



## Regular article

# Influence of mate preference and laying order on maternal allocation in a monogamous parrot species with extreme hatching asynchrony



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## ABSTRACT

It is well established that in many avian species, prenatal maternal resource allocation varies both between and within clutches and may affect offspring fitness. Differential allocation of maternal resources, in terms of egg weight and yolk composition, may therefore allow the female to adjust brood reduction and to fine-tune reproductive investment in accordance with the expected fitness returns. The adaptive value of such maternal resource allocation is thought to be context-dependent as well as species-specific. We investigated the effects of female preference for her mate on the allocation of prenatal maternal resources in the budgerigar, *Melospiza undulatus*, a monogamous species of parrot that shows an extreme hatching asynchrony. We assessed mate preferences in a two-way preference test and allowed females two breeding rounds: one with the preferred and one with the non-preferred partner. We found no effect of preference on either latency to lay or clutch size, but females mated with the preferred partner laid eggs that contained significantly more yolk. Their eggs also contained significantly more androstenedione but not testosterone. Our results suggest that in this species, female preference may influence maternal resource allocation, and that the functional roles of each androgen in the yolk should be considered separately. In addition, we found a significant effect of laying order on egg and yolk weight as well as on yolk testosterone and androstenedione levels. These measures, however, did not change linearly with the laying order and render it unlikely that female budgerigars compensate for the extreme hatching asynchrony by adjusting within-clutch allocation of prenatal maternal resources.

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## Introduction

Early maternal allocation of resources provides a non-genetic mechanism for the female to modify the phenotype of the offspring in accordance with the environmental conditions that she experiences and that her offspring are likely to face after hatching (Mousseau and Fox, 1998). In oviparous animals, such as birds, the egg provides a sealed system in which the embryo develops and once the egg is laid, investment in the offspring through maternal resources is restricted. Birds are therefore excellent subjects for studying the causes and consequences of differential maternal allocation during the prenatal phase.

In birds, maternal resources that determine egg quality include egg weight and various yolk compounds (e.g. antibodies, antioxidants, androgens; Blount et al., 2002; Groothuis et al., 2005a; Krist, 2011; Müller et al., 2004; von Engelhardt and Groothuis, 2011). These maternal resources may vary both within and between clutches. Within

clutches, species-specific deposition patterns of maternal resources over the laying order have been documented for several species (e.g. androgen deposition and egg weight; Groothuis et al., 2005a; Muller and Groothuis, 2013; Slagsvold et al., 1984). This has typically been interpreted in the context of hatching asynchrony, which is caused by the fact that females may lay more than one egg, but eventually start incubating before the clutch is completed. The resulting hatching spread and associated size hierarchy in the nest negatively affect the survival of chicks from later-laid eggs as they experience a competitive disadvantage compared to their older siblings (Massemin et al., 2002). It has been proposed that differential allocation patterns of maternal resources within a clutch enable the female to adjust brood reduction, thereby maximizing her own fitness (Schwabl, 1996; Wagner and Williams, 2007). An increase in maternal allocation with the laying order may counteract the competitive disadvantage of the chicks from later-laid eggs, because chicks that hatch from eggs with heavier yolks or higher levels of the maternal androgens androstenedione (A4) and/or testosterone (T) may hatch earlier, beg more vigorously, grow faster and have higher survival rates (e.g. Eising et al., 2001; Groothuis et al.,

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2005a; Krist, 2011; Schwabl, 1996; von Engelhardt and Groothuis, 2011; Wagner and Williams, 2007). A decrease in resources on the contrary may further enhance brood reduction (Groothuis et al., 2005a). However, the situation may be more complex, as in some species certain maternal resources such as yolk androgens have mainly negative effects on offspring fitness (Groothuis et al., 2005a, b; von Engelhardt and Groothuis, 2011). Together with the fact that species vary considerably with respect to within-clutch allocation patterns, this suggests that the adaptive value of maternal allocation is species-specific and may differ according to the type of resource. To increase our understanding of the phylogenetic and life-history factors that potentially underlie within-clutch allocation patterns, studies that measure different parameters of egg quality in a large variety of species of different taxa are necessary (Gil et al., 2007; Love et al., 2009).

Variation in maternal allocation between clutches has been attributed to a range of environmental determinants and factors intrinsic to the female (e.g. social density, food availability, condition, age; Christians, 2002; Hargitai et al., 2009; Remes, 2011; Safran et al., 2008, 2010; Vergauwen et al., 2012; reviewed in: von Engelhardt and Groothuis, 2011). Reproduction is costly for the female, and there is thus a trade-off between investment in the current reproductive attempt and future reproduction (Williams, 1966). Hence, females are thought to adjust their reproductive effort in accordance to the expected fitness return. One important factor that may influence the reproductive decisions of the female is mate quality (Burley, 1988). Females may experience higher fitness returns when investing more heavily in reproduction when mated with a more attractive male (differential allocation hypothesis; Burley, 1988; Sheldon, 2000), because attractive males may provide more direct benefits such as parental care or territory quality and indirect benefits in terms of offspring genetic quality (Andersson, 1994). The effects of male attractiveness on maternal allocation have been examined in a variety of species, but the resulting data are inconclusive (reviewed in: Cucco et al., 2011; Horvathova et al., 2012; Kingma et al., 2009). Interestingly, in most studies, male attractiveness was determined based on previous work and it was not specifically tested whether females indeed preferred the males that were considered to be more attractive (e.g. Alonso-Alvarez et al., 2012; Garcia-Fernandez et al., 2013; Gil et al., 1999, 2004; Grana et al., 2012; Kingma et al., 2009; Safran et al., 2008; but see: Bluhm and Gowaty, 2004; Cucco et al., 2011; von Engelhardt et al., 2004). In order to estimate male attractiveness as perceived by the female, it is necessary to allow females to actively choose between potential partners.

The budgerigar, *Melopsittacus undulatus*, is a small monogamous species of parrot (Juniper and Parr, 1998). Female budgerigars of self-selected pairs show a shorter latency to lay and produce larger clutches (Massa et al., 1996), which indicates that mating preferences may be an important factor influencing maternal allocation. It has not yet been investigated whether females flexibly adjust maternal allocation of resources, such as yolk weight and androgen deposition, according to mate preference. Unlike many other bird species, parrots produce clutches with extreme hatching asynchrony (budgerigar broods hatch over a span of up to 16 days). Despite the apparent lower competitive abilities of younger chicks, brood reduction is uncommon (Brockway, 1964; Stamps et al., 1985). To the best of our knowledge, it has not been reported in the literature whether or not female budgerigars compensate for the competitive disadvantage of younger chicks as caused by the extreme hatching asynchrony via differential prenatal maternal allocation to the eggs, as has been found for many species with less pronounced asynchrony.

In the current study, we assessed female preferences in a two-way choice test (von Engelhardt et al., 2004). Subsequently, the females were allowed two consecutive breeding rounds in a cross-over design. In one breeding round, they were paired with their preferred partner (i.e. the more attractive male as perceived by the female) and in the other with the non-preferred partner (i.e. the less attractive male as

perceived by the female). Our aims were twofold. First, we tested whether females increase the allocation of resources when they are paired with the preferred partner by studying the effects of female preference on latency to lay, clutch size and the following six maternal resources that have been shown to influence egg quality: egg weight, yolk weight and the concentrations and the total amounts of the androgenic hormones T and A4 in the yolk. Finally, we asked whether maternal allocation varies over the laying order by investigating within-clutch variation in these six maternal resources.

## Material and methods

### Ethics statement

The budgerigars of this study were domesticated animals, which were used to human presence. Because budgerigars are social birds, we always allowed the birds at least vocal interactions with each other. We did not observe abnormal behavior performed by any of the birds during the experimental procedures or during the daily routine checks. Handling time was minimized and did not exceed 3 min per individual for any of the procedures. All experimental procedures were performed in agreement with the Belgian and Flemish laws.

### Study species and housing

We randomly selected 39 unpaired female and 76 unpaired male budgerigars from our captive stock population. The birds had been obtained from local breeders as juveniles and had been maintained in our captive stock for at least one and up to two years. All females showed a green plumage and were adults of approximately one year old with no breeding experience. The males varied in plumage coloration and were approximately between one and two years old. Before the experiment, the birds had been housed in two single-sex outdoor aviaries (8 m wide × 2.5 m deep × 2.3 m high). One week before the start of the preference tests (see 'Preference tests'), the birds were moved to indoor single-sex cages (males: 120 cm wide × 40 cm deep × 50 cm high, females: 150 cm wide × 40 cm deep × 80 cm high). The birds were housed in groups of up to 10 individuals and there was no visual or auditory contact between members of the opposite sex. Throughout the experiment, the birds were maintained on a light regime of 15:9 (L:D), unless stated otherwise. Food (commercial budgerigar seed mix, Nifra Van Camp bvba, Belgium), greens and water were provided ad libitum.

### Male stimulus sets

The females were allowed to choose between two males of a stimulus set (see 'Preference tests'). The males of a stimulus set were matched for body weight. We also matched males with higher and lower UV reflectance of the chest feathers, because female budgerigars may show mating preferences based on this trait (Griggio et al., 2010a; Zampiga et al., 2004). The color of the chest was measured with an USB4000 spectrophotometer (Ocean Optics, Duiven, The Netherlands), using an Ocean Optics DH-2000 BAL deuterium/halogen lamp. Before the measurement session, we took a dark current measurement on the chest of a randomly selected live bird and a white standard reference measurement (WS-1, Diffuse Reflectance Standard, Ocean Optics, Duiven, The Netherlands) for calibration purposes (Cuthill et al., 1999; Lahaye et al., 2014). Next, the chest of all males was measured three times by the same person (Lahaye et al., 2014). From the measurements, we calculated UV chroma as the proportion of total reflectance occurring between 320 and 400 nm ( $R_{320-400}/R_{320-700}$ ) (Montgomerie, 2006). For each male, we first calculated UV chroma separately for the three spectra that were measured, and the mean of these three values was used in the statistical analyses (Lahaye et al., 2014). Each stimulus set contained a male with a higher value for UV chroma of the chest

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