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Genetic and environmental influences on fitness-related traits in an endangered shorebird population

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ABSTRACT

Adaptation depends on the additive genetic variance for fitness and its component traits. Yet estimating additive genetic variance and heritability for wild populations is challenging because determining relatedness of individuals is difficult. We used 20 years (1994–2013) of phenotypic records from mark-recapture data and a multi-generational pedigree to estimate quantitative genetic variation in three fitness-related traits in Great Lakes piping plovers (*Charadrius melodus*), an endangered wild shorebird. Genetic and environmental components of variance as well as heritabilities were estimated using Bayesian inference for animal models. Phenotypic variation in age-corrected chick mass was composed of a significant additive genetic component ($h^2 = 0.27$; 95% credible interval: 0.16–0.38), and hatch year, common maternal environment, and hatch site effects. Conversely, natal dispersal distance and female breeding time were not significantly heritable ($h^2 = 0.03$; 95% CI: 0.0–0.11; $h^2 = 0.08$, 95% CI: 0.0–0.22, respectively). Rather, environmental factors (e.g., breeding site) are the main sources of variation in these two traits. Variation in female breeding time was minimally influenced by her mate and was moderately repeatable. The low potential for natal dispersal and breeding time to evolve may limit the ability of this population to adapt to climate change long-term. However, trait alteration could occur by a phenotypically plastic response, allowing rapid adjustment to novel environmental conditions and short-term persistence. Depending on the relative contribution of genetic and environmental influences on the trait(s) of interest, results from quantitative genetic studies can also help identify management priorities for endangered populations.

1. Introduction

Nearly every alteration to a population's environment, whether it is natural or anthropogenic, is a potential source of new or intensified directional selection on traits important for fitness (Gienapp et al., 2008). Responses of populations to such challenges include dispersing to a new location, adjusting the phenotype non-genetically (i.e., phenotypic plasticity), adapting via genetic changes through evolution, or extirpation (Serbezov et al., 2010). While dispersal may lead to local extirpation, but persistence elsewhere, plasticity and adaptation can prevent local extinction. Phenotypic plasticity may enhance short-term persistence of populations as the environment changes, but there are limits to plastic responses and they are unlikely to provide long-term persistence in the face of continuous directional environmental change (Gienapp et al., 2008), such as habitat loss and global climate change. Persistence through major, lasting environmental changes depends on adaptation, with its rate dependent on the additive genetic variance for fitness-related traits. Although genetic variability may be less critical than other determinants of population persistence in the short-term, it can play a decisive role in ultimately allowing a population to persist in and adapt to a changing environment; thus, extirpation is the final consequence of the inability of a population to adapt with sufficient speed to novel conditions (Falconer et al., 1996; Lande and Shannon, 1996).

Because an evolutionary response is necessary for long-term viability of wild populations, disentangling the genetic and environmental influences on morphological and life-history traits is becoming increasingly pertinent to conservation (Lane et al., 2011). Due to the relative ease with which parents and their offspring can be marked and identified, studies of bird populations have played an important role in the application of quantitative genetic methods to natural populations (Merilä and Sheldon, 2001). However, although more than 30 years of research into the genetics of wild bird populations suggests that life-history

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traits are to some extent heritable, little is still known about how quantitative genetic parameters vary among traits, populations, and species (Postma and Charmantier, 2007). This study uses long-term data from a natural shorebird population to quantify the genetic and environmental components of variance of three fitness-related traits: age-corrected chick body mass, natal dispersal distance, and female timing of breeding.

Body mass is an important component of parental and offspring fitness in many vertebrate species (Haramis et al., 1986; Festa-Bianchet et al., 1998; Saunders et al., 2014). Although there is considerable evidence that skeletal measures of body size are heritable in wild animal populations, it is often assumed that the non-skeletal component of body weight is determined primarily by environmental factors, such as nutritional status (Merilä et al., 2001). Yet analyses of cross-fostering experiments of collared flycatchers (*Ficedula albicollis*) and blue tits (*Parus caeruleus*) suggest a significant genetic component to variation in relative body weight as well (Merilä et al., 1999, 2001).

Natal dispersal, defined as the movement of an individual from its natal site to a new site for first breeding, is a major component of gene flow and therefore another important trait for adaptation of populations. Evolution of natal dispersal has frequently been attributed to the social and environmental context faced by individuals (e.g., inbreeding avoidance, resource competition; Charmantier et al., 2011), but heritability estimates for vertebrates are still limited (but see: Massot and Clobert, 2000; Hansson et al., 2003; Gienapp and Merilä, 2010). This scarcity is largely due to the need to obtain estimates from realized dispersal events over sufficiently large spatial and temporal scales (Doligez et al., 2012), which can be challenging because of the need to track an unbiased sample of parent and offspring movements.

Timing of breeding is an important fitness-correlated trait as it is the main determinant of the time a migratory bird has available for raising young (Pulido et al., 2001). It further determines the fitness of offspring, as earlier breeding leads to more time for chick growth prior to autumn migration (Harris et al., 1994). Seasonal declines in chick survival, and consequently reproductive success, have been documented in numerous precocial species (Guyn and Clark, 1999; Traylor and Alisauskas, 2006; Brudney et al., 2013; Catlin et al., 2013).

Quantitative genetic models (Falconer et al., 1996) allow estimation of components of variance observed in a phenotypic trait by jointly analyzing data on the trait and genealogical relationships in a pedigree. Specifically, the 'animal model' approach allows simultaneous estimation of components of variance that can be attributed to genetic, environmental, and other unknown factors (Shaw, 1987; Kruuk, 2004). Heritability of the phenotypic trait can then be estimated from the fraction of the variance that can be attributed to the additive genetic effects. Only recently has the animal model framework been used for wild animal and plant populations, resulting in applications to conservation issues (e.g., harvesting strategies, habitat fragmentation effects) and management for species of conservation concern (Coltman et al., 2003; Stockwell et al., 2003; Law and Stokes, 2005).

Teasing apart the genetic and environmental underpinnings of fitness-related traits in piping plovers (*Charadrius melodus*) will help identify which have the greatest potential to evolve relative to other traits, allowing for more accurate predictions of the impact of local and global environmental changes on the long-term persistence of this endangered population. Because of their endangered status, piping plovers in the Great Lakes region of North America are thoroughly monitored throughout the entire known breeding range, so young are likely to be encountered even if they disperse to a new breeding location (LeDee et al., 2010). Additionally, the resighting probability of breeding adults is near perfect (LeDee et al., 2010); thus, individuals that return to breed will likely be encountered. This intensive monitoring makes the Great Lakes piping plover population ideal for accurately estimating heritabilities of natal dispersal distance and timing of breeding in particular.

We used long-term (1994–2013) phenotypic records from mark-recapture data and a multi-generational social pedigree to examine the quantitative genetic influences on three fitness-related traits in the Great Lakes piping plover population. Our objectives were to: (1) estimate the heritabilities of chick mass, natal dispersal distance, and female timing of breeding; (2) quantify the genetic and environmental variance components of these traits; and (3) determine the evolvability of each trait as measured by the coefficient of additive genetic variation. Results from this study will help predict the short- and long-term consequences of climate change to an endangered population, as well as identify management priorities, given the relative contributions of genetic and environmental influences on traits essential to fitness.

2. Methods

2.1. Focal species and study area

The Great Lakes population of piping plovers nests on wide, sparsely vegetated sand and cobble beaches along the shoreline of lakes Michigan, Superior, and Huron (U.S. Fish and Wildlife Service [USFWS], 2003), and winters primarily along the U.S. Atlantic coastline from North Carolina to Florida and the Bahamas (Stucker et al., 2010; Gratto-Trevor et al., 2012). Since being listed as federally endangered in 1986 (USFWS, 1985), the population has fluctuated between 17 and 71 known breeding pairs (Saunders et al., 2014). Females typically produce a four-egg clutch, and both parents incubate and assist in rearing precocial young. Nests are protected by wire exclosures to reduce egg predation (Melvin et al., 1992) and recreational activities are managed to reduce human disturbance in breeding areas (USFWS, 2003). This study used data from all known nesting locations during 1994–2013 (Fig. 1).

2.2. Field data collection

Surveys were conducted at historical, recent, and potential nesting sites to locate breeding pairs. Plovers were banded using U.S. Geological Survey (USGS) metal bands and Darvic color bands (Avinet Inc., Dryden, NY, USA). Unmarked or brood-marked (i.e., previously marked as chicks) incubating adults were trapped on the nest (Lincoln, 1947), sexed, and given unique color band combinations. Chicks were caught by hand, weighed with a Pesola spring scale to the nearest gram, and given brood-specific color band combinations, typically at 5–15 days of age (Roche et al., 2010). Because all nesting sites were monitored throughout the breeding season, hatch dates were known and therefore, the age of every chick was known. Breeding pairs were monitored every one to four days from nest initiation until all chicks disappeared or fledged. Data collected during monitoring included identity of plover pairs (based on individual color bands), locations of nests, hatch dates, and numbers of chicks that survived to fledging age.

2.3. Data summary and pedigree construction

Similar to body condition, we assumed that relative age-specific chick body mass was a good indicator of survivability (Saunders et al., 2014). We calculated the residual body mass (hereafter referred to as chick mass) as the residuals from a regression of $\log_e$-body mass on known age at banding (to account for differences in body size associated with age; Schulte-Hostedde et al., 2005). Because structural measurements of chicks were not available,