Biological Conservation 180 (2014) 196–205

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Can river management improve the piping plover's long-term survival on the Missouri River?

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ARTICLE INFO

Article history:
Received 16 April 2014
Received in revised form 2 October 2014
Accepted 6 October 2014

Keywords:
Piping plover
Charadrius melodus
Maternal effects
Cohort effects
Missouri River

ABSTRACT

The goal of many animal conservation efforts is to improve short-term demography, but there is growing interest in the potential for producing more fit individuals, resulting in long-lasting demographic impacts. The environments that animals experience prior to independence from their parents can have profound, life-long effects on individual fitness and population demography that managers can potentially exploit. Environmental variables can affect fitness directly through early mortality, delayed maturity, reduced probability of recruitment, decreased fecundity, or a combination of these factors. We studied the imperiled piping plover (*Charadrius melodus*) nesting on the Missouri River to determine if body condition affected their long-term survival, and, if so, whether these factors could be used to improve conservation and management. We captured and measured adult and hatchling piping plovers during the breeding season (April–August, 2005–2012) to obtain measures of condition (mass, wing-chord length, culmen length). We assessed the effect of environmental variables on plover growth, and the effect of chick condition at fledging on subsequent survival as an adult. Plover chicks grew faster and achieved larger body size if they hatched earlier in the season, were exposed to lower density, and were hatched in higher quality habitat compared to other chicks. Plovers that were heavier at fledging had a higher survival rate (as much as 9%) than lighter plovers during their first year as well as in subsequent years, which could make a significant impact on population viability and an individual's lifetime fitness. Where the factors that affect development are manageable, they offer an opportunity for conservation to capitalize on these long-term effects. For example, habitat creation, restoration, and protection projects should ensure that adequate food resources are available or created not only to maximize reproductive output, but also to improve the condition of offspring where possible.

1. Introduction

Habitat protection is a commonly recommended approach to imperiled species conservation (e.g., IUCN, 2013; USFWS, 2013). These recommendations imply that setting aside habitat will invoke demographic benefits (e.g., stationary or increasing population, maintained or improved rates of reproduction and/or survival, etc.). However, it is well known that some habitats that appear to support populations can, in fact, be "sinks" that attract organisms, but that cannot sustain their numbers without continual immigration from source populations (Hanski, 1998). Sink populations may require conservation interventions to insure that mortality and emigration are at least balanced by reproduction and immigration. Such interventions are common, especially for species in anthropogenically-altered habitats or subject to overexploitation (e.g., Guimaraes et al., 2014; Inman et al., 2013; Wellicome et al., 2013; Wiens et al., 2014). The goals of these interventions usually are to improve local survival and reproduction, with expected response time to be nearly immediate.

A logical extension of this goal, however, would be to manage populations to produce more fit individuals. Such individuals would be expected to have higher reproduction and survival at the time and place of the intervention, but could also be expected to have improved demographics in future years, and for dispersive species, in other populations. To that end, interventions to improve individual fitness at early life-stages could have long-lasting impacts.

The period of animal development prior to maturity can have important effects on an individual's fitness (Cam and Aubry, 2011; Cam et al., 2003; Desai and Hales, 1997; DuRant et al., 2013; Lindström, 1999; Metcalfe and Monaghan, 2001). The environmental conditions experienced at these early life stages may affect growth and survival prior to independence (Burness et al.,

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http://dx.doi.org/10.1016/j.biocon.2014.10.004
0006-3207/

2000; de Kogel, 1997; Gebhardt-Henrich and Richner, 1998; Green and Cockburn, 2001; Haywood and Perrins, 1992), adult phenotype (Boag, 1987; de Kogel, 1997; de Kogel and Prijs, 1996), survival prior to recruitment as a breeder (Cam et al., 2003; Magrath, 1991), age at recruitment (Cam et al., 2003), reproductive fitness (Haywood and Perrins, 1992; Schluter and Gustafsson, 1993), and even adult survival (Albon et al., 1987).

Nutrient limitation during key pre- and post-natal stages can slow growth and maturation (Catlin et al., 2013; Desai and Hales, 1997; Gebhardt-Henrich and Richner, 1998; Martin, 1987). Such limitations can be direct (e.g., reduction in food abundance or quality) or mediated through indirect, environmental effects that are related to food abundance, quality, or availability (e.g., precipitation, temperature, etc., Albon et al., 1987; Clinchy et al., 2013; Gebhardt-Henrich and Richner, 1998; Schekkerman et al., 2003).

In addition to individual effects, the environmental factors that affect ontogeny also can manifest at the family- or cohort-specific level (Cam and Aubry, 2011; Mousseau and Fox, 1998; Sæther, 1997), which can create a disconnect between current environmental conditions and population dynamics in longer-lived species (Beckerman et al., 2002; Cam and Aubry, 2011; Cam et al., 2003). There is increasing interest in understanding maternal and cohort effects on individual fitness as well as population dynamics (Mousseau and Fox, 1998; Sæther, 1997). Whether it is offspring placement (e.g., den site, nest location, territory quality, etc.) or investment (e.g., propagule size, clutch size, parental care, etc.), maternal or 'silver spoon' effects can have profound impacts on offspring fitness (Lloyd and Martin, 2004; Mousseau and Fox, 1998; van de Pol et al., 2006). Moreover, cohort-level effects can have complex interactions with density-dependent population dynamics, such that cohort effects act to change future densities and negative feedback from those densities (Beckerman et al., 2002).

The interest in using and applying indirect effects such as maternal (Arlinghaus et al., 2010; Garnier et al., 2012; Gibbs and Van Dyck, 2009; Schuler and Orrock, 2012) or cohort effects (Wittmer et al., 2007) to inform conservation has increased, but the necessary data and linkages are unavailable in many instances. Where relationships among environmental factors and long-term survival and fecundity are known to affect species of conservation concern, this information ought to be used to improve the specificity of population models (Arlinghaus et al., 2010) and, where possible, to manage a population for the greatest average fitness (Garnier et al., 2012; Gibbs and Van Dyck, 2009).

Our primary objective in this study was to describe the links between environmental conditions during early development (with specific attention paid to conditions related to management), individual condition, and short- and long-term survival, using a 'near threatened' (IUCN, 2013) shorebird, the piping plover (*Charadrius melodus*), as an example. Previous work established that land and water management practices (flow control and habitat creation) can have direct impacts on survival to fledging (i.e., first flight) and time to achieve first flight (Catlin et al., 2013), but long-lasting effects have not been adequately explored.

The first step in achieving the study objective was to establish what if any effect juvenile condition had on lifelong survival. Although pre-breeding survival can be affected by early conditions (Cam et al., 2003; Magrath, 1991), there is relatively little evidence for long-lasting effects of early conditions on survival of breeders (Cam and Aubry, 2011). We hypothesized that condition at fledging would be positively correlated with annual survival, and that the effect would extend into adulthood.

After estimating the effect of offspring condition on annual survival, we investigated potential maternal effects (Lloyd and Martin, 2004; Mousseau and Fox, 1998; van de Pol et al., 2006). We explored the relationships among parental condition, parental investment (egg mass), and the condition of young birds at fledging. We hypothesized that there were positive correlations among parental condition, parental investment, and juvenile condition.

Finally, we estimated the effect of various environmental (e.g., weather, location) and management-related (related to flow, habitat availability, and habitat creation) factors on the condition of individuals at fledging. Flow can affect demography directly through flooded nests (McGowan and Ryan, 2009) and habitat limitation affecting growth and survival (Catlin et al., 2013), but flooded nests also lead to later initiation and hatching dates and increased density as flows increase through the breeding season. Habitat creation can alleviate some of these issues (Catlin, 2009; Catlin et al., 2011b) and even the choice of habitat placement can affect demography (Catlin et al., unpublished data). We hypothesized that factors that tended to increase habitat availability and quality would be correlated with offspring condition, and that manageable factors such as flooding, flow control, and habitat creation and placement could have significant impacts on fledgling condition.

2. Methods

2.1. Study species

The piping plover (hereafter 'plover') is a small, temperate-breeding shorebird that nests on open or sparsely vegetated beaches, river sandbars, and lake-shores on the Atlantic Coast and interior rivers and lakes of North America (Elliott-Smith and Haig, 2004). The average lifespan of a plover is approximately 5 years (D. Catlin, unpublished data). Plovers are serially monogamous but have low mate-fidelity between years, with males establishing territories typically near their previous year's nest site (Elliott-Smith and Haig, 2004). Territorial pairs defend both nesting and foraging habitats from other pairs and broods (Elliott-Smith and Haig, 2004) even when they do not have an active brood (D. Catlin, pers. obs.). Most plovers breed by age three, and 35–56% breed by age one (Saunders et al., 2014). Females lay eggs in a small depression in the sand, often lined with shells or pebbles, within their mate's territory. Females lay a single clutch (modal clutch size 4 eggs), but can renest repeatedly following nest loss (at least 4 nest attempts, D. Catlin, unpublished data). Once a clutch is complete, both the male and female incubate the eggs for approximately 28 days until hatching (Elliott-Smith and Haig, 2004). Chicks are precocial and active within hours of hatching, gleaning small insects from the surface of moist sandy areas. Both parents share brooding and tending responsibilities, but there is some evidence that females can leave prior to fledging (23–35 days post-hatch; Catlin et al., 2013; Elliott-Smith and Haig, 2004).

2.2. Study area

We studied plovers on the Gavins Point Reach of the Missouri National Recreational River ('river'; 42°51′N, 97°29′W) in 2005–2012 and on Lewis and Clark Lake ('lake'; 42°51′N, 97°47′W) in 2007–2012. Plover nesting habitat in both areas consisted of sandbars that were usually unconnected to the shore. Most sandbars used for nesting were deposited by the river during relatively high flows in the late 1990s (USFWS, 2003) and in 2011. Plovers also used engineered sandbars built by the U.S. Army Corps of Engineers (USACE) to augment naturally deposited sandbars (Catlin, 2009; Catlin et al., 2011b). Releases from the Gavins Point Dam are controlled by the USACE (USACE, 2006), which accounts for the majority of the water flowing by sandbars downstream of the dam. Although protection of endangered species and their habitat is a part of how the USACE manages water releases (USACE, 2006),