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Evidence of reproductive senescence of released individuals in a reinforced bird population

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ABSTRACT

In free-ranging populations, age-dependent variation in fitness related parameters, in particular the pattern of senescence, has major eco-evolutionary implications and potential influence on population dynamics. Despite the recent surge of studies of senescence in the wild, senescence patterns in species for which population dynamics assessments are crucial, such as translocated populations, remain virtually unexplored. Based on a 15-year nest survey of a North-African Houbara bustard population in Morocco, we investigated age variation in the breeding performance of captive-bred females released in the wild. We identified 781 females, from 1 to 10 years of age, on 1094 nests. We examined how age influenced nest initiation date, clutch size, egg volume, daily nest survival and daily brood survival, as well as whether age-dependent patterns varied according to environmental conditions. Most breeding parameters exhibited variation, suggesting an increase in breeding performance with age in young females (those from 1 to 3 years old). In older females (> 7–8 years old), the egg volume and clutch size decreased with age, in concordance with expectations from senescence theories and previous empirical results obtained from captive Houbara bustards. Finally, our analysis uncovered a significant interaction between age and the amount of precipitation prior to the breeding season on clutch size, suggesting differential abilities of females of different ages to increase their breeding investment. Our study suggests that life histories in translocated individuals are not affected by translocation protocols and provides insights for implementing age dependencies in population viability assessments.

1. Introduction

In wild animals, variation in fitness-related parameters with age has major eco-evolutionary implications (Charmantier et al., 2006) and a potentially strong influence on population dynamics and viability (Robert et al., 2015a; Chantepie et al., 2016). Although age-demography relationships can exhibit a diversity of patterns (Jones et al., 2014), most studies of vertebrates, both in captivity and in the wild, describe a characteristic bell-shaped trend of fitness related parameters divided into youth, adulthood and senescent stages (Lynch et al., 2010; Oro et al., 2014). The increase in performance in early ages can be explained (non-exclusively) by the selection of good quality individuals (the selection hypothesis, Lescroël et al., 2009), by the increase in experience or physiology (the constraint hypothesis, Curio, 1983) and the adaptive restraining of reproductive effort by young individuals (the restraint hypothesis, Curio, 1983). For ageing individuals, a decrease in demographic parameters is expected; this process is referred to as senescence. Senescence is caused by internal physiological degeneration (Kirkwood and Austad, 2000) occurring in relation to the decrease of the force of selection with age (Charlesworth, 1994). In the field of evolutionary ecology, it has been argued for decades that animals in the wild fail to senesce due to high extrinsic mortality probability (Medawar, 1952, Kirkwood and Austad, 2000, discussion in Nussey et al., 2013). However, in recent years, new evidence enabled by longitudinal individual-based population surveys has clearly demonstrated that senescence commonly occurs in free-ranging populations (Nussey et al., 2008, 2013).

In addition to age variation, wild populations exhibit temporal and spatial variation in demographic parameters due to external factors (Parmesan, 2006), and the link between individual age and breeding performance or survival may be condition dependent (Reichert et al., 2010). It has been suggested that the effects of environmental conditions will be stronger on age classes with poor intrinsic abilities and conditions (Bunce et al., 2005; Pardo et al., 2013), so that differences in demographic parameters between ages will be greater in stressful environments (Bunce et al., 2005; Nussey et al., 2008). In contrast, if low-

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quality individuals temper their reproductive investment to reduce costs when conditions are poor (Cubaynes et al., 2011; Robert et al., 2012), one may expect that differences in average reproduction performance between age classes will be greater in favourable environments (discussion in Oro et al., 2014; Robert et al., 2015b).

Conservation translocations are increasingly used to manage threatened species and to maintain or establish viable populations in the long term (Armstrong and Seddon, 2008). Translocated populations are likely to suffer demographic costs in terms of survival (Hardouin et al., 2014) and reproduction (Sarrazin et al., 1996), especially in translocations relying on captive breeding (Robert, 2009). Thorough assessments of these demographic costs and of their potential effects on the life history of released individuals are nevertheless rarely done, because they require high quality demographic data, which are generally lacking due to insufficient monitoring effort (Bertolero et al., 2007). Although now commonly documented in the wild in many taxa (Nussey et al., 2013), the effects of potential translocation costs on realized senescence patterns remain virtually unexplored (but see Chantepie et al., 2016 for a recent exception concerning actuarial senescence).

Here, we argue that the documentation of senescence patterns in translocated populations is of strong importance for (1) assessing whether translocated individuals senesce in the wild despite potential demographic translocation costs or phenotypic changes; and (2) improving the reliability of long-term assessments of the success of individual translocation programmes. We aim to investigate how breeding performance varies according to the age of released captive-bred individuals in a reinforced bird population and whether such age-related patterns vary according to environmental conditions. We used data collected from a longitudinal nest survey of the North-African Houbara bustard (*Chlamydotis undulata undulata*, hereafter Houbara) in eastern Morocco completed between 2002 and 2016. Previous studies on captive populations of Houbara have shown strong senescence trends in female breeding parameters (Chantepie et al., 2015; Preston et al., 2015) affecting egg productivity and chick mass at hatching. However, those results were obtained from captive populations subject to controlled environmental conditions (food and water ad libitum). Further investigation is needed to corroborate if similar age patterns occur in captive-bred females released in the wild. Since populations in the wild are exposed to higher levels of environmental stressors, one can expect mitigated age-dependent patterns and variation in breeding parameters as functions of environmental conditions. The Houbara is found in semi-desert habitats where meteorological conditions are highly variable between years and where water is a primary limiting factor (Gamoun, 2016). Under such environmental conditions, variation in temperature and precipitation may have major consequences on food resource availability, ecological processes (Brown et al., 1997; Gamoun, 2016), and breeding performance in bird species (Morales et al., 2002; van Heezik et al., 2002; McCreedy and van Riper, 2014).

We focused on five breeding parameters: nest initiation date, clutch size, egg volume, daily nest survival, and brood survival. Senescence in breeding parameters is expected to be primarily caused by physiological degradation (Angelier et al., 2006). Egg production (size and number) is known to be highly influenced by physiological conditions (Williams, 2001; Christians, 2002). Conversely, laying date as well as nest and brood survival are highly influenced by external factors (e.g., meteorological conditions, nest predators) and can be positively influenced by female competence, which is expected to increase with age (see discussions in Wooller et al., 1990 and Pärt, 1995, 2001). Therefore, we expected that clutch size and egg volume would experience particularly strong reductions in older individuals. In contrast, since female competence is expected to increase sharply with age in young females, we expected strong reductions in the precocity of nest initiation, nest survival, and brood survival in the youngest females.

Based on previous studies of birds in captive conditions and knowledge of the species' biology, we hypothesized three functional age classes (see Chantepie et al., 2015, 2016): youth, adulthood and senescent ages, and made the following predictions:

1. Breeding performance will be lower in young birds (i.e., age < 2 - years based on knowledge of the distribution of recruitment age, Preston et al., 2015) and in senescent individuals compared to adults, with more marked reduction in the precocity of nest initiation, nest survival and brood survival in younger females and more marked reduction in clutch size and egg volume in senescent individuals.
2. Meteorological conditions (temperature and precipitation) prior to the breeding season will constrain the breeding performance of all individuals. However, young, adult, and senescent individuals will respond differently to varied meteorological conditions.

2. Methods

2.1. Biological model and study area

The Houbara is a medium-sized bustard inhabiting semi-desert steppes from North Mauritania to Egypt. It is a ground-nesting, gyneparental incubating species breeding from mid-February to mid-June. Females generally lay two or three eggs, at 2.5-day intervals, which they incubate on average for 23 days (Gaucher, 1995). Houbara chicks are nidifugous but rely on the dams to be fed for the first ten days after hatching and fledge at a mean age of 60 days (Saint Jalme and van Heezik, 1996; Hardouin et al., 2012).

Over the last few decades, the Houbara population has greatly declined throughout the species' range due to habitat degradation, poaching and over-hunting (Lacroix et al., 2003; Saint Jalme and van Heezik, 1996). This population decline led to the creation, in 1995, of the Emirates Center for Wildlife Propagation (ECWP) based in eastern Morocco (Lacroix et al., 2003). The ECWP captive breeding programme aims to increase the population size of the threatened Houbara throughout its range via regular releases of captive-bred individuals.

The present study was conducted in eastern Morocco (see Fig. A, Supplementary Appendix A). The study area encompasses an area of 50,000 km^2 and is characterized by an arid climate marked by irregular rainfall and cold winters. Hunting is allowed from October to January and is delimited to specific hunting areas totalling 64% of the managed area.

2.2. Release and tagging procedure

From 1996 to 2016, 108,486 birds were released in North Africa (94,374 in the study area). Within the study area, the overall number of birds released progressively increased over the years (from 28 in 1996 to 9084 in 2016), with an increase in the number of release sites and a decrease in the group size per release (Hardouin et al., 2014). The numbers of birds in release groups varied between sites (from 4 to 498, median = 18). Houbara were released at an average age of 8 ± 3 (standard deviation) months in spring (from March to May), autumn (from September to November) and, since 2003, at an average of 3 ± 0.6 months of age in summer (June). Autumn releases were conducted in non-hunting areas to avoid direct mortality and disturbance due to hunting. Over the study period, all released Houbara were individually marked with either aluminium rings (1996–2005) or electronic transponders (2006–2016). A total of 3014 individuals were also equipped with transmitters (see Supplementary Appendix B and Hardouin et al., 2015).

2.3. Data collection

2.3.1. Breeding parameters

Five breeding parameters were assessed from survey data collected from 2002 to 2016 (the number of years of survey data varied among