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Effects of inbreeding and parental incubation on captive breeding success in Hawaiian crows

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ABSTRACT

Inbreeding can reduce individual or population fitness and is predicted to have particularly severe effects on early life traits. Detecting inbreeding depression remains a challenge, however, especially in endangered species or long-lived taxa. Ample and detailed data are needed to study the effects of inbreeding at various life stages. We used 17 years of captive breeding records of the Hawaiian crow (*Corvus hawaiiensis*) to study the effects of individual and parental level of inbreeding on survival through early life. Using pedigree data to calculate inbreeding coefficients for over 300 eggs, we find that the individual's inbreeding coefficient, but not the parents', has a very strong effect on embryo and chick survival. Inbreeding levels of chicks that survived to 2 years (reproductive age) are 31% lower than those of embryos and chicks that died. Highly inbred embryos have a > 5 times reduced survival probability as a consequence of individuals carrying on average 6.9 haploid lethal equivalents for survival to 2 years. Further, offspring survival is greatly improved by longer parental incubation. Individuals surviving to 2 years had, on average, twice as many days of parental incubation prior to artificial incubation (four vs. two). Our study contributes to evidence that the strength of inbreeding depression is particularly severe in early life traits. It shows that the negative effects of inbreeding on reproductive success should be accounted for even in benign captive environments where survival is maximized and suggests that parental incubation should be favored over artificial incubation in avian captive breeding programs.

1. Introduction

Inbreeding, the mating between related individuals, can cause a reduction in individual fitness and population viability (inbreeding depression; Keller and Waller, 2002; Wright et al., 2008). Inbreeding depression has been shown to occur in wild (e.g. Billing et al., 2012; Frankham, 2010; Nielsen et al., 2012; Walling et al., 2011) as well as captive populations (Boakes et al., 2007; Fuerst-Waltl and Fuerst, 2012), affecting a broad array of traits. Thus, inbreeding and the associated effects of inbreeding depression are of considerable importance in studies of evolution, ecology and conservation (Frankham, 2010; Keller and Waller, 2002). Since inbreeding is particularly likely to happen in small and isolated populations, its negative effects on fitness have also become a major concern in the management of endangered populations.

Inbreeding depression can affect multiple life history stages and is predicted to be particularly severe early in life (Keller and Waller, 2002). Reduced fertility or offspring survival due to inbreeding have been detected in a number of taxa (e.g. Kruuk et al., 2002; Saccheri et al., 1998; Van Oosterhout et al., 2007; Walling et al., 2011), including species of conservation concern (e.g. Jamieson et al., 2007; Swinnerton et al., 2004). However, detecting inbreeding depression and at what stage it occurs still remains a challenge, especially in species with small population sizes (such as endangered species) or long-lived taxa. Large sample sizes and detailed information on inbreeding levels and phenotypic data are needed (Boakes et al., 2007), which limits the implementation of such studies in general and makes it particularly hard to differentiate inbreeding effects during various life history stages. For example, in birds, inbreeding has been shown to reduce overall hatching success of eggs (Briskie and Mackintosh, 2004; Spottiswoode and Moller, 2004, and references therein). This could be the result of inbreeding depression in the parents (e.g. due to lower fertilization success or poorer egg quality) or in the offspring itself (e.g. embryonic developmental problems). Because parent and offspring inbreeding levels are not expected to correlate

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(Falconer, 1989; but see Reid et al., 2006), it is necessary to study both offspring and parental inbreeding in order to quantify the effects of inbreeding on reproductive success.

The captive population of the last surviving Hawaiian crows (*Corvus hawaiiensis*), also called 'alala, provides a rare opportunity to quantify the effects of offspring and parental inbreeding on early life fitness. Once abundant on the Big Island, the species declined dramatically in the 20th century (Fig. 1). Fortunately, a captive breeding program was initiated well before the species was declared extinct in the wild in 2003. The last individual to supplement the captive population was brought in from the wild as an egg in 1996 and the captive population has steadily increased over the past decade. Detailed pedigree data and records on egg survival and reproductive success have been collected for all living birds as part of the captive breeding program (U.S. Fish and Wildlife Service, 2009). Despite intense efforts to maintain genetic diversity in the captive population through selective breeding, some levels of inbreeding have been inevitable due to the small population size and reproductive rates have been low (U.S. Fish and Wildlife Service, 2009). A gradual decrease in fertility has been observed over the years so that fertility in 'alala is now lower than that of other captive-bred Hawaiian forest birds (Switzer, 2012). Also, a high proportion (61%) of 'alala embryos die during development or while hatching, and 15% of hatched chicks die before reaching independence (Switzer, 2012).

The aim of this study was to identify the main effects contributing to poor reproductive success observed in 'alala. We then quantified whether and to what extent embryonic or parental inbreeding depression can explain the observed low embryo and chick survival. We tested this using pedigree-based inbreeding coefficients that span over 8 generations and include over 700 eggs. We also assessed whether age of the parents, a factor known to affect reproductive success (e.g. Rebke et al., 2010), may explain variation in embryo and chick survival. Furthermore, since natural incubation preceding artificial incubation of eggs has been shown to improve hatching success in some captive bird populations (Burnham, 1983; Robertson et al., 2006; Smith et al., 2011), we also tested for the effect of initial parental incubation on embryo and chick survival.

The availability of detailed phenotypic data on eggs, embryos, chicks and adults over many years, as well as on the individuals' genetic relationships and inbreeding levels, makes this an unusually good opportunity to test for parental and offspring inbreeding depression in a long-lived and highly endangered species. Since little is known about the factors that cause hatching failure in captive bird populations (Smith et al., 2011) and since offspring survival can be an important limitation on the contribution of captive populations to ex situ conservation efforts, our study is not only of importance to the conservation of 'alala, but may also be of value to the captive management of other species.

2. Materials and methods

2.1. Captive breeding of 'alala

The 'alala is an iconic Hawaiian endemic that was historically abundant in low and mid elevation forests on the Big Island (Perkins, 1903). Its dramatic decline began in the early 1900s along with habitat destruction and the introduction of ungulates and novel avian diseases (Banko et al., 2009). In order to save the species from extinction, captive breeding attempts began in the 1970s and 1980s, but initially struggled on many levels (Banko et al., 2009; U.S. Fish and Wildlife Service, 2009). In 1996, the captive conditions improved substantially when a modern facility was established on the Big Island, significant operational improvements were made to the facility on Maui and captive holding and breeding protocols were standardized for both facilities (i.e. standardized egg incubation protocols, very similar housing/aviary structures, veterinary control and care). Since then, captive propagation has produced over 120 chicks (Switzer, 2012) and the captive population has increased in number despite the species' extinction in the wild (Fig. 1). The 'alala is now the only species in Hawaii whose recovery depends entirely on captive propagation. The ultimate aim of the 'alala recovery program is reintroduction of the birds back into the wild to hopefully secure their long-term survival outside of captivity (U.S. Fish and Wildlife Service 2009; VanderWerf et al., 2013).

'Alala breeding pairs are carefully selected each year according to low inbreeding coefficients and genetic representation in the flock, among other criteria (Switzer, 2012). Breeding occurs from April to July and pairs are housed in separate aviaries where they are intensely monitored for mating, egg laying and incubation

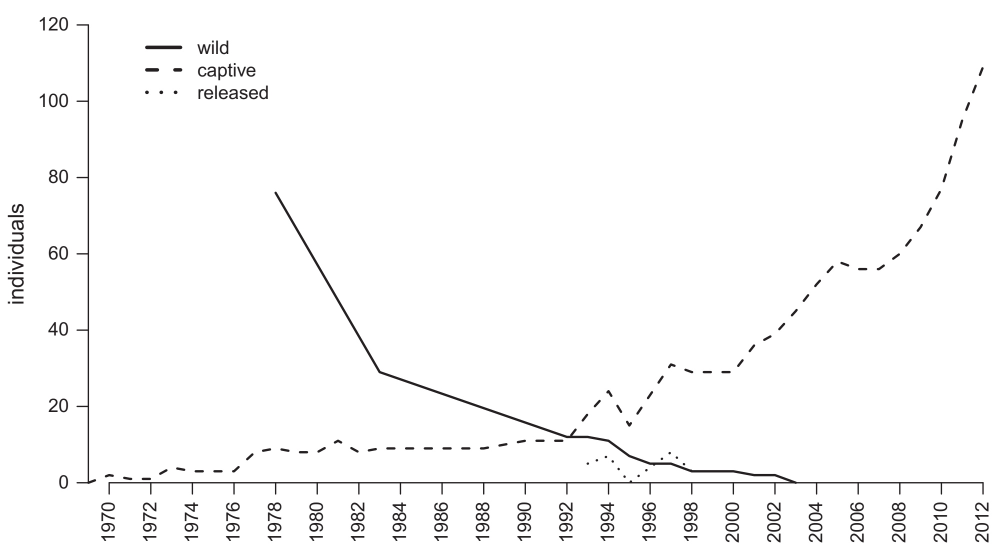

Fig. 1. 'Alala population size since the first individuals were taken into captivity in 1970. The captive population (dashed line) has continually increased while the population in the wild (solid line) went extinct in 2003. The dotted line shows a few individuals that were released into the wild in the 1990s, all of which either died in the wild or were brought back into captivity in 1999. All individuals alive today have been born and are living in captivity at the two breeding facilities.