

Individual quality and double-brooding in a highly synchronous songbird population

Author(s): Allison Cornell and Tony D. Williams

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populations of species in at least 64 avian families are known to pursue multiple broods (Bennett and Owens 2002), and in some species the number of broods has been used to predict reproductive success with better accuracy than the success of one brood (Sæther and Bakke 2000). Nevertheless, although double-brooding can have seemingly obvious and significant consequences for individual fecundity, second brood success is often not quantified in avian breeding studies (Holmes et al. 1992, Ogden and Stutchbury 1996, Nagy and Holmes 2004, Weggler 2006). In addition, the fitness consequences of double-brooding in adults (survival, future fecundity) as a result of increased reproductive effort are relatively poorly studied (but see Geupel and Desante 1990, Morton et al. 2004, Nagy and Holmes 2005b, Husby et al. 2009). Previous studies have suggested that double-brooding can be associated with lower survival (Bryant 1979, Brinkhof et al. 2002) or no survival cost (Geupel and Desante 1990, Morton et al. 2004, Nagy and Holmes 2005b, Husby et al. 2009), but few studies have considered the effects on future fecundity, likely due to a combination of low return rates and the difficulty of repeatedly finding nests belonging to the same individuals.

Numerous studies have suggested that the timing of breeding—laying date of the first clutch—is the most important factor determining the propensity for double-brooding: The incidence of second clutches generally declines the later the first clutch is initiated (Geupel and DeSante 1990, Verboven et al. 2001, Brinkhof et al. 2002, Parejo and Danchin 2006, Husby et al. 2009, O'Brien and Dawson 2013, Hoffmann et al. 2015). A higher frequency of double-brooding among early-laying females could occur simply because these females then have more time to rear a second brood, or because their initially early laying date makes them less affected by seasonal declines in the quality of the rearing environment (e.g., the feeding

renesting interval after egg removal of 5 days), so that we excluded any potential replacement clutches in experimental years in which first clutches were removed. Only known control birds were used from experimental years, and experimental birds were excluded from analysis in the subsequent year of treatment to minimize potential carry-over effects. No egg removal (and experimentally delayed laying) occurred in 2012–2014, so we restricted some analyses to these years, where indicated, to understand population-level annual trends (see Results).

During the period when starlings had their first broods, we were successful in banding 398/419 (95%) of all females with nests that survived until hatching across years. We missed banding the remaining individuals largely due to early nest failure or abandonment, hence our restriction of first broods to the peak laying period to exclude replacement nests of birds of unknown status (unbanded birds). Females that failed to fledge offspring from their first clutch laid replacement clutches in only 19 instances, 12 of which were successful in fledging young (~8% of all single-brooders or 16% of failed single-brooders). We included productivity resulting from replacement clutches in the total annual productivity analysis, but not in the calculation of first brood productivity. None of the individuals that laid a replacement clutch attempted to double-brood. We checked all nest boxes regularly during the second brood window, beginning ~

experienced total brood failure of their second brood (hereafter, failed double-brooders, compared with successful double-brooders who fledged young from both broods). Neither the proportion of single- to double-brooders nor successful to failed double-brooders varied among years (number of broods: $\chi^2_2 = 1.17$, $p = 0.56$; success of the second brood: $\chi^2_2 = 1.79$, $p = 0.41$). When the single-brooders that failed to rear any chicks from the first brood (hereafter, failed single-brooders, compared with successful single-brooders who did fledge chicks from the first brood) were excluded, the frequency of double-brooding did not vary among years: 49% of 46 (2012), 52% of 46 (2013), and 60% of 27 (2014; $\chi^2_2 = 0.94$, $p = 0.63$).

Mean annual productivity estimated as brood size at fledging from all breeding attempts was almost twice as high for double-brooding females as for all single-brooding females ($t_{1,61} = 108.02$, $p < 0.001$; Table 1, Figure 1). Furthermore, brood size at fledging for first broods alone was significantly higher for double-brooding females than for all single-brooding females ($t_{1,56} = 18.80$, $p = 0.001$, controlling for clutch size; Table 1). Productivity resulting from replacement clutch/F19934520197 (for all) annu productiv2j(a4(s

offspring than successful single-brooders ($t_{1,47} = 24.31$, $p < 0.001$, controlling for clutch size; Table 1). Among double-brooders who were successful in fledging offspring from the second brood, brood size at fledging from the second clutch was reduced compared with the first clutch (paired t -test, $t_{52} = 3.82$, $p < 0.001$).

single-brooders, all $p > 0.09$). Size-corrected body mass for 3 yr (2012–2014; $n = 88$) also showed no difference between all single-brooders and double-brooders ($t_{1,84} = 2.62$, $p = 0.19$) or between successful single-brooders and double-brooders ($t_{1,15} = 1.89$, $p = 0.19$).

annual fecundity in European Starlings (based on the number of chicks fledged), and, given that 25% of our birds only breed on site once, this is a powerful representation of lifetime fecundity. However, on average, only 38% of individual females were double-brooding. Furthermore, 39% of females that initiated a second clutch experienced total failure of their second brood, and thus accrued no fecundity advantage from their decision to double-brood. So, on average, only 23% of females in our study population obtained higher breeding produc-

second clutch showed similarly high first brood productivity when compared with successful double-brooders. Thus, regardless of the success of the second brood, all of the double-brooding females were of equally high quality based on the success of their first broods. Instead, perhaps a date-dependent decrease in environmental quality during the second brooding window makes second broods a risky investment (for doubling reproductive effort) with a high failure rate, despite the proven ability of parents to successfully rear offspring from first broods. Consistent with this idea, even successful double-brooding females had lower brood size at fledging from their second breeding attempt compared with their first breeding attempt. There is existing evidence to suggest that the seasonal window for second broods may be more challenging due to difficult environmental conditions or lower food availability (Rodenhouse and Holmes 1992, Silkamaki 1998, Nagy and Holmes 2005a). Regardless of the low probability of success, a double-brooding strategy clearly has a high potential payoff in doubling fecundity within the year if individuals can manage potential costs to survival and/or future fecundity.

Although there is clearly additional reproductive effort involved in doubling egg production, incubation, and chick provisioning for a second brood, we were not able to identify a cost for double-brooders. Double-brooding had no negative effect on the timing of breeding or breeding productivity in the year following double-brooding (future fecundity), and double-brooding females actually had higher local return rates (survival). In other words, double-brooding females did not show the predicted tradeoff between current reproductive effort and our indices of survival and future reproduction as predicted by life-history theory (Reznick 1985, Stearns 1992). Several other studies have also shown this lack of a tradeoff between double-brooding and various indices of survival (Geupel and DeSante 1990, Morton et al. 2004, Nagy and Holmes 2005b, Husby et al. 2009), although double-brooding birds had lower survival in the Northern House-Martin (*D. erythrorhynchos*; Bryant 1979) and Eurasian Coot (*Fulica marila*; Brinkhof et al. 2002). In our population of European Starlings, regardless of the success of the first brood, single-brooders had a significantly lower return rate than double-brooders (Figure 3). Because we have not attached long-term tracking equipment to our birds, we do not know what proportion of individuals fail to return due to mortality vs. a search for new breeding grounds. It is possible that successful single-brooders that decide not to pursue a second brood may require additional self-maintenance to support their return the following year. Thus, these single-brooders deliberately choose not to invest in a second brood that is unlikely to pay off. On the other hand, double-brooders do increase their reproductive effort by rearing a second clutch, but may do so

they can manage the consequences of the additional effort without compromising their return rate and subsequent year's reproductive success. This ability may be due to a combination of unmeasured components of quality, such as genetic or physiological traits, or pairing with high-quality mates. So, in conclusion, a small proportion (~20%) of high-quality female European Starlings effectively doubles their potential breeding productivity through double-brooding without apparently paying any costs in the variables that we measured or experiencing simple tradeoffs in our indices of survival and future fecundity in the way that life-history theory predicts (as has been reported elsewhere; Ardia 2005, Weladji et al. 2008, Hamel et al. 2009).

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Author contributions: T.D.W. supervised the research; A.C. collected the data; A.C. and T.D.W. wrote the paper (or substantially edited the paper); and A.C. analyzed the data.

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