (the equivalent of changes in air temperatures for marine organisms) caused by El Niño events. A severe drought along the migratory flyway of North American shorebirds caused birds to leave stopover sites with insufficient fuel reserves to reach better areas (Myers and Lester, 1992). Droughts may also increase the incidence of wide-ranging wildfires (Davis and Zabinski, 1992). Prolonged droughts in tropical rainforest biomes may lead to crowding of freshwater shrimp in remaining water pools and consequent prolonged decreases in reproductive output (Covich et al., 2003). However, some populations may experience short-lived bonanzas during extreme climatic events due to increased food availability. Thus, Andean condors *Vultur gryphus* experienced a pulse of reproduction after an El Niño event induced high carrion abundance in some areas (Wallace and Temple, 1988). Folivorous insects may benefit from droughts through reduced plant defences (Rubenstein, 1992; but see Murphy and Weiss 1992). Although examples of positive effects on populations of long-term changes in climatic conditions have been reported (e.g. Kitaysky and Golubova, 2000; Gaston et al., 2005; Halupka et al., 2008; David and Gillon, 2009; David and Handa, 2010; D'Alba et al., 2010), there is scant information on positive effects of extreme events (e.g.

Holmgren et al., 1996; Kinzelbach et al., 1997), as they are probably deleterious for most organisms, especially for events related to thermal changes and for temperature-constrained animals. In general, we can expect changes in individual performance in relation to extreme climatic events which may have implications at the population level.

3 Extreme Weather and Reproductive Failure

Some extreme weather events may induce massive reproductive failure where most adults do not breed or attempt reproduction but fail to produce any offspring. There are several population studies including extreme environmental conditions for which actual failure rates can be estimated (Table 1). Mean failure rate during normal conditions was 27.2% ($SE = 6.0$), $n = 14$, but 79.0% ($SE = 6.0$), $n = 14$ during extreme conditions, a difference of almost a factor three. This difference is highly significant (paired t-test based on square-root arcsin-transformed values: $t = 8.00$, $df = 13$, $P < 0.0001$). Evidence for these is particularly strong for some marine organisms. During the 1982–1983 El Niño Southern Oscillation (ENSO), an entire seabird community disappeared (Schreiber and Schreiber, 1984). Recruitment failure has also been observed in marine fishes during such events (Peterson et al., 2006). Elevated sea-surface temperatures also lead to increased reproductive failure in baleen whales (Leaper et al., 2006). During the ENSO years of 1983 and 1993 a variety of seabirds suffered widespread mortalities and breeding failures in the Gulf of Alaska (Bailey et al., 1995). Atmospheric cooling in the Arctic after the 1991 Pinatubo eruption resulted in higher proportions of non-breeders and low hatching and fledging success, which led to an almost complete reproductive failure for waterfowl and waders across the Arctic in that year (Ganter and Boyd, 2000). The exceptionally cool and rainy summer of 1981 led to severely reduced breeding success of both seabirds and land birds in Finland (Hildén et al., 1982). Saltmarsh nesting birds experience increasingly frequent and catastrophic flooding of nests in Europe's largest estuary (van de Pol et al., 2010). Severe droughts may also result in near total reproductive failure (e.g. Durst et al., 2008). All these examples indicate that breeding failure rates may increase by an order of magnitude in relation with extreme climatic events.

Abandoning clutches or broods is the usual proximate cause of breeding failure. Desertion of offspring is presumably endocrinologically mediated by elevated

Table 1   Examples of studies investigating the effects of extreme environmental conditions on complete reproductive failure

Species	Extreme event	Complete reproductive failure in normal years	Complete reproductive failure in extreme years	Reference
Anous stolidus	Cyclones	21.4%	74.5%	King et al., 1992
Baelophus wollweberi	Drought (La Niña)	15%	82.5%	Christman, 2002
Chamaea fascista, Pipilo maculates, Pipilo crissalis, Aimophila ruficeps	Drought (driest year in 150 years)	12% (no attempt at reproduction) 1.36–3.14 fledglings per pair	93.3% (no attempt at reproduction) 0.00–0.12 fledglings per pair	Bolger et al., 2005
Ficedula albicollis	Cold spring	8%	23%	Wiggins et al., 1994
Geospiza fortis	Drought	17.1% (raised no fledglings)	100% (no attempt at breeding)	Boag and Grant,1984
Larus occidentalis	Heat wave	0% (good locality during same year)	90% (poor locality during same year)	Salzman, 1982
Neotoma lepida	Drought (half of normal precipitation)		100% (no individual in breeding condition)	Smith,1995
Pagodroma nivea	ENSO	48.7%	79%	Chastel et al., 1993
Puffinus pacificus	High sea- surface temperature	3.4%	50%	Smithers et al., 2003
Ptychoramphus aleuticus	High sea-surface temperature	30%	100%	Sydeman et al., 2006
Phalacrocorax pelagicus	ENSO	20%	52%	Hodder and Graybill, 1985
Phalacrocorax penicillatus	ENSO		100% (no attempt at reproduction)	Hodder and Graybill, 1985
Sterna benghalensis	Cyclones	67.6%	100%	King et al., 1992
Sterna bergii	Cyclones	48.2%	90.5%	King et al., 1992
Sterna fuscata	Cyclones	52.5%	88.7%	King et al., 1992
Sus scrofa	Drought	10% (non-breeding females)	83.1% (non-breeding females)	Fernández-Llario and Carranza 2000, Massei et al., 1996
Xantocephalus xantocephalus	Drought (>2 SE below 71-year average)	55.6%–58.8%	100%	Fletcher and Koford, 2004

Species are listed in alphabetic order.

levels of corticosterone or other stress hormones (Love et al., 2004). Thus, elevated parental corticosterone levels were found in a year of total breeding failure in blue-footed boobies *Sula nebouxii* (Wingfield et al., 1999). Breeding failure may also be associated with parental mortality during the reproductive event (Ankney and MacInnes, 1978). Female salamanders defer these episodic survival costs of breeding by not reproducing when risks of adult mortality are high (Church et al., 2007). This failure may in some cases be directly related to exposure after storms (Sealy et al., 1986). Failure of reproductive organ recrudescence is a frequently undetected cause of null reproductive output (Koerth and Guthery, 1991). Skipped breeding is probably due to hormonal signals related to nutritional condition of breeders. Advancing the date of breeding as envisaged in some models on responses to climate change in fact involves increasing the risk of confronting adverse conditions prior to breeding in some areas (Jonzén

et al., 2007). Thus, it can be equated in some circumstances with increased reproductive effort. We may consequently fail to detect any advancement of breeding in cases when selection does not favour increases in reproductive effort (e.g. Sanz et al., 2003; Visser et al., 2004).

4   Extreme Weather and Adult Survival

Effects of climate on survival of adults are more difficult to monitor in natural populations than breeding success. However, a few studies have demonstrated reduced adult survival rates during extreme weather conditions (Table 2). The ratio of survival rate in normal and extreme years was 0.349 ($SE = 0.086$), $n = 6$ studies, differing significantly from the expected value of one when survival values were similar under the two conditions (one-sample t-test, $t = 4.04$, $df = 5$, $P = 0.010$). Thus survival rate in extreme years was around one third of what it was in normal years. Clearly, there is

Table 2   Examples of studies investigating the effects of extreme environmental conditions on adult survival rate

Species	Extreme weather condition	Survival in normal years	Survival in extreme years	Reference
Ambystoma tigrinum	Drought 2002	100% Females 2000–2001	55% Females 2001–2002	Church et al., 2007
Cepphus columba	ENSO 1983	3 dead birds 1981, 7.4 km beach	27 dead birds 1983, 7.4 km beach	Hodder and Graybill, 1985
Geospiza fortis	Drought 1977	93 % females 91% males (March-December 1976)	17% females 50% males (March-December 1977)	Boag and Grant, 1984
Hirundo rustica	Extreme drought in North Africa	27% females 34% males	15% females 19% males	Møller and Szép, 2005
Tyto alba	Severest winter in 68 years	57%	25%	Altwegg et al., 2006
Uria aalge	ENSO 1983	0.25±0.10 dead birds/km beach July (1978–1982)	3.38 dead birds/km beach July 1983	Hodder and Graybill, 1985

Species are listed in alphabetic order.

further need for clearly showing a link between climatic extremes and adult survival. However, one possible conclusion from such studies is that the relationship between weather and survival observed during regular years is likely to underestimate the importance of climate variation for population dynamics.

The impact of extreme climate on population dynamics may operate mainly through effects on adult survival during the non-breeding season (e.g. cold winter spells in temperate latitudes), or alternatively through effects on recruitment due to juvenile survival (e.g. weather anomalies during the breeding season). Thus, in a 68-year study of barn owls *Tyto alba* including two extremely harsh winters, survival decreased non-linearly with winter harshness for adults but linearly for juveniles (Altwegg et al., 2006; Table 2). Thus, extreme climate seems to have a relatively larger impact on adults than on juveniles in this population (Altwegg et al., 2006). In contrast, large fluctuations in adult population size in wood frogs primarily occurred due to drought-induced catastrophic larval mortality (Berven, 1995). In elk *Cervus virginianus* populations, the severity of snow-pack conditions only had effects on adult survival during the most extreme winter, while it had a pronounced effect on recruitment, the most severe conditions resulting in virtual elimination of a juvenile cohort (Garrott et al., 2003). The two alternative models have especially been studied in birds, leading to predicted differences for species differing in habitats and life histories (Sæther et al., 2004). While selection induced by changes in recruitment may favour reduced reproductive effort per breeding attempt and increased iteroparity (see above), the first scenario may in fact select for semelparity or maximized reproductive effort (Rubenstein, 1982; 1992). Thus, there is evidence in a small rodent that adaptations to an increasingly harsh environment affecting adult survival during the early Holocene favoured a switch from iteroparity to semelparity (Smith and Charnov, 2001).

5   Phenotypic Plasticity and Micro-evolution

Organisms can react to environmental changes by either showing phenotypic plasticity or micro-evolutionary adaptation. Phenotypic plasticity occurs when an individual develops a phenotype depending on the environment experienced. Such plasticity can either be fixed after exposure to environmental conditions during development as is the case for body size, or the phenotype can be re-set annually as is the case for laying date or clutch size. Phenotypic plasticity may ensure responses to variable environments, but perhaps not account for adjustments to extreme environmental conditions. Environmental variability can have different effects on life histories depending on its predictability (Levins, 1968). Predictable variation may select for phenotypic plasticity, where reaction norms express the usual range of environmental variation experienced by populations (Schlichting and Pigliucci, 1998; Meyers and Bull, 2002). Extreme weather events are so rarely experienced that they may provide little or no selection on reaction norms to cope with such situations. Theory shows that as the range of environmental conditions increases, optimal phenotypic plasticity may become unachievable (Via and Lande, 1985; Van Tienderen, 1991; de Jong, 1995; Fischer et al., 2009). Although some degree of tolerance to certain strong environmental disturbances may be expected (e.g. Penteriani et al., 2002), coping mechanisms may only be effective below a threshold of climatic extremes as shown for alpine and arctic birds (Martin and Wiebe, 2004). It is presumably more difficult to infer that habitat quality

has decreased from changes in the frequency of rare and unpredictable events than from trends in climatic means (van de Pol et al., 2010).

Optimal phenotypes in stochastically fluctuating environments are different from optimal phenotypes in constant environments (Tuljapurkar et al., 2009). Selection occurs as a consequence of differences in fitness among individuals linked to abiotic or biotic selective agents. While numerous studies have quantified and shown extensive evidence of selection (Kingsolver et al., 2001) that can readily change phenotypes across just a few generations, given additive genetic variation (Hendry and Kinnison, 1999), there are relatively few examples of what happens under extreme conditions. A textbook example is the study of selection on Darwin's finches during the extreme El Niño year 1977, resulting in a change in beak and tarsus length linked to changes in availability of seeds of different size (Grant and Grant, 1995; 2002). A second textbook example concerns viability selection on morphology in house sparrows *Passer domesticus* during a blizzard, leading to dramatic changes in morphology after selective mortality (Bumpus, 1899). Other examples of less extreme events that caused dramatic mortality are known (Jones, 1987; Møller, 1994; Brown and Brown, 1999; 2000; Møller and Szép, 2005). With the exception of these few examples, we know very little about the intensity of selection during normal and extreme environmental conditions, and we are unaware of any studies dealing with life history with the exception of selection on arrival date in cliff swallows *Petrochelidon pyrrhonota* (Brown and Brown, 1999) and barn swallows *Hirundo rustica* (Brown and Brown, 2000; Møller, 1994), where early arriving individuals suffered from excess mortality during extremely cold springs.

Selection may affect different phenotypes to a varying degree. When the difference in phenotype between survivors and non-survivors (or successful and failed breeders) is distinct, we are dealing with truncation selection that eliminates all individuals on one side of a certain threshold in trait value (Milkman, 1978; Crow and Kimura, 1979). We expect that the extent to which selection acts as truncation selection should increase with extremeness of the environment. Extreme weather may operate as an all-or-nothing process by creating conditions which require top behavioural and physiological performance. As environmental conditions become more extreme, an increasing number of individuals will find their environmental tolerance overwhelmed, resulting in excess mortality beyond a certain threshold (i.e. truncation selection). This is not just a hypothetical possibility, as evidenced by more than 15,000 excess human deaths in France alone during the extreme heat wave in 2003 (INSERM, 2003[1]). Moreover, even if truncation selection also operates during normal conditions, the threshold may shift towards including only the most extreme phenotypes during unusual climatic events (Mitton, 1997). Truncation selection is usually more efficient (requires fewer deaths or failures) in shifting the mean and variance of traits than non-truncation selection where fitness is a smooth function of trait value (Crow and Kimura, 1979). Thus, if there is a clearer distinction between selected and other individuals due to their ability to cope with extreme environmental conditions this could facilitate micro-evolutionary adaptation to climatic extremes. However, to what degree extreme weather induces clear thresholds in life history trait values is currently unknown. There is a clear need for theoretical explorations of life history implications of extreme events, in contrast to mere stochastic variation.

Extreme environmental conditions may result in micro-evolutionary adaptation to these extreme conditions. In the example with the extreme ENSO event and Darwin's finches, there was a micro-evolutionary change in beak morphology subsequent to selection (Grant and Grant, 1995; 2002). A similar case was reported for body size in sand martins *Riparia riparia* after a climatically-driven population crash (Jones, 1987). However, the phenotype later converged towards the variant that was predominant in the population before the extreme event. For life history traits we are only aware of a micro-evolutionary change in arrival date of cliff swallows following extreme selection during a cold spring, because arrival continued to be late in subsequent years despite the fact that there was intense selection for early arrival due to increased reproductive success (Brown and Brown, 2004). However, even in this case arrival date returned to pre-selection levels after a few years.

Breeding failure increases the temporal variance in reproductive output of phenotypes and thereby reduces geometric mean fitness. The geometric mean is the appropriate fitness measure in stochastic environments,

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[1] INSERM, 2003. Impact de la canicule sur la mortalité: les premiers résultats de la mission d'expertise de l'Inserm. Available at http://www.inserm.fr/fr/ questionsdesante/dossiers/sante_environnement/att00000579/25septembre2003.pdf.

and it is normally lower than the arithmetic mean (Cohen, 1966). Some authors have questioned the capacity of temporal stochastic variation to have an important effect on reproductive effort (e.g. Sibly et al., 1991; Cooch and Ricklefs, 1994; Roff, 2002). However, this conclusion rests on considering large differences between "good" and "bad" years as unrealistic and extreme. Here we are dealing with precisely such "unrealistic", but increasingly frequent scenarios. Extreme events in many cases imply "extremely poor" conditions. Benton and Grant (1999) included density dependence in their models of reproduction and related optimal effort in stochastic environments to that in constant or deterministic environments. They concluded that a marked decrease in optimal reproductive effort was most likely when the deterministic effort was low (long-lived prudent reproducers) and the environmental variance high (frequent extreme events). Massive reproductive failures imply extremely high environmental coefficients of variation, probably far above the 20% postulated by Cooch and Ricklefs (1994). Breeding output in extreme and normal years may differ by at least one order of magnitude (Table 1). Thus, the conclusion by Roff (2002) about expected small changes in reproductive effort induced by environmental stochasticity probably does not apply to mass breeding failure during extreme climatic events. Levels far below the 50% reductions in optimal effort maximally predicted by Benton and Grant (1999) would in fact imply an important selection pressure for reduction in reproductive effort. However, this reduction would only apply to conditions of moderate to high energy availability (Fischer et al., 2009).

Another possible response to fluctuating environmental conditions is partial brood reduction (Lack, 1954). Given uncertainty in conditions during the impending breeding event, selection may favour an "optimistic" clutch size that can be reduced either passively or by active intervention if conditions deteriorate (Lack, 1954). Models of brood reduction that have incorporated geometric mean fitness have shown that selection will favour the overproduction of offspring provided that the costs in bad years are more than balanced by the gains in good years (Temme and Charnov, 1987; Forbes, 1991; Ford and Ydenberg, 1992; Konarzewski, 1993). However, extreme climatic events may rather induce selection for desertion of the entire brood than partial brood reduction that appears more suitable for the normal range of breeding conditions. Trying to breed in extremely poor conditions may jeopardize the survival

of adults (e.g. Gaston et al., 2002) and select for desertion. Thus, selection should minimize pre-breeding survival costs, potentially leading to abandonment of the breeding attempt (Jönsson et al., 1995). Parental death at the nest is the extreme consequence of high pre-breeding costs (Ankney and MacInnes, 1978). Death after storms has sometimes been observed in small birds during incubation, a potential consequence of high pre-breeding costs (Sealy et al., 1986).

6 Life History Consequences of Extreme Climate

Two possible consequences of extreme weather events on life histories are reduction in adult and juvenile survival rate and increased frequency of reproductive failure. Life history theory predicts that increased temporal environmental stochasticity should lead to increased iteroparity and reduced reproductive effort per breeding attempt (Charlesworth, 1994). This would reduce the negative effect of catastrophic years on lifetime reproductive success. In extreme cases, skipping reproduction entirely in some years would be selected if there are high survival risks for breeding adults derived from the preliminary costs of attaining breeding condition (Ankney and MacInnes, 1978; Church et al., 2007). In contrast, elevated spatial stochastic variability should select for enhanced dispersal or migration (Levin et al., 1984; Roff, 1975). Theory also predicts selection for genetic variability in offspring, a phenomenon that has been called "spreading the risk" (den Boer, 1968) or "bet-hedging" (Slatkin, 1974). Thus, offspring variability related to increased migration, more frequent dormancy, more variable diapause (Danks, 2004) or hatch delay (Khatchikian et al., 2009), variation in aestivation (Winne et al., 2006), or in any trait allowing avoidance of effects of local extreme events may be favoured. However, whereas there is abundant evidence that fecundity-related traits are heritable, there is no convincing evidence that generation of random offspring variation has a genetic basis (Roff, 2002). Thus it seems much more likely that selection in temporally stochastically variable environments will cause changes in reproductive effort than in bet-hedging.

Extreme events may also disproportionately affect the survival of specific age classes. If juveniles are more strongly affected than adults, increased iteroparity or reduced reproductive effort would be favoured as in the case of reproductive failure (see above). However, an increased adult mortality between breeding events driven by climate should favour reduced age at first

reproduction and therefore higher reproductive effort (Gadgil and Bossert, 1970; Michod, 1979). Moreover, different age classes that inhabit different environments such as marine habitats and streams in the case of anodromous fish may experience differential sensitivity to extreme climate (Rubenstein, 1982; 1992). Life history theory predicts that reduced juvenile survival with respect to adult survival should select for iteroparity or reduced reproductive effort, while the opposite would be the case if climate mainly affects adult life stages (Rubenstein, 1992).

Life history theory leads us to expect that more frequent extreme weather events may either increase phenotypic plasticity or, more probably, induce evolutionary changes leading to either reduced reproductive effort, or, alternatively, enhanced effort or semelparity. In the first scenario, compensatory responses such as enhanced fecundity can be sufficient in some populations to accommodate the effects of extreme weather conditions (Kalcounis-Rueppell et al., 2002). In the second scenario, selection for either alternative may depend on the stage of the life cycle at which extreme climate has the strongest effects, adult survival between breeding attempts or reproductive output. Selection for prudent phenotypes that invest less in reproduction may affect population dynamics in a scenario of global change and reduced population sizes for many organisms. Moreover, an increase in stochasticity reduces the long-term population growth rate compared to that in a constant environment (Sæther et al., 2004). Selection for lower fecundity will aggravate this effect. Some populations are mainly sustained by intense reproduction and will probably fare poorly if selection mainly favours reduced fecundity. Chronic reproductive failure and reduced reproductive drive in mass spawning populations may induce deleterious Allee effects (Knowlton, 2001). Inbreeding depression in small populations may preclude adjustment of life history traits to climate change (e.g. Schiegg et al., 2002). Moreover, intermittent recruitment in some populations may only result in population persistence if compensated by relatively high adult survival (Griffiths et al., 2010). Both intermittent recruitment and lowered survival elicited by extreme weather is a recipe for population extinction.

A strategy of retaining resources for another bout of breeding, when survival prospects between breeding seasons are low, may not be favoured. Thus, it is important to identify the life cycle phase most affected by extreme climatic events, which may differ geographically or depending on habitat. The capacity to escape extreme events through migration may also affect how climatic extremes impinge on life histories. Thus, a scenario of dramatically lowered survival probabilities may be especially prevalent in less mobile organisms. In fact, migration is presumed to have evolved as a response to spatially heterogeneous environments in terms of survival probability (Southwood, 1962; den Boer, 1968; Dingle, 1996), allowing highly mobile organisms such as birds to escape extreme weather disturbances (e.g. Boyle et al., 2010).

7   Evidence for Changes in Life Histories

From the theoretical arguments raised above it is possible to predict micro-evolutionary changes in reproductive effort. These changes should be most evident in populations of short-lived organisms given their short generation times and the very recent global climate changes with respect to extreme climatic events. The literature has been scanned for evidence of either reduced or increased fecundity in relation to the frequency of extreme climatic events. However, evidence for reduced reproductive effort derived from long-term population studies is scant and contradictory. In a German eagle owl *Bubo bubo* population, a conspicuous decrease in the number of young per successful brood was detected, which was compensated by a decrease in the proportion of total breeding failures (Dalbeck and Heg, 2006). The average clutch size of arctic-breeding geese declined during the warming period from 1951 to 1986 (MacInnes et al., 1990). In contrast, no trend in clutch size during 12 years of study was detected in wood warblers *Phylloscopus sibilatrix* (Wesolowski and Maziarz, 2009). In shrikes, no trend was detected throughout the last century (Tryjanowski, 2002). In some birds advancement of breeding has been accompanied by larger clutches (Husek and Adamik, 2008). No long-term trend in the fecundity of freshwater coregonids was found between the 1970s and the 1990's (Harrod and Griffiths, 2004). The capacity to detect evolutionary changes in life history induced by extreme climatic events is limited by our ignorance about what factors may be driving these potential trends and by the short period during which these changes in climate have been acting. Sustained changes in average climatic conditions may have stronger effects than stochastic variation and have received a great deal of attention in the literature (Jentsch et al., 2007). We also ignore at present if breeding failure and adult mortality induced by weather extremes strikes randomly at populations, or if certain phenotypes are disproportionately penalized by

climatic stochasticity. If there is truncation selection due to climatic extremes, we may expect detectable effects in the phenotypic composition of populations evidenced by marked shifts in certain life history traits.

It is important to make the distinction between genetic or evolutionary and phenotypic responses including a plastic component (Møller and Merilä, 2004; Gienapp et al., 2008). Moreover, deteriorating environmental conditions may mask a predicted evolutionary response in breeding value by showing contrary trends in phenotype (e.g. Merilä et al., 2001). However, as stated above, extreme climatic events are presumed to exceed the capacity to expand reaction norms due to inherent costs of evolving an extreme plasticity covering such emergencies (DeWitt et al., 1998; Scheiner, 1993). Furthermore, the complex genetic architecture of life history traits and the multiplicity of trade-offs involved may preclude or delay evolutionary responses to selection (Sheldon et al., 2003). Detection of evolutionary responses to extreme climatic events is thus marred by methodological complications that may preclude our ability to predict population-level consequences.

8   Future Prospects

Research into the life history consequences of extreme weather may make use of data recorded during long-term population studies. The longer the period covered by these studies, the higher the probability that it will include one or more extreme climatic events affecting either adult survival or breeding output. This effect with respect to so-called 'unusual' events was detected in population studies with durations up to six years, with no further increase for longer durations (Weatherhead, 1986). This finding was explained by the tendency of researchers to assign the term 'extreme' or 'unusual' in relation to how much these conditions affect results and interpretation obtained during a multi-year study. With increasing number of years, unusual events become less important for general conclusions and presumably therefore are evaluated as less 'unusual'. Both in Weatherhead's (1986) and our study, the terms 'extreme' resp. 'unusual' have been adjudicated by the authors themselves, which implies a certain degree of subjectivity. We have assumed in this review that authors have derived their interpretation about the rarity of the events from clear meteorological standards for the time of year and area considered. To avoid subjectivity in the characterization of climatic conditions as extreme, authors should clearly state how rare the event was in relation to the present climatological distribution

of the variable in question for the locality and time of year. Given presumed shifts in distributions of meteorological variables due to global change, it is imperative to establish some pre-change standard distributions to estimate impacts of extreme climate in the future. The 5% cut-off point should be applied in relation to these pre-change standards. However, this need would not affect studies measuring the impact of hurricanes, cyclones or heavy storms which are extreme by definition. There is also much need for studies reporting positive effects on reproduction and survival of extreme climatic events. The bias in the literature towards reporting only negative consequences may need correction.

Increased frequency of climatic extremes may be detected as higher incidence of seasons with low average breeding success with low variance among individuals or breeding pairs. One way of exploring this type of data is to plot seasonal variances in breeding success in relation to seasonal average breeding success (Moreno et al., 2003). Thus, for short-lived organisms these functions frequently drop to a low variance near maximum average breeding success. Other more long-lived species show curvilinear functions increasing from conditions of very low average breeding output with low variance (mass failure) to medium average success with high variance (Moreno et al., 2003). We should expect more frequent climatically-driven mass failures to be expressed as shifts from monotonically declining variance to mean functions to concave-down functions including low averages with low variances (near total failure). Extreme climatic events would lead to changes in the form of the mean- to variance function in breeding success (Fig. 1). Such shifts would predict serious problems for populations highly dependent on annual recruitment.

We propose a number of empirical tests of the effects of extreme environmental conditions on life history traits which can be addressed in future studies. Although it is mostly unknown which phenotypes are more strongly affected by reproductive failures, one prediction would be that failure will be more frequent in individuals in poor condition. Thus, we can expect that late breeders or individuals laying smaller clutches should be critically affected by extreme climate. Also, individuals in poor pre-breeding condition could suffer higher mortality during the breeding event. More ornamented phenotypes could also signal their capacity to withstand extreme conditions given that sexually selected ornaments are usually condition-dependent. Alternatively, extreme weather may hit at random among
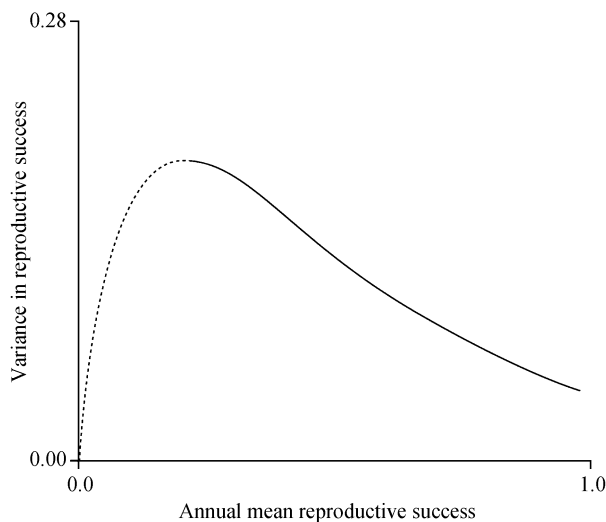
Fig. 1 Schematic presentation of a shift towards lower variances in reproductive success associated with lower means induced by climatically driven increases in reproductive failure as derived from the model by Moreno et al. (2003)

Line in bold represents the normal decreasing trend in variance with improved conditions shown by many populations while the dotted line represents the increasing frequency of mass failures due to climatic extremes which lead to reduced variances (most individuals fail).

phenotypes. Food availability, health state or access to predators could interact synergistically with extreme weather disruptions to accentuate the effects of climate even further. Experiments of food supplementation, medication or protection of nests from predators offer a possible avenue of research on these crucial interactions. As life history theory is based on the existence of trade-offs between post-reproductive survival and reproductive effort, it is possible that reproductive costs are especially strong during extremely poor breeding conditions. Increasing or reducing reproductive effort through clutch or brood size manipulations could answer if reproductive costs relate to extreme climatic conditions while breeding. The same tests may also relate to adult survival between reproductive events. Thus, individuals showing poor condition either directly or through their fecundity and/or ornamentation patterns could be those most affected by mortality induced by extreme climatic conditions. Food availability, health state or predator pressure could also affect mortality induced by weather. Finally, reproductive costs could also have delayed effects on mortality between reproductive events and interact with extreme climatic events.

The possibility that extreme weather will induce truncation selection or shift the threshold of truncation towards extreme trait values has not been explored. Truncation selection should be detected by comparing life history traits of failed and successful breeders or of killed and surviving adults. A shift in thresholds would require comparing normal and extreme conditions. It is probably easier to find truncation with respect to breeding failure than to adult mortality given the problems in finding individuals killed by weather events and with known life history traits. A consequence of more intense truncation selection would be a faster microevolutionary response to the incidence of extreme climatic events with increasingly smaller effects of repeated weather events.

We propose a number of reviews and meta-analyses that may clarify the importance of extreme climatic events for evolutionary changes in life histories. Habitat quality may be crucial in explaining effects of extreme climate. Thus, in several seabird studies reported in Table 1, some colonies or parts of colonies were much more heavily affected than others by weather or by climatically induced oceanographic disturbances. In this scenario, habitats at the distribution margins may turn into population sinks due to extreme weather events. This prediction assumes negative impacts of extreme events, which may not be true as positive effects have also been reported (e.g. Holmgren et al., 1996; Kinzelbach et al., 1997). Moreover, intensity of selection will be higher in poor marginal habitats. Alternatively, extreme weather may hit indiscriminately so habitat quality under normal conditions may not have any predictive value for extraordinary climatic circumstances. On the other hand, extreme environmental conditions may increase the amount of environmental variance expressed in life history traits and reduce the amount of genetic variation on which selection can act (Hoffmann and Parsons, 1997; Hoffmann and Merilä, 1999). This would delay or prevent adaptation to future climate scenarios. Thus, there is a need to study the heritability of life history traits in relation to habitats with varying frequency and intensity of weather perturbations. Furthermore, it is unknown to what degree extreme conditions impose truncation selection in natural populations, or whether they shift the selection threshold to more extreme phenotypic values. Truncation selection is more efficient than gradual selection for the same level of breeding failure or mortality and could allow adaptation to future climate scenarios. The amount of genetic variation and population size may also facilitate evolutionary adaptation to increased frequency of extreme events. Other factors that may interact with climate to

determine the impact of weather disturbances are population density, body size, migration or mobility and type of distribution. We may predict that large, mobile and homogeneously distributed animals may have a higher resilience against climatic extremes. More dense populations may also suffer more strongly from extreme weather. Larger animals may store sufficient body reserves to allow survival or breeding activities during extreme weather, especially if disturbances are of short duration. Many mobile animals may avoid the full impact of weather disturbances through migration in altitude or irruptive movements. Populations of animals with clumped distributions during breeding (colonial) or of a higher degree of sociality (living in aggregations) may suffer heavily from local weather disturbances, while more homogeneously distributed animals may experience relatively fewer losses. This means that stochasticity may be stronger for animals living or breeding in aggregations. There may be also density-dependent effects on climate-driven reproductive failure or mortality. All these associations remain to be tested through comparative studies.

The conservation implications of sensitivity to extreme climate are crucially important (McCarty, 2001). The issue is which species or populations may be most resilient to increased frequency of extreme events and if selection may be intense enough to permit adaptation or alternatively trigger extinction vortices. For instance selection for reduced reproductive effort as suggested above may select for extremely prudent reproducers that skip breeding as soon as conditions turn adverse, as these may have the highest probability of breeding again after a heavy weather disturbance. Selection for these phenotypes may trigger an extinction vortex for many populations. On the other hand selection for semelparity may increase sensitivity of future phenotypes to extreme events by eliminating whole cohorts in certain populations affected by locally and temporally restricted weather disturbances. Finally, selection for increased plasticity may be prevented by the costs of enlarging reaction norms in integrated phenotypes. Extreme climate events have the potential to put to the test organismic performance as no other environmental factor.

We strongly believe that thorough analysis of existing long-term individual-based and population-based data will provide us with important insights into the effects of extreme environmental conditions on life history traits. Finally, we also believe that exhaustive meta-analyses of life history variation and selection on life history during normal and extreme environmental conditions will broaden our understanding of future evolutionary scenarios related to extreme climate.

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