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A mechanistic approach to understanding range shifts in a changing world: What makes a pioneer?

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ABSTRACT

A species' range can be thought of as a manifestation of the ecological niche in space. Within a niche, evolution has resulted in traits that maximize fitness. Across millennia, natural oscillations in temperature have caused shifts in the geographic location of appropriate habitat and with corresponding changes in species' ranges. Contemporary climate change and human disturbance may lead to rapid range expansion or contractions with largely unknown consequences. Birds provide an excellent case study of this phenomenon with some taxa expanding range and others contracting even to the point of extinction. What leads some populations to expand while others contract? Are there physiological and behavioral attributes of "pioneers" at the forefront of a range shift/expansion?

The concept of allostasis provides a framework with which to begin to evaluate when a species will be able to successfully expand into new habitat. This tool allows the integration of normal energetic demands (e.g. wear and tear of daily and seasonal routines) with novel challenges posed by unfamiliar and human altered environments. Allostasis is particularly attractive because it allows assessment of how individual phenotypes may respond differentially to changing environments. Here, we use allostasis to evaluate what characteristics of individuals and their environment permit successful range expansion. Understanding variation in the regulatory mechanisms that influence response to a novel environment will be fundamental for understanding the phenotypes of pioneers.

1. Introduction

The geographical range of a species has evolved to maximize fitness in a particular ecological niche (MacArthur, 1972). Species ranges are often highly plastic, contracting or expanding to match spatial shifts of their ecological niches (Sexton et al., 2009). Changes in geographical range following climatic variations have occurred for hundreds of millions of years (e.g. Wright and Stigall, 2013), and are being documented with current changes in the Earth's climate (Parmesan and Yohe, 2003). In addition to inducing range shifts, global climate change has lead to increases in the frequency, duration and intensity of extreme weather events (Meehl et al., 2000; Field et al., 2012; IPCC, 2012). For example, the incidence of catastrophic weather such as floods, droughts, storms, heat waves and cold spells has risen almost 10-fold in the past 50 years (Easterling et al., 2000; Beniston and Stephenson, 2004). These environmental perturbations are further compounded by human disturbance, invasive species, changes in population dynamics, and pollution. Most organisms will face major challenges in coping with one or more of these environmental challenges in the coming decades. Rapid environmental shifts can result in either deleterious or improved conditions for an individual or population. The culmination of these changes in abiotic, biotic and anthropogenic factors may lead to geographical shifts in species' ranges at an unprecedented rate. Predicting which populations or individuals will have the capacity to shift their range as conditions change remains a challenge. Failure to adapt or shift home range may lead to population reductions or extinction. Clearly, rapid global change has placed significant and novel challenges on organisms that may not have been experienced during their evolutionary history.

The literature on dispersal biology provides a starting point to identify phenotypes that may allow individuals to successfully

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explore and track emerging opportunities, and shift their range when necessary (Chaine and Clobert, 2012). To complement this literature, we suggest that the concept of allostasis, or maintenance of stability through change (McEwen and Wingfield, 2003), and accompanying physiological and behavioral coping mechanisms allow us to make predictions about the factors limiting range expansion under a variety of ecological scenarios. We argue that this approach will facilitate modeling of mechanistic approaches in turn generating biologically relevant hypotheses and predictions to enable further experimental tests to identify "what makes a pioneer" at hormonal and physiological levels in vertebrates.

2. Species dispersals, range shifts and introductions

Dispersal biology includes natal and breeding dispersal and can occur over different spatial scales. We considered pioneering individuals at the forefront of a range expansion of breeding distribution to be a special case of dispersal and not necessarily linked directly to post-juvenile or reproductive dispersal. To that end we follow the Bowler and Benton (2005) definition of dispersal as "any movement between habitat patches, areas of suitable habitat separated in space from other such areas, irrespective of the distance between them". Ecological invasions have been defined similarly by Vermeij (1996) as, "the geographical expansion of a species into an area not previously occupied by that species" that is consistent with the dispersal concept. Both broad definitions describe range shifts motivated by a diversity of factors from population dynamics to climate change. We have opted to follow a dispersal-based approach in that both pioneering events and invasions can be thought of as dispersal that can occur at any time in the life cycle. Here we focus on dispersal of populations into new geographic ranges resulting from climate change and shifts in native habitat.

Range expansions take a variety of forms, can include non-breeding as well as breeding ranges, and changes in habitat use may be driven by different abiotic and biotic factors. Climate change (Parmesan and Yohe, 2003), deforestation (Addis et al., 2011), urbanization (McKinney, 2008), changes in food availability (Rolshausen et al., 2009), translocation by humans (Liebl and Martin, 2012), or exclusion by introduction of novel predators and competitors (Olson et al., 2005; White et al., 2006) can all result in species leaving historic ranges and/or colonizing new habitats.

Range shifts, broadly considered, include more than just absolute changes in the geographic area occupied by a species. Temporal shifts in how species occupy space within the existing range (such as breeding on wintering grounds or overwintering on former breeding grounds) also constitute an important change in habitat use and should be considered independently (Clark, 2010; Badyaev, 2009; Stein and Badyaev, 2011; Newman et al., 2006; Atwell et al., 2012).

Range changes may occur when the quality of old habitats deteriorate, previously uninhabitable areas become more favorable, or both simultaneously. As a result, critical features of the newly occupied habitat such as climatic conditions, food resources, and important competitors may be very similar to or different from the historic range. Given the diverse nature of range expansions, we propose that finding a mechanistic framework that can be applied across different types of shifts will be helpful for making predictions about when and how colonization attempts will be successful and when and how they will fail. The concept of allostasis, which examines individual energetic balance across fluctuating environmental conditions and periods of energetic demand (allostatic load), may provide the common currency needed to make such predictions especially from a mechanistic point of view.

3. What makes individuals within expanding populations pioneers or followers, and what characteristics do those that endure show?

As humans it is easy to imagine, based on popular literature, that a pioneer is epitomized by the intrepid explorer, strong and bold, pushing back frontiers despite hardships and challenges. Although some pioneers of western settlements in North America were fearless explorers, in reality the vast majority were immigrants from the Old World, vulnerable to the harsh conditions of the frontier while they attempted to "tame" a vast wilderness. This point is illustrated by a stanza of the poem "The New Collosus" (1883) by Emma Lazarus that is inscribed beneath the Statue of Liberty: "*Give me your tired, your poor/your huddled masses yearning to breathe free/The wretched refuse of your teeming shore/Send these, the homeless, tempest-tost to me/I lift my lamp beside the golden door*".

Who, then, are the pioneers? Are they "bold and intrepid explorers," the "wretched refuse" of the larger population, or perhaps a diverse mixture of phenotypes? Further, are the individuals that disperse from original habitats the same as, or different from, the individuals that successfully persist in the newly colonized territory? The dispersal literature describes a three step process: dispersal from the old habitat (emigration), transition, and settlement in the new habitat (immigration) (Clobert et al., 2009; Bowler and Benton, 2005). Each step of dispersal provides a selective screen; some individuals will emigrate, few survive transition, and fewer still establish in the new habitat. Investigations showing phenotypic differences of populations in recently colonized areas versus those from sites that have been established for long periods (e.g. Duckworth and Badyaev, 2007; Hanski et al., 2004; Lindstrom et al., 2013). While the bulk of our discussion concerns the mechanistic traits that enable individuals in range expanding populations to establish and persist in new habitat, next we briefly address recent findings on the dispersal phase of range change. We highlight these examples to emphasize that "successful pioneers" must arise from a subset of the individuals that leave the historic range.

Behavioral traits associated with dispersal include aggression (e.g. Duckworth and Badyaev, 2007), exploration (e.g. Dingemanse et al., 2003), and sociability with asocial individuals dispersing further (e.g. Cote et al., 2010). Furthermore, the behavioral traits of a disperser may differ across contexts: dispersers from high density populations tend to be asocial, while dispersers from low density sites are generally more social (Cote and Clobert, 2007). The physiological or morphological traits and mechanisms underlying behavioral differences in dispersing individuals are not well known. The first cane toads, *Rhinella marina*, to arrive on new sites of an invasion front in Australia had longer legs than individuals in established populations (Phillips et al., 2006). Additionally, condition-dependent dispersal appears also to be important though directionality differs across systems (reviewed in Clobert et al., 2009). In some cases, individuals in poorer condition have a higher propensity for dispersal (Bowler and Benton, 2005; Roff and Fairbairn, 2001; Sinervo et al., 2006). Studies in naked mole rats (*Heterocephalus glaber*), side-blotched lizards (*Uta stansburiana*) and Belding's ground squirrels (*Urocitellus beldingi*) have shown that dispersing individuals often have a higher body mass than non-dispersers (Bowler and Benton, 2005; Sinervo et al., 2006; Holekamp, 1986; O'Riain et al., 1996). However, mechanisms remain to be determined. A few investigations have described distinctive patterns in testosterone, glucocorticoids, and serotonin