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PERSPECTIVE

Observational field studies reveal wild birds responding to early-life stresses with resilience, plasticity, and intergenerational effects

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ABSTRACT

An extensive experimental literature documenting negative impacts of early stresses such as food deprivation, elevated corticosterone, and brood enlargement on numerous morphological, physiological, and behavioral traits of adult birds has left the impression of generalized developmental vulnerability to stress in birds. However, descriptive studies of wild populations, most of them recent, are indicating that natural stresses can sometimes elicit resilience or flexible variation in adult life history traits, and that such plasticity can neutralize impacts of stress on fitness. Experiments, almost entirely in captivity, were not designed to detect such effects, and most were not suited for this purpose in that treatments did not mimic natural stresses, effects were seldom measured over the lifespan, and fitness consequences were rarely assessed. Future research needs to take into account that early stresses can elicit positive developmental responses, that the direction of effects of stresses can depend on their magnitude, and that a deficit in one fitness component can be compensated by modification of others. Different styles and types of research can shed more light on avian developmental plasticity by characterizing natural stresses more precisely, measuring their effects on diverse variables including fitness over the lifespan, conducting field experiments, and adopting a life history framework.

Keywords: phenotypic plasticity, developmental stress, resilience, intergenerational effects

Estudios observacionales de campo revelan que las aves silvestres responden al estrés en la vida temprana con resiliencia, plasticidad, y efectos intergeneracionales

RESUMEN

Un extenso cuerpo de literatura experimental documentando los impactos negativos que tienen distintos tipos de estrés durante la vida temprana, incluyendo la restricción del alimento, la corticosterona elevada y el aumento del tamaño de la nidada, sobre numerosos rasgos morfológicos, fisiológicos y conductuales de las aves adultas, principalmente en cautiverio, ha dejado una impresión de vulnerabilidad generalizada al estrés en las aves. Sin embargo, estudios descriptivos de poblaciones silvestres, en su mayoría recientes, indican que el estrés natural puede también provocar resiliencia o variación flexible en rasgos de historia de vida durante la adultez, y que dicha plasticidad puede neutralizar los impactos del estrés sobre la adecuación. Los trabajos experimentales, realizados principalmente en cautiverio, no sólo no fueron diseñados para detectar dichos efectos, sino que tampoco eran adecuados para ese propósito debido a que los tratamientos no imitaban los estreses naturales, los efectos pocas veces eran medidos a lo largo de la vida, y las consecuencias sobre la adecuación rara vez fueron evaluadas. La investigación futura debería de tomar en cuenta que el estrés durante la vida temprana puede provocar respuestas de desarrollo positivas, que la dirección de los efectos puede depender de la magnitud del estrés experimentado, y que la deficiencia en un componente de la adecuación puede ser compensada con la modificación de otros. La investigación mas variada tendrá mas posibilidad de mejorar nuestro entendimiento acerca de la plasticidad del desarrollo en las aves si caracteriza con mayor precisión los estreses naturales, si mide sus efectos en diversas variables incluyendo la adecuación de por vida, si incluye experimentos de campo y si además adopta un marco de historia de vida.

Palabras clave: plasticidad fenotípica, estrés, desarrollo, resiliencia, efectos transgeneracionales

INTRODUCTION

The proposal that environmental stresses in infancy induce phenotypic deficits in adults (e.g., diminished physiological, morphological, behavioral or life history traits) is now

extensively supported by research on diverse animal species including humans and other mammals (Lummaa and Clutton-Brock 2002, Nussey et al. 2007, Monaghan 2008). Since the publication of reviews by Lindström (1999) and Metcalfe and Monaghan (2001), along with the

Nowicki et al. (1998) nutritional/developmental stress hypothesis for the importance of early stresses in sexual selection, experimental research on birds has abundantly supported the proposal. The notion that adverse conditions such as poor weather or food availability, disease, and high population density experienced pre- or post-natally before maturity (Lindström 1999) have profound and long-term impacts on avian development has become a refrain. We suggest, however, that while phenotypic deficits can certainly be generated in adult birds by exposure to stress in infancy, the prevalence and importance of similar effects in nature is still largely unknown. We further suggest that accumulating evidence from wild birds indicates that, although stresses can indeed impose deficits in adulthood, developing birds sometimes meet them with resilience (absence of a deficit where one is expected) and developmental plasticity comparable to that reported for fish (Auer 2010), and that these adaptive responses deserve further exploration and analysis. Exploration needs to encompass the lifespans of ecologically and taxonomically diverse avian species, and experimental studies can potentially provide special insight into natural developmental processes by using treatments that mimic natural stresses and including measures of fitness in their response variables.

Before considering the evidence, a word about inferential methods in a field that has been dominated by experiments but where results of longitudinal studies of wild populations are beginning to demand a new perspective. Because they are powerful tools for demonstrating causal effects of experience on development, experiments are the research method of choice in this field, and their results have largely shaped our understanding of effects of early stresses. However, nearly all have been carried out in captivity and with little regard to whether treatments fall within the range of stresses encountered in nature. Yet confident extrapolation of results to natural contexts depends on the extent to which treatments mimic natural stresses (e.g., in their nature, magnitude, and timing) and the extent to which their physical and social contexts mimic natural environments.

To determine the relationships between early environments and developmental outcomes in nature, descriptive studies of wild birds are also required; these cannot reliably identify causes, but they can detect candidate relationships and provide compelling confirmation of causal inferences from experiments. Less often appreciated is that descriptive studies can also provide persuasive evidence that suspected causes have no effect, for example when infants exposed to stress perform as well as unstressed individuals in adult life. Experiments that do not mimic natural stresses and environments may sometimes tell us more about contingencies that potentially constrain phenotypic evolution than about how particular stresses actually

generate phenotypic variation in nature. For example, an experimental brood enlargement that results in the fledging of underperforming offspring may tell us why birds avoid producing, reduce, or abandon overly large broods, but does not necessarily imply that underperforming adults fledged from overly large broods will be found in nature.

Observational Studies of Wild Birds

For wild birds, numerous analyses of effects of early environments on traits in the nestling, fledgling, and juvenile periods have been published, but extremely few studies have considered effects after sexual maturity, and estimation of effects on longevity or fitness is rare (Cam and Aubry 2011, Saino et al. 2012). We summarize the relevant findings for the species for which effects after sexual maturity have been reported, divided into 4 short-lived species (maximum lifespans 12–16 years, $X = 14.6$) and 5 long-lived species (maximum lifespans 18–43 years, $X = 27.0$).

Short-lived species. The 3 studies carried out on short-lived species suggest that early stresses in some cases impact adult fitness or lifespan and in other cases do not, that life history traits can be resilient to a variety of early stresses, and also that stress-induced deficits in adult traits can be part of a pattern of adjustment over one or more seasons that leaves fitness unaffected.

The Great Tit (*Parus major*) has been the flagship species for negative effects of early stress on adult traits in wild birds since Haywood and Perrins (1992) found that underweight female fledglings laid fewer eggs when they recruited. However, continued scrutiny of female Great Tits dealing with diverse early stresses has documented both resilience and flexible modification of reproductive parameters. Thus, when underweight fledglings produced smaller first clutches, their brood size, the body mass of their nestlings, and their reproductive success were unaffected (Visser and Verboven 1999, Tilgar et al. 2010). Similarly, neither late fledging nor small fledging size affected offspring's reproductive success (Visser and Verboven 1999); neither poor natal sites nor natal years affected reproductive success or lifespan (Wilkin and Sheldon 2009); and rate of reproductive senescence was unaffected by natal season quality, fledge date, brood size, maternal age, nest density, or first-winter food availability (Bouwhuis et al. 2010). Underweight female fledglings actually nested earlier on their first breeding attempt (Perrins and McCleery 2001), possibly a mechanism that allows normal reproductive success when the clutch is small. Male Great Tits, while apparently unaffected by poor growth, are susceptible to poor natal environments. Reduced body size or mass of male fledglings did not compromise their reproductive success (Visser and Verboven 1999), despite their underweight condition at first

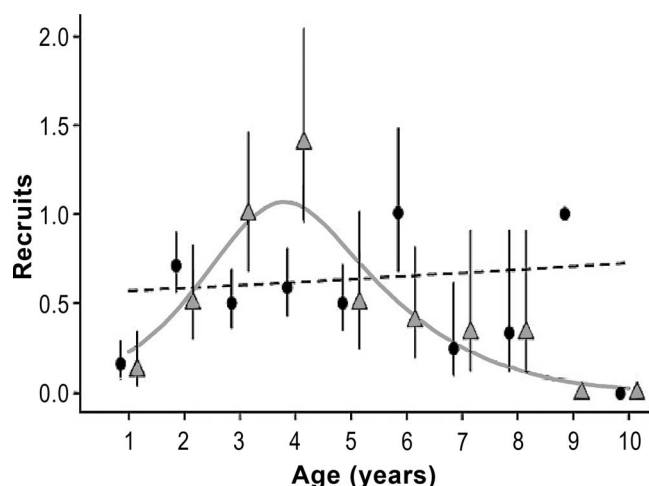


FIGURE 1. Life history plasticity of Mauritius Kestrels in response to habitat degradation. Kestrels from natal territories in agricultural habitat with altered prey community (gray triangles and curve), which suffered increased mortality as young adults, increased their production of recruits ($X \pm se$) in early life compared to kestrels from intact forest (black dots, dashed curve), thereby achieving similar lifetime fitness. (figure 1B in Cartwright et al. 2014)

breeding (Perrins and McCleery 2001), but late fledging (Visser and Verboven 1999) and poor natal sites (Wilkin and Sheldon 2009) did, with poor natal sites also affecting their lifespan. Oddly, however, poor natal years enhanced males' reproductive success and lifespan (Wilkin and Sheldon 2009).

Female Mauritius Kestrels (*Falco punctatus*) neutralized the impact of an anthropogenic stress on their fitness by adjusting an important life history parameter. Individuals that fledged in areas where prey populations had been altered by converting natural forest habitat to agriculture probably suffered nutritional stress in the nestling period, and they showed increased mortality in early adult life (Cartwright et al. 2014). Nonetheless, they achieved similar lifetime fitness to females raised in natural forest areas by increasing reproductive investment (fledgling/recruit production) in early life at the expense of investment in late life (Figure 1).

By contrast, late-fledged male and female wild Barn Swallows (*Hirundo rustica*) showed shorter longevity and diminished lifetime reproductive success (Saino et al. 2012), and female Pied Flycatchers (*Ficedula hypoleuca*) that fledged in poor condition laid smaller eggs (Potti 1999), although effects on fitness were not measured.

Long-lived species. Longitudinal field studies of 5 taxonomically and ecologically diverse species suggest that in long-lived bird species, not only life history traits but also behavioral and physiological traits can be resilient to early stresses. As in short-lived species, adult fitness is impacted by early stress in some cases but maintained in

others by compensating for a deficit in one life history trait by adjusting another, and the sexes can differ in their vulnerabilities. Observations also suggest that in long-lived species, effects of early stress can be mitigated and postponed or compensated by intergenerational effects.

The first studies of long-lived species showed how poor early environments can prejudice reproduction of one or both sexes and, in some cases, affect lifetime fitness. Black-legged Kittiwakes (*Rissa tridactyla*) that received less extended parental care performed worse on a composite index of reproductive performance (Cam et al. 2003). Red-billed Choughs (*Pyrrhocorax pyrrhocorax*) born after a period of unfavorable weather had reduced lifespans and produced fewer fledglings over the lifetime and, in the case of males, reduced reproductive success at age 3 years (Reid et al. 2003). Similarly, choughs that fledged in an unfavorable region showed poor adult survival, irrespective of the region they bred in (Reid et al. 2006). Oystercatchers (*Haematopus ostralegus*) that fledged in poor quality natal territories bred in poor quality territories (generally distinct from their natal ones) and showed diminished lifetime reproductive success (van de Pol et al. 2006). Tawny Owl (*Strix aluco*) sexes clearly differ. Females raised in territories where prey density was low showed diminished annual reproductive success (Appleby et al. 1997) and, strikingly, those raised in a year of low prey density showed consistently diminished annual reproduction during at least 16 years (Millon et al. 2011), although their annual survival was unaffected. Males, however, were resilient; low prey density in the natal year or territory failed to prejudice their annual survival up to ≥ 9 years or their annual reproductive success up to ≥ 12 years. In neither sex was the rate of senescence in reproductive success accelerated by low prey density in the natal year.

The Blue-footed Booby's (*Sula nebouxi*; Figure 2) broad resilience to severe early stresses, combined with adjustment of life history parameters including positive and negative intergenerational effects, illustrates the range of responses that long-lived birds can make. In broods of 2 chicks, a 4-day age disadvantage routinely results in the junior chick experiencing violent aggressive domination and psychological subordination on a daily basis during more than 12 weeks, along with reduced feeding and growth coupled with elevated corticosterone during ≥ 3 weeks (Drummond et al. 1986, Nuñez de la Mora et al. 1996, Drummond and Canales 1998). Nonetheless, compared to senior fledglings, juniors showed similar annual survival and probability of recruiting at all ages up to ≥ 20 years (Drummond et al. 2011), similar cell-mediated immune responsiveness at all ages up to ≥ 8 years (only females were tested; Carmona-Isunza et al. 2013), similar aggressive defense of nest and brood at all ages up to ≥ 13 years (Sánchez-Macouzet and Drummond 2011), and no deficit in annual reproductive success at any age up to ≥ 16

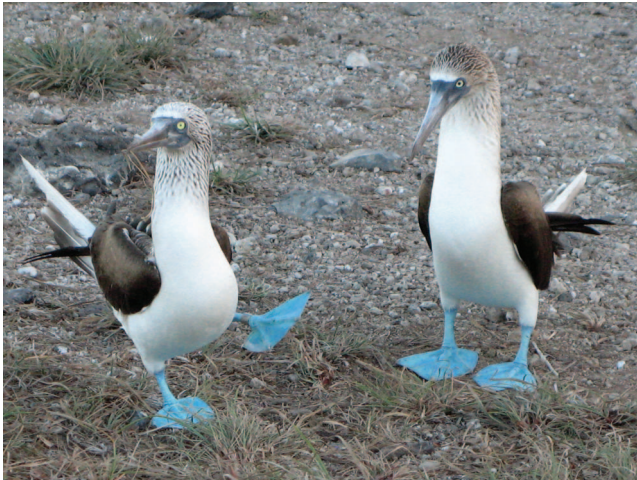


FIGURE 2. Blue-footed Boobies (*Sula nebouxi*) show plasticity. By making life history adjustments, boobies that grew up during an el Niño event or suffered aggressive sibling dominance as a nestling survive and breed as successfully as their peers.

years (Figure 3). Intriguingly however, fledglings produced by juniors in their first 3 years of life (when female juniors, at least, are temporarily underweight) were less likely to recruit than those produced by seniors (Figure 4). This cost is small because few boobies recruit before age 4 years (mean recruiting age: females 3.85 years, males 4.32 years; Drummond et al. 2003), and those that do produce few fledglings. Thus, junior boobies are resilient to multiple stresses of their nestling environment but pass a delayed and minimized cost to their earliest progeny. In contrast, the exigencies of El Niño Southern Oscillation (ENSO),

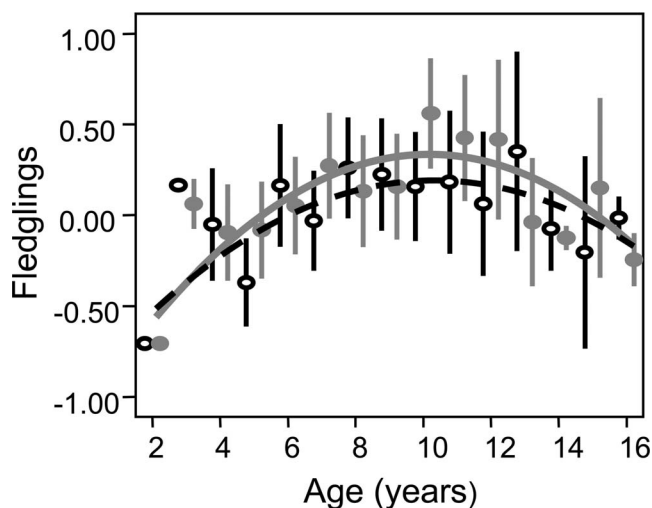


FIGURE 3. Qualified resilience of junior Blue-footed Booby siblings. Despite experiencing the stresses of subordination during the nestling period, junior boobies of both sexes (gray curve) produced as many fledglings annually as their siblings (black curve) over the age span. (figure 2C in Drummond and Rodríguez 2013)

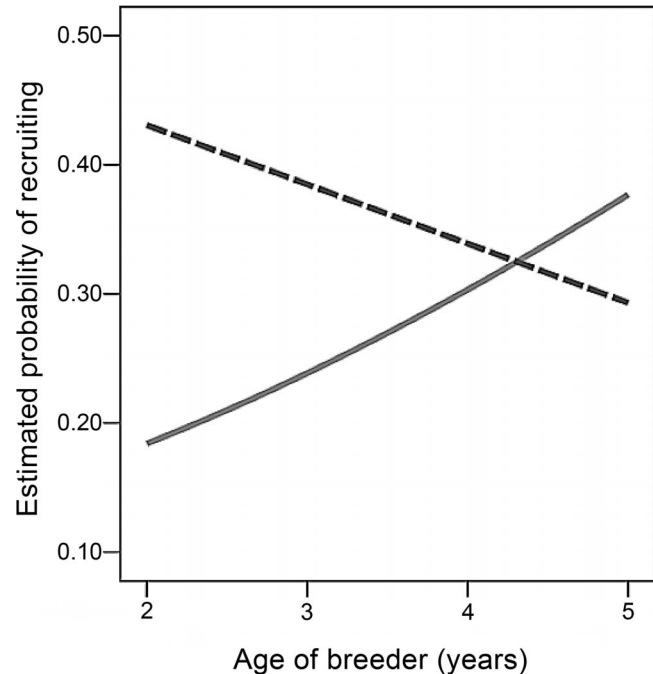


FIGURE 4. Negative effect of natal stress on the next generation of Blue-footed Boobies. Offspring fledged by former juniors of both sexes in their first 3 years of life were less likely to recruit (continuous gray curve) than those fledged by former seniors (dashed black curve). (figure 3 in Drummond and Rodríguez 2013)

which has major impacts on breeding parameters (Ancona et al. 2011), are met with flexible life history adjustments that seem to obviate costs altogether. Despite fledging roughly 15% underweight, chicks that faced warm water conditions in the natal year managed, over at least the first 10 years of life, to achieve similar longevity and accumulated reproductive success to those experiencing cold water by recruiting at a younger age and skipping breeding seasons more frequently (Figure 5). Poor conditions were even associated with an intergenerational benefit; the daughters of females hatched in warm water years showed enhanced reproductive success over the first 10 years (Figure 6).

To summarize findings for wild birds, all 9 short- and long-lived species that experienced one or more stresses in early life showed a deficit of some sort in adult life. However, in 3 species, 1 sex was relatively resilient, and in only 5 species are there reliable grounds for concluding that adult deficits impacted lifetime fitness: Great Tits (males only), Barn Swallows, Red-billed Choughs, Oystercatchers, and Tawny Owls (females only). Moreover, in 3 cases, adult deficits were associated with flexible adjustment of other life history traits that seemed to nullify impact on fitness: female Great Tits, female Mauritius Kestrels, and Blue-footed Boobies of both sexes facing

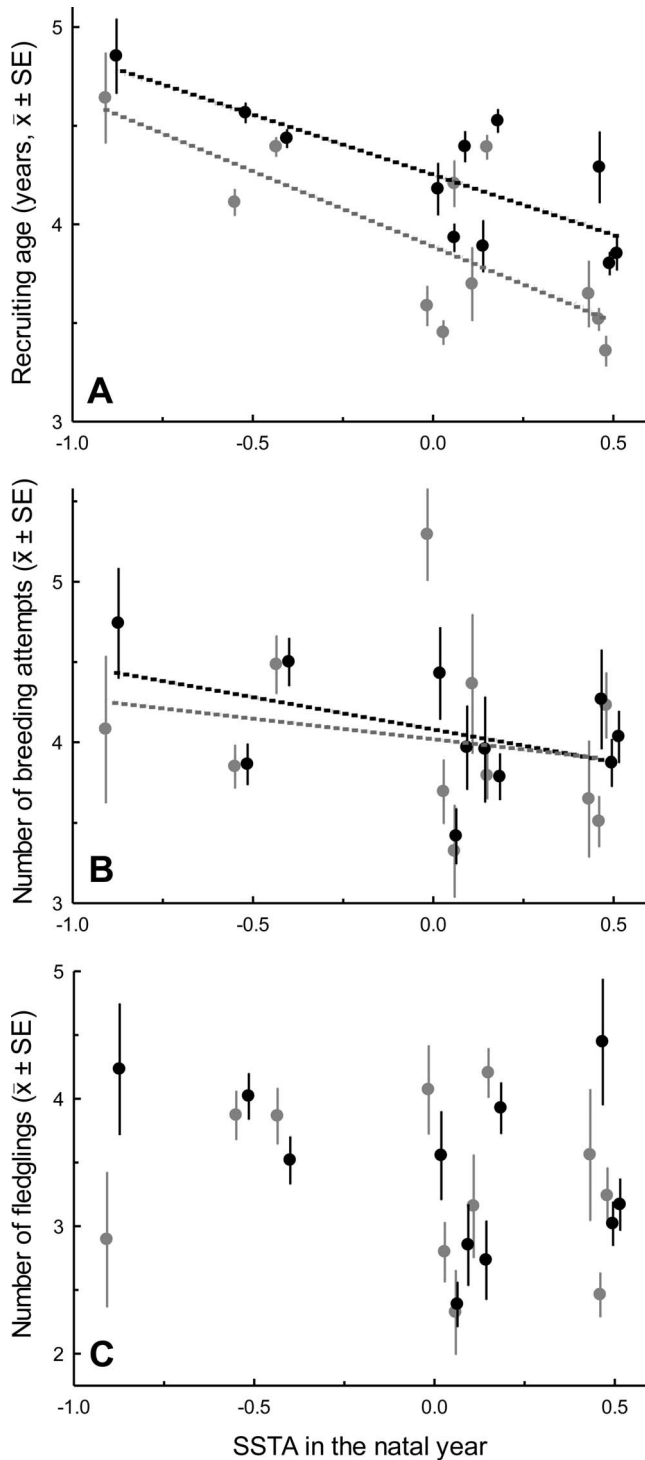


FIGURE 5. Life history plasticity of Blue-footed Boobies in response to sea surface temperature anomalies (SSTA) in the natal year. Warmer waters were associated with females (gray) and males (black) (A) recruiting earlier in life and (B) breeding less frequently during the first 10 years of life, thereby (C) achieving similar reproductive success over that period to boobies from years with cooler waters. (figure 1 in Ancona and Drummond 2013)

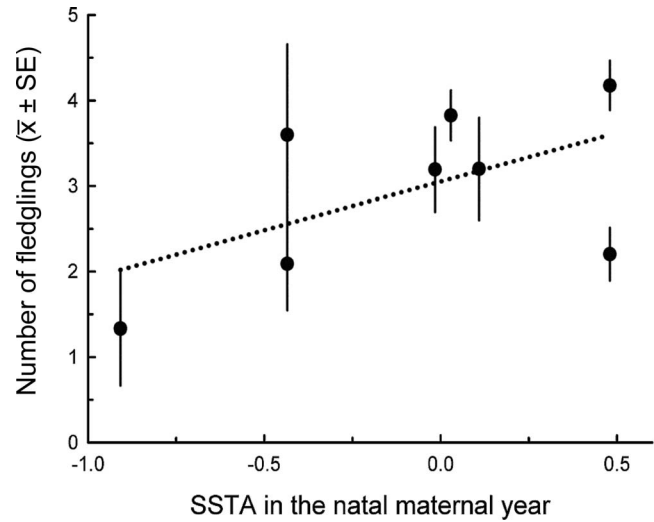


FIGURE 6. Positive effect of natal stress on the next generation of Blue-footed Boobies. Sea surface temperature anomalies (SSTA) in females' natal years were positively related to the number of fledglings produced by their daughters over those daughters' first 10 years of life. (figure 5 in Ancona and Drummond 2013)

warm waters. In addition, flexibility in the Blue-footed Booby included intergenerational components, with subordinate chicks of both sexes passing the cost of dominance to their very first fledglings and female chicks that experienced warm waters at birth, producing daughters with high reproductive success. Importantly, tits, boobies, and kestrels demonstrate that when asking whether early stresses cause profound deficits or elicit developmental plasticity, it can be insufficient and potentially misleading to measure a few traits in early adulthood. To avoid false negatives while testing for plasticity, measurements of multiple life history traits and fitness across the lifespan are sometimes necessary. Another caution is that developmental impacts revealed by some observational studies could be overestimated or spurious. As recognized by van de Pol et al. (2006), we can seldom discount the alternative explanation that they actually represent underperformance by the progeny of inferior individuals obliged to reproduce in suboptimal contexts. Field experiments in which parents are randomly assigned to experimental vs. control treatments (e.g., nestling parasites removed vs. left in the nest) are also needed.

Experimental Studies

The plethora of experimental studies (summarized in Table 1) has convincingly shown that poor quality food, food deprivation, compensatory growth, brood enlargement, elevated corticosterone, social isolation, and parasitic infection during early development can have negative

TABLE 1. Experimental demonstrations that stresses in early life induce deficits in adulthood. Birds exposed to food stress and/or compensatory growth (F), brood enlargement (B), elevated corticosterone (C) or parasitic infection (P) during the nestling or fledgling periods showed deficits in the listed traits.

Trait	Stress	Species	Reference
Body size or mass	F	Zebra Finch (<i>Taeniopygia guttata</i>)	Boag 1987
	B	Zebra Finch (<i>T. guttata</i>)	de Kogel and Prijs 1996
	B	Zebra Finch (<i>T. guttata</i>)	Naguib et al. 2004
	F	Pheasant (<i>Phasianus colchicus</i>)	Ohlsson and Smith 2001
Tendency for mass loss	F	Zebra Finch (<i>T. guttata</i>)	Krause et al. 2009
Fluctuating asymmetry	F	Western Scrub Jay (<i>Aphelocoma californica</i>)	Pravosudov and Kitaysky 2006
Brain morphology	F, C	Zebra Finch (<i>T. guttata</i>)	Buchanan et al. 2004
	F	Zebra Finch (<i>T. guttata</i>)	Nowicki et al. 2002
	P	Canary (<i>Serinus canaria</i>)	Spencer et al. 2005a
	F	Western Scrub Jay (<i>A. californica</i>)	Pravosudov et al. 2005
Plasma antioxidants	F	Zebra Finch (<i>T. guttata</i>)	Blount et al. 2003
Metabolic rate	B	Zebra Finch (<i>T. guttata</i>)	Verhulst et al. 2006
	F, C	Song Sparrow (<i>Melospiza melodia</i>)	Schmidt et al. 2012
Stress (HPA axis) response	C	Zebra Finch (<i>T. guttata</i>)	Spencer et al. 2009
	F	Western Scrub Jay (<i>A. californica</i>)	Pravosudov and Kitaysky 2006
Testosterone	B	Zebra Finch (<i>T. guttata</i>)	Naguib et al. 2004
Immune response	B	Zebra Finch (<i>T. guttata</i>)	Naguib et al. 2004
Cognition, learning	F	Zebra Finch (<i>T. guttata</i>)	Fisher et al. 2006
	F	Zebra Finch (<i>T. guttata</i>)	Bonaparte et al. 2011
	C	Black-legged Kittiwake (<i>Rissa tridactyla</i>)	Kitaysky et al. 2003
	F	Western Scrub Jay (<i>A. californica</i>)	Pravosudov et al. 2005
	B	White Leghorn Chicken (<i>Gallus gallus domesticus</i>)	Lindqvist et al. 2007
	F	Pheasant (<i>P. colchicus</i>)	Ohlsson et al. 2002
	B	Collared Flycatcher (<i>Ficedula albicollis</i>)	Gustafsson et al. 1995
	F, C	Zebra Finch (<i>T. guttata</i>)	Spencer et al. 2003
Song traits	F	Zebra Finch (<i>T. guttata</i>)	Brumm et al. 2009
	B	Zebra Finch (<i>T. guttata</i>)	Holveck et al. 2008
	F	Zebra Finch (<i>T. guttata</i>)	Nowicki et al. 2002
	F	Zebra Finch (<i>T. guttata</i>)	Zann and Cash 2008
	F, C	Zebra Finch (<i>T. guttata</i>)	Spencer et al. 2005b
	B	Blue Tit (<i>Cyanistes caeruleus</i>)	Dreiss et al. 2006
	P	Canary (<i>Serinus canaria</i>)	Spencer et al. 2005a
	F	Swamp Sparrow (<i>Melospiza georgiana</i>)	Searcy et al. 2010
	F	European Starling (<i>Sturnus vulgaris</i>)	Buchanan et al. 2003
	F	Swamp Sparrow (<i>M. georgiana</i>)	Searcy et al. 2010
	F, C	Zebra Finch (<i>T. guttata</i>)	Spencer et al. 2005b
	B	Zebra Finch (<i>T. guttata</i>)	Riebel et al. 2009
Song preference strength	F	Zebra Finch (<i>T. guttata</i>)	Woodgate et al. 2010
Activity level in mate choice	C	Zebra Finch (<i>T. guttata</i>)	Spencer et al. 2010
Incubation effort	C	Zebra Finch (<i>T. guttata</i>)	Spencer and Verhulst 2007
Competitive ability	C	Zebra Finch (<i>T. guttata</i>)	Spencer and Verhulst 2007
Neophobia	C	Zebra Finch (<i>T. guttata</i>)	Spencer and Verhulst 2007
Flight	F	Zebra Finch (<i>T. guttata</i>)	Criscuolo et al. 2011
Laying date/timing	F	Zebra Finch (<i>T. guttata</i>)	Blount et al. 2006
	B	Zebra Finch (<i>T. guttata</i>)	Alonso-Alvarez et al. 2006
Clutch size	F	Zebra Finch (<i>T. guttata</i>)	Gorman and Nager 2004
	P	Great Tit (<i>Parus major</i>)	Fitze et al. 2004
Reproductive output	F	Zebra Finch (<i>T. guttata</i>)	Gorman and Nager 2004
	B	Collared Flycatcher (<i>F. albicollis</i>)	Gustafsson and Sutherland 1988
	P	Great Tit (<i>P. major</i>)	Fitze et al. 2004
Mortality	B	Zebra Finch (<i>T. guttata</i>)	de Kogel 1997
	F	Zebra Finch (<i>T. guttata</i>)	Birkhead et al. 1999

effects on an impressive list of morphological, physiological, behavioral, and life history traits in adulthood. Characteristics and reproduction of affected individuals' offspring can also be affected; female Zebra Finches (*Taeniopygia guttata*) that grew up in enlarged broods

produced small or low-condition daughters that showed diminished hatching success and nest success (Naguib and Gil 2005, Naguib et al. 2006, Alonso-Alvarez et al. 2007). Nonetheless, generalizing from these studies to wild birds requires caution. First, taxonomic representation is

poor; deficits have been induced in adults of 12 species, including only 3 nonpasserines, and 63% of experiments were on Zebra Finches (Table 1). Second, as we explain in the following paragraphs, results are more mixed than is generally appreciated, the external validity of most experiments is questionable, and because they do not measure across the lifespan or analyze fitness, experiments generally have a limited capacity to detect developmental plasticity.

Substantial negative effects of experimental stresses are by no means universal. Effects can be meager despite prolonged or severe stress, sometimes 1 sex is unaffected or less affected (e.g., de Kogel 1997, Spencer et al. 2010, Schmidt et al. 2012), and it is commonly only 1 or 2 of several response variables that shows any effect at all. For example, Song Sparrow (*Melospiza melodia*) chicks subjected to 54 days of either food ingestion limited to 65% of ad libitum consumption or twice daily corticosterone boosts at an acute stress level were unaffected at age 7 months in their body size and composition (lean or fat mass) or peak metabolic rate, and only females' standard metabolic rates showed an increase (Schmidt et al. 2012). Similarly, although food-stressed female Zebra Finch nestlings were less active in mate choice trials at age 190 days, their general activity levels and their choices among males were unaffected (Riebel et al. 2009, Woodgate et al. 2010). The resilience shown by the Zebra Finch nestlings and fledglings studied by Honarmand et al. (2010) may have been even greater; despite experiencing nutrition deficient enough to induce poor growth and elevated baseline corticosterone levels at 0–17 days or 17–35 days, followed by compensatory growth, these birds showed no adult deficits in biometry, size of male cheek patch, baseline corticosterone, or survival through 1200 days.

Sometimes effect of early stressors on adults are positive, raising the question of whether they represent adaptive plasticity. Adult female Zebra Finches raised on a low quality nestling diet outperformed controls on a behavioral test after 3–4.5 hr of food restriction, exploring for food more promptly and feeding sooner (Krause et al. 2009); adult Zebra Finches that had been dosed twice daily with corticosterone at 12–28 days solved a novel foraging challenge more quickly than controls, apparently because they were better at learning rather than being more motivated (Crino et al. 2014); adult Zebra Finches from enlarged broods sang more and showed stronger immune responses than those from reduced broods while showing no deficit in laying date or clutch characteristics (Tschirren et al. 2009); and male Zebra Finch chicks that hatched later than their nest mates (implying disadvantage in nest mate competition) were more attractive to females (Mainwaring et al. 2012). More significantly, although Zebra Finches from enlarged broods delayed reproduction by 15 days, their fecundity and longevity were unaffected, and their

decrease in reproductive value with age was actually slower (Alonso-Alvarez et al. 2006), arguably showing adaptive plasticity capable of nullifying fitness impact. Positive effects of early stresses have also been documented in juveniles of species with precocial young. Juvenile Japanese Quail (*Coturnix japonica*) displayed enhanced behavioral flexibility in a spatial memory task immediately after exposure during ages 2–3 weeks to repeated negative stimuli (unpredictably timed confinement, handling, and loud noise; Calandreau et al. 2011); and at 7 weeks, juvenile Domestic Fowl (*Gallus gallus*) showed superior associative learning indicative of enhanced coping ability after experiencing intermittent social isolation during the first 3 weeks (Goerlich et al. 2012).

Because the aim of these experiments has generally been to determine whether particular adult traits of model species can be negatively impacted by stress rather than to explore effects across the lifespan of naturalistic stresses and evaluate fitness consequences, their scope for revealing developmental resilience and plasticity and how these vary among avian species is limited. Understandably, experimental treatments fall short of mimicking the nature, magnitude, timing, duration, and stochasticity of stresses in wild populations (parameters that are seldom known), so their external validity is usually doubtful. Here, experimental tests of compensatory growth may provide an object lesson in the difficulty of mimicking natural challenges. After observing accelerated growth when normal food supply was restored to food-deprived Collared Flycatchers (*Ficedula albicollis*) in the natural habitat, Hegyi and Török (2007) concluded that catch-up growth had failed to manifest in several species tested in captivity because the artificial diets used were inauthentic. Experiments often expose chicks to experiences that their parents have probably been selected to keep them from and that may rarely be experienced in nature, such as growing up in an overly large brood or experiencing 2–7 weeks of twice-daily doses of corticosterone equivalent to the amount that chicks might secrete during capture and handling by a predator. Further, the scope for deploying evolved repertoires for ameliorating or compensating for experimental stresses is usually limited because parents and chicks nearly always face them in impoverished (i.e. captive) environments (for an exemplary exception, see Fitze et al. 2004). Thus, until experimentally elicited effects are confirmed by descriptive field observations, we should be skeptical about how often such consequences occur in nature. Also, an important lesson from female Great Tits, Mauritius Kestrels, and Blue-footed Boobies is that, in nature, birds sometimes compensate successfully for stress-induced deficits by making life history adjustments.

In addition, we may have misled ourselves by so often affirming the existence of “long-term effects” of early

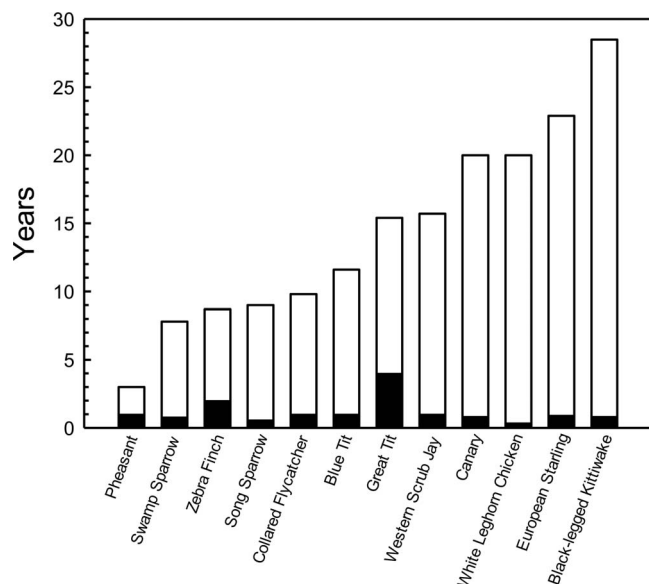


FIGURE 7. Maximum ages at which experimental studies documented deficits in adulthood due to early stresses (black bar) in relation to the maximum lifespan of each species (open bar). The studies and species are listed in Table 1. Maximum lifespans were obtained from reference works (e.g., *Birds of North America* and *Handbook of Models for Human Aging*) and specialized databases (e.g., the website of the European Bird Banding Organization, *Longevity Records of North American Birds*, and the *Animal Aging and Longevity Database*). For the Zebra Finch and Canary, we used maximum lifespans recorded in captivity.

stresses when experimental subjects are seldom monitored long enough to determine whether experimentally induced deficits are temporary or permanent. Although subjects have been monitored until the ends of their lives (e.g., Birkhead et al. 1999), adult traits are generally measured on a single occasion not long after sexual maturation, and only 6 experimental studies have documented trait deficits beyond the first year of life (Figure 7). However, adult birds with deficits induced by early stress can sometimes recover; for example, male Zebra Finches that produced few offspring in their first season because their mothers had been nutritionally stressed before laying recovered normal output in the next season (Gorman and Nager 2004). In their review of effects of developmental exposure to corticosterone, Schoech et al. (2011) lament the general lack of information on persistence of physiological and behavioral effects and on fitness consequences.

Indeed, in experiments fitness consequences of stress-induced deficits in adult traits are very seldom measured (Table 1), so the subject's ability to compensate for deficits goes largely untested. A notable exception is a field experiment by Gustafsson and Sutherland (1988) showing reduced fecundity in Collared Flycatchers that developed in enlarged clutches. In more typical laboratory experi-

ments, it is usually uncertain whether and how demonstrated deficits in adult traits (and any correlated traits) would affect fitness in natural environments. And here our intuition can let us down, as illustrated by a study of the effects of natural variation in problem-solving ability among Great Tits. In nature, poor problem-solvers foraged extensively in space and time (probably because they were inefficient) and laid small clutches, but their fitness did not suffer because they deserted their nests less often than good problem-solvers (Cole et al. 2012).

When weighing the relevance of experimental analyses of impacts of early stresses, it is salutary to bear in mind the findings of Bolund et al. (2010). Their particularly thorough descriptive study of a colony of Zebra Finches casts doubt on the extent to which effects of standard (manipulated) experimental treatments on captive birds can be extrapolated to natural environments. They tested for effects of unmanipulated variation in the early environment on 23 traits of hundreds of cross-fostered members of 3 generations of finches living in socially complex captive environments. Importantly, nestling growth showed extreme variation due to severe undernourishment of some birds, and the authors' quantitative genetic analysis permitted estimation of the entire environmental component of early growth, including nutrition, while accounting for effects of individual genotypes. To measure effects on fitness, paternity of 2087 eggs and offspring was determined using microsatellites. Bolund et al. (2010) concluded that Zebra Finches are remarkably resilient to food shortage during growth and can compensate for poor growth conditions while incurring little in the way of long-term costs.

In surprising contrast with predictions of the developmental stress hypothesis (Nowicki et al. 1998), and with earlier inferences based on experimental brood enlargement, corticosterone treatment, or food restriction of the same species (de Kogel and Prijs 1996, Spencer et al. 2005b), this statistically powerful study provided no evidence that stressful early conditions affect male traits important for female choice. Moreover, although early environment affected both sexes' body size and mass strongly and their beak color moderately, it had no effect on male or female plumage characters, male song traits, or male attractiveness (measured both in mate choice trials and socially complex aviary interactions), and little or no impact on the longevity or fitness of either sex. The Zebra Finch, the workhorse of experimentally demonstrated effects of early stress, turns out to have a hitherto unsuspected capacity to neutralize most expected impacts of undernourishment on reproductive and life history traits, and ultimately on fitness, by making flexible developmental responses.

DISCUSSION

Our understanding of how stresses during infancy affect birds during their adult lives has advanced since Nowicki et al. (1998), Lindström (1999), and Metcalfe and Monaghan (2001) highlighted the general importance of early stresses in their seminal papers. Experiments have probed the susceptibility of (mostly captive) nestlings and fledglings to diverse imposed stresses and given us a preliminary list of physiological, behavioral, and morphological traits of adult birds that can be positively and negatively affected or that show resilience. The accelerating trickle of descriptive studies can now help us put the experimental findings into perspective.

Some of those 9 species studied in nature confirm expectations of induced long-term deficits in adult traits, for example documenting reduction in lifetime fitness of both short- and long-lived species and showing how impairment in annual reproductive success of Tawny Owls can persist over their long lifespan. Others demonstrate a surprising resilience and life history plasticity in response to natural early stresses, including diverse stresses faced by female Great Tits and the chronic, multiple, and anthropogenic stresses faced by Blue-footed Boobies and Mauritius Kestrels. The deficits, resilience, and developmental plasticity documented in wild birds by purely descriptive methods now give rise to a growing agenda for research on mechanisms of the types contemplated by current developmental theory (e.g., Del Giudice et al. 2011, Sih 2011, Constantini 2013) and outlined below.

Integrating the largely disjunct findings from lab and field will require characterizing the early stresses actually experienced by different species in nature, documenting their phenotypic effects, describing correlated changes in other traits that mitigate or annul their effects on fitness, and testing causation with experiments grounded in natural history. The need to base experimental challenges on known characteristics of natural stresses, including their magnitude, frequency, timing, duration, and stochasticity, to elucidate adaptiveness of plastic developmental responses is increasingly recognized by students of birds and other taxa (e.g., Parker and Maestripietri 2011). Combinations of stresses, such as habitat change and climate change, are increasingly recognized as important, and details of how stresses are experienced can be critical. For example, in fishes the challenge of changing early in life from a high food ration to a low food ration can affect learning ability later in life, independent of amount consumed (Kotrschal and Taborsky 2010). In birds, susceptibility of the brain to natural stresses probably varies temporally in relation to life-history stage and season (Buchanan et al. 2013), and the response elicited by

an experimental boost in corticosterone may depend on additional environmental information, given that different stressors can evoke its secretion (Henriksen et al. 2011).

Exploration of adaptive responses needs to take into account that early stresses, both mild and severe, can sometimes strengthen behavioral capacities of adult vertebrates (Champagne et al. 2008, Oomen et al. 2010) and even enhance their capacity to withstand other types of stresses (reviewed in Constantini 2013). Assessment of adaptive developmental responses needs to be informed by field observations and will often need to embrace the age span because developmental effects of early exposure to stress can emerge at any time in an animal's life (Constantini 2013). Similarly, assessment of effects of early stress will sometimes require probing for them in the range of conditions experienced in the field because adults express some deficits only when re-exposed to the original stress (Dmitriew and Rowe 2007).

Particular attention should be paid to the magnitude of experimental stimuli when examining the developmental outcomes of natural stresses because direction of response can depend on it (Constantini et al. 2010). For example, moderate environmental challenges to infants are thought to promote future resilience (Macrì 2013), and although at high levels glucocorticoids can prejudice development of learning abilities, at low levels they can have positive effects (references in Diamond et al. 1992). Experiencing mild heat stress at 42–45 days made Zebra Finches better able to withstand oxidative stress at 177–180 days (Constantini et al. 2012), and 24 hr of maternal deprivation enhanced hippocampal synaptic plasticity and emotional learning of rats in adulthood, particularly in stressful contexts (Oomen et al. 2010).

The finding that no reproductive fitness penalty was paid when nately stressed Great Tits, Blue-footed Boobies, and Mauritius Kestrels reduced their clutch sizes, skipped more breeding seasons, or suffered increased annual mortality shows that birds can sometimes compensate for loss in one fitness component by gain in another. This finding cautions against automatically assuming that stress-induced deficits, even in fitness components, imply a net cost to fitness. Interestingly and consistent with life history theory (Stearns 1992, Roff 2002), nately stressed tits, boobies, and kestrels neutralized fitness cost not by postponing but by bringing forward their schedules of reproductive effort. The mechanisms by which these adjustments occurred are unknown; early stress can extend lifespan in some animals (Sayer and Cooper 2002, Gems and Partridge 2008) and is thought to evoke trade-offs between neural structures that enhance some cognitive functions while depressing others (Crino et al. 2014), with potentially ramifying ecological and life history consequences. Thus, dosing Zebra Finches with corticosterone during the nestling/fledgling period enhanced their

performance on a foraging task in adulthood by boosting one type of learning while probably diminishing song learning (Crino et al. 2014). The potential complexity of the causal routes from early stress to adult phenotypes was illustrated by observation of common lizards (*Zootoca vivipara*) largely maintained in socially complex 100 m² outdoor enclosures. Experimental food deprivation in the first 2 months of life depressed growth (while enhancing long-term immunocompetence) but also had delayed effects on growth, body size, early survival, and reproduction, themselves partly due to effects of the initial deprivation on intercohort social interactions (Mugabo et al. 2010).

That scrutiny of only 9 short- and long-lived species in nature should turn up notable variation in life history plasticity, with differences among species, populations, and sexes, and should encourage us to widen the search for flexible responses to early stresses. The jury is still out on whether poor natal environments can make birds better able to deal with similar environments during adulthood, as contemplated by the predictive adaptive response and thrifty phenotype hypotheses (reviewed by Monaghan 2008). It is now clear, however, that in some circumstances birds can at least evade or make compensatory adjustments for long-term developmental impacts of poor environments, and we should further characterize these coping mechanisms and their limitations. In doing so we should embrace greater taxonomic and ecological diversity and a broader range of life history and other traits. Understanding life history plasticity in response to early stresses associated with ecological variation, anthropogenic change, and social interactions is of more than theoretical interest. Plasticity is relevant to conservation because it has the potential to facilitate rapid population responses to climate change while possibly slowing microevolutionary response (Charmantier et al. 2008).

We should explore intergenerational effects of early stresses. Although seldom sought, these have been documented in diverse taxa (Burton and Metcalfe 2014), including 4 species of birds. Application of experimental stresses to captive nestlings or juveniles induced deficits in their offspring: diminished size, hatching success, and nest success in female Zebra Finches (Naguib and Gil 2005, Naguib et al. 2006, Alonso-Alvarez et al. 2007); reduced spatial learning or corticosterone responsiveness in breeds of Domestic Fowl (Lindqvist et al. 2007, Goerlich et al. 2012); and increased fearfulness in Japanese Quail (Guibert et al. 2012). In nature, however, intergenerational effects are unlikely to be just a matter of imposed deficits and, on present evidence, sometimes reflect adaptive plasticity. A hint of such potential comes from the offspring of white leghorn chicks exposed to unpredictable light–dark rhythms (Lindqvist et al. 2007) which, despite their poor spatial learning, were more competitive and grew faster

than controls. More persuasive, perhaps, are the 2 intergenerational effects so far observed in free-living birds that can be interpreted as strategic deferral of costs or compensatory adjustment for them. Thus, subordinate booby chicks may manage to sustain normal survival, recruitment, and annual reproductive success throughout their lifespan by passing the costs of sibling conflict to their first fledglings (Figure 4), and female booby chicks may compensate for costs (if any) incurred during a warm-water infancy by somehow boosting the breeding success of their daughters (Figure 6).

Our major recommendation is to achieve a more happy marriage between descriptive and experimental methods. We should expand the number of species described in the field to well above the paltry 9 that we could find and follow individual birds over their lifetimes. Of equal importance, experiments on the effects of early experience on adult traits need to be conducted on wild birds. For these, 1 year will often be sufficient for tracing effects in short-lived species, but follow-up over periods of years is clearly necessary for detecting some of the most interesting and important effects (e.g., Fitze et al. 2004).

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