

Individual Quality and Double-brooding in a Highly Synchronous Songbird Population

Final version published as:

Cornell, A. and Williams, T.D. 2016. Individual Quality and Double-brooding in a Highly Synchronous Songbird Population. *Auk* 133: 251-260.
DOI: 10.1642/AUK-15-165.1

Author Affiliation

Allison Cornell

Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada
Author for correspondence: acornell@sfu.ca

Tony D. Williams

Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada

ABSTRACT:

Multiple brooding, the production of more than one set of offspring per breeding season, is a life history trait potentially doubling or tripling fecundity, but the factors responsible for variation in occurrence of multiple brooding *within species* remain poorly understood. We investigated the potential causes and consequences of double-brooding in the highly-synchronously breeding European starlings (*Sturnus vulgaris*), where we predicted that ‘date’ (clutch initiation) would have little effect on double-brooding propensity compared to individual ‘quality’. Double-brooding effectively doubled annual fecundity in European starlings (based on annual number of chicks fledged), but on average only 38% of individual females was double-brooded. Furthermore, 39% of females that initiated a second clutch experienced total failure of their second brood, thus accrued no fecundity advantage from their decision to double-brood. As we predicted variation in propensity for, and success of double-brooding was independent of laying date, but also of other putative measures of individual ‘quality’ (clutch size, egg mass, relative age, and provisioning rate). However, we found no evidence of a cost of double-brooding; double-brooded females had significantly higher return rate, and similar breeding productivity in the year after double-brooding compared with single-brooding females. Thus, a small proportion (~20%) of “high quality” female European starlings effectively double their potential breeding productivity through double-brooding without apparently paying a cost or experiencing simple trade-offs.

Keywords: multiple brooding, breeding phenology, individual quality, lay date

INTRODUCTION

Birds have evolved a variety of strategies for maximizing fecundity despite the constraints of clutch size per brood, and one such mechanism is to produce multiple broods of offspring in a single breeding season, which can potentially double or triple fecundity (Lack 1947, Rockwell et al. 1987, Martin 1995, McCleery et al. 2004, Weggler 2006). At least 64 avian families are known to pursue multiple broods in some species' populations (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, 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 effects on future fecundity, likely due to a combination of low return rates and the difficulty of repeatedly finding nests for the same individuals.

Numerous studies have suggested that timing of breeding, i.e. laying date of the first clutch, is the most important factor determining 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 lay date makes them less affected by seasonal declines in quality of the rearing environment, e.g. feeding of earlier second broods can still be relatively synchronous with the seasonal peak in food supply (date hypothesis; Verboven and Verhulst 1996, Husby et al. 2009). Alternatively, early laying females might be “high quality” individuals (the quality hypothesis) such that females differ in their intrinsic ability to produce and raise a second brood. For example, Hoffmann et al. (2015) suggested that high-quality, early laying females might be better able to sustain the energetic investment costs of producing both first and second clutches. Similarly, O’Brien and Dawson (2013) showed that the highest quality female mountain bluebirds (*Sialia currucoides*), which were naturally early breeders, were better able to compensate for the effects of experimentally-delayed breeding, whereas lower quality females were much less likely to double-brood when their first attempt was delayed.

Here we investigate the potential causes and consequences of double-brooding in free-living European starlings (*Sturnus vulgaris*) in the context of the individual quality versus date hypotheses. In our study population females are facultatively double-brooded (~40% of females produce a second clutch; see Results) even though egg-laying is highly synchronous for first broods: mean egg-laying date varies by ± 4 days among years, and 80% of nests are initiated within a 5-day period within years (Williams et al. 2015). We therefore predicted that “date” would not be a strong driver of propensity to double-brood in this population, such that we could identify phenotypic components of individual “quality” (*sensu* Wilson and Nussey 2010) that were associated with a double-brooding strategy. Our specific objectives were a) to quantify how much more successful double-brooding females are compared to females that produce only a single brood, in terms of total breeding productivity, and where this increased productivity

comes from, i.e. how important is additive productivity from the second brood, versus higher first brood productivity; b) to determine if propensity for, and/or success of, double-brooding is associated with putative measures of individual quality (lay date, egg and clutch size, relative age, chick provisioning rate, size-corrected body mass); c) to test whether success of second broods is explained by within-season nest-site fidelity or nest switching between first and second broods; and d) to determine if there is a ‘cost’ of double-brooding in European starlings in terms of reduced local return rate of individual females between years or breeding productivity the following year.

METHODS

We used 10 years of breeding data (2004-2014) from our long-term European starling study at Davistead Farm, Langley, British Columbia, Canada (49.17°N, 122.83°W), which comprises c.150 nest boxes mounted on posts around pastures and on farm buildings. All nest boxes are surrounded by, and potentially equidistant from similar high quality foraging areas (pasture), predation of the nest is low, and many boxes where birds do not return are occupied in subsequent years. In each year we followed the same basic field protocol: nest boxes were checked daily from April 1 to determine laying date and clutch size, all newly-laid eggs were measured ($\pm 0.001\text{g}$), and nests were monitored until either failure or fledging to quantify productivity. In several years we conducted experiments which involved catching females at clutch completion and removing eggs to stimulate laying of replacement clutches (e.g. Love and Williams 2008). Therefore, we restricted analysis to clutches initiated during the first peak of egg-laying in each year, defined as a 12-day period from the earliest first nest initiation date (based on a mean 5-egg clutch, two further days for determination of clutch completion and a

minimum re-nesting interval after egg removal of 5 days), so that we excluded any potential replacement clutches in experimental years where 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 restrict some analyses to these years, where indicated, to understand population level annual trends (see Results). During first broods we were successful in banding 398/419 (95%) of all females with nests that survived until hatching across years. Individuals that we missed were 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). Single-brooders that failed in fledging offspring from their first clutch laid replacement clutches in only 19 instances, 12 of which were successful in fledging young. Productivity resulting from replacement clutches are included in the total annual productivity analyses but not in the calculation of first brood productivity. None of the individuals laying replacement clutches laid a double-brood. We checked all nest boxes regularly during the second brood window, beginning ~31 days (10 days of incubation, 21 days to fledge) after clutch completion of the earliest first brood and trapped and identified 160/198 (81%) of females with nests that survived to hatch across years. Only known individuals (numbered Federal metal bands) that laid clutches during both first and second brood windows were classified as “double-brooders”, unbanded birds (single or double-brooded) were not included in any analysis.

Local return rate and relative age (age = 1 in the first year birds were encountered and banded as adults) were determined by the recapture of banded individuals in subsequent years. Our detection probability was high, as only 5/125 individuals or 4% “skipped” years in our

records. Due to the multiple years included in this dataset, lay date was calculated as a residual based on the annual mean laying date. In order to assess parental provisioning (nest visit) rates we conducted 30-min surveys from 09:00-14:00 on days 6, 7, and 8 post-hatching, three times (75% of nests) or twice (25% of nests). Therefore, we obtained either 1-hour or 1.5-hours of data per nest, and we standardized the timing of observations. Days 6-8 were chosen as they represent the period of most rapid chick growth, and we used the mean nest visit rate over 3 days. Fowler and Williams (2015) conducted a detailed analysis of these data and showed that nest visit rate was highly correlated among successive days (hence the decision to use the mean), i.e. nest visit rate was repeatable. Nest visit rate was also repeatable within-years between first- and second-broods confirming it does capture individual variation in provisioning. We have used this standardized approach in our previous studies and it does have the power to detect treatment effects in provisioning rate in experimental studies (e.g. Rowland et al 2007, Verspoor et al 2007, Love and Williams 2008). For some analyses, individuals that pursued second broods but failed to fledge offspring from the second nest were grouped as “failed” double-brooders. Individuals that fledged ≥ 1 offspring from the second clutch were grouped as “successful”. Because many single-brooding individuals fledged zero young (“failed” single-brooders, see Results section), we excluded these birds where indicated to avoid favorable bias of double-brooders. Values in the tables and Results sections are presented as means \pm standard deviation.

All analyses were completed in R Studio version 0.98.1028 (R Core Team 2013) using *pscl* (Zeileis et al. 2008), *lme4* (Bates et al. 2014), *lmerTest* (Zeileis and Hothorn 2002), *nlme* (Pinheiro et al. 2013), and *stats* (R Core Team 2013) packages. Linear mixed-effects models were used to compare single and double-brooders’ and failed and successful double-brooders’ breeding productivities, individual quality metrics, nest visit rate, and subsequent year’s lay date

with band number (individual) as a random factor. Clutch size was only incorporated in the models where noted. Analysis of return rates was done using fit generalized linear mixed-effects models with binomial distribution controlling for individual (band number) and year as random factors. Significance was determined by comparing the fit of the models with and without the terms of interest using likelihood ratio tests (as in Jones et al. 2014). Subsequent year productivity was analyzed using zero-adjusted Poisson (ZAP) or hurdle model similar to Jones et al. (2014) due to the high distribution of zeros and few repeat measures (no random effect of individual). These models are suitable for data with a high proportion of “true” zero values (c.f. Martin et al 2005) because they treat zeros simultaneously as a count metric and as negative binomial, which cannot be simply modeled with a normal, binomial, or Poisson distribution. The significance of the terms of interest was determined by comparing the fit of the models with and without the terms of interest using likelihood ratio tests.

RESULTS

Productivity and Double-brooding

In 2012-2014 (years when we did no manipulation of laying date), 43% of 65 (2012), 36% of 89(2013), and 44% of 43 (2014) of individual females double-brooded, but for these double-brooding females 42% of 27 (2012), 29% of 28 (2013), and 42% of 19 (2014) of birds experienced total brood failure during their second brood (hereafter “failed double-brooders” compared to “successful double-brooders” who fledge young from both broods). Neither the proportions of single to double-brooders, or 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 to “successful single-brooders” who do fledge chicks from the first brood) are 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 in double-brooding females compared with all single-brooding females ($F_{1,61} = 108.02$, $P < 0.001$; Table 2; Figure 1). Furthermore, brood size at fledging for first broods alone was significantly higher in double-brooding females compared with all single-brooding females ($F_{1,56} = 18.80$, $P = 0.001$, controlling for clutch size; Table 2). Productivity resulting from replacement clutches ($n=12$) are included in the total annual productivity analyses but not in the calculation of first brood productivity. If we restrict analysis to successful single-brooders then breeding productivity in first broods was similar for single- and double-brooding females ($F_{1,47} = 2.25$, $P = 0.14$; Table 2), however overall double-brooders still produce more total annual offspring than successful single-brooders ($F_{1,47} = 24.31$, $P < 0.001$, controlling for clutch size; Table 2). Among double-brooders who were successful in fledging offspring from the second brood, brood size at fledging for the second clutch was reduced compared to the first clutch (paired t -test, $t_{52} = 3.82$, $P < 0.001$).

Productivity of first broods for all single-brooding females had a bimodal distribution with 73/157 (46%) of females failing to fledge any offspring. Similarly, in double-brooding females, brood size at fledging for second broods had a bimodal distribution, with 34/87 (39%) second-brooding females failing to fledge any offspring from their second brood. Females that fledged no offspring from their second brood ($n = 34$) were just as successful in their first broods as individuals who did fledge second brood chicks ($n = 53$, respectively; $F_{1,16} = 0.03$, $P = 0.87$; controlling for clutch size; Table 2).

Double-brooding and Individual Quality

Mean relative laying date for first clutches was not significantly different between single- and double-brooding females either including all single-brooders ($F_{1,73} = 1.17, P = 0.28$) or excluding the failed single-brooders ($F_{1,55} = 0.43, P = 0.51$). Furthermore, single-brooders did not differ from double-brooders in the clutch size of their first brood ($F_{1,63} = 0.26, P = 0.61$), mean egg size (controlling for clutch size, $F_{1,65} = 1.72, P = 0.19$), or relative age ($F_{1,62} = 3.44, P > 0.05$; Table 1; excluding failed single-brooders all $P > 0.09$). Size-corrected body mass for 3 years (2012-2014, $n = 88$) also showed no differences between all single-brooders and double-brooders ($F_{1,84} = 2.62, P = 0.19$) or between successful single-brooders and double-brooders ($F_{1,15} = 1.89, P = 0.19$).

Among double-brooding females, comparing failed double-brooders with successful double-brooders (fledge ≥ 1 chick) there was no difference in relative laying date of the first clutch ($F_{1,22} = 2.36, P = 0.14$), clutch size of the first clutch ($F_{1,18} = 1.35, P = 0.26$), mean egg size (controlling for clutch size, $F_{1,13} = 1.36, P = 0.22$), or relative age ($F_{1,18} = 0.55, P = 0.47$; Table 1). Overall, 48% ($n = 54$) of successful double-brooding females retained the same nest box between breeding attempts compared with 62% of failed double-brooding females ($\chi^2_1 = 1.06, P = 0.30$). Lay date of the second brood was related to nest box fidelity, with birds retaining their box laying earlier (-0.26 ± 4.77 days relative to mean laying date for year) than birds switching their box (1.49 ± 3.23 days) (Welch's two-sample t -test, $t_{81} = -2.03, P < 0.05$). However, among successful double-brooding females, mean number of offspring fledged from the second brood did not differ between birds that switched boxes (2.82 ± 1.28 chicks) and birds

that retained first brood boxes (2.93 ± 1.26 chicks; Welch's two-sample t -test, $t_{51} = 0.29$, $P = 0.77$).

Provisioning rate (nest visits/chick/30 min) of first broods did not differ for double-brooding females compared to single-brooding females ($F_{1,27} = 3.06$, $P = 0.09$; Table 1). Similarly, neither male visit rate or total visit rate (sum of male and female visits) per chick differed at nests of single- and double-brooders ($P > 0.35$ in both cases). When these analyses were conducted as per nest visit, rather than per chick, there was also no relationship (female: $F_{1,12} = 1.19$, $P = 0.30$; male: $F_{1,12} = 0.49$, $P = 0.50$; total: $F_{1,12} = 0.01$, $P = 0.91$, controlling for brood size and individual as random factors). There was no difference in mean female provisioning rate of the first brood among successful and failed double-brooders ($F_{1,11} = 0.01$, $P = 0.91$; Table 1), nor for male or total nest visit rate ($P > 0.80$ in both cases). No significant difference was found when these groups were analyzed per nest rather than per chick (female: $F_{1,6} = 0.19$, $P = 0.68$; male: $F_{1,6} = 0.02$, $P = 0.90$; total: $F_{1,6} = 0.09$, $P = 0.77$, controlling for brood size and individual as random factors).

Potential Costs of Double-brooding

Double-brooding females had higher local return rates (72%) than all single-brooding females (56%), and successful single-brooders (57%) ($\chi^2_{4,5} = 5.17$, $P = 0.02$, $\chi^2_{4,5} = 3.07$, $P = 0.08$, with relative age as a covariate, and individual and year as random effects; Table 2, Figure 3).

However, the local return rate of double-brooders was independent of the success of the second brood (failed double-brooders, 81% vs. successful double-brooders, 67%; $\chi^2_{4,5} = 0.22$, $P = 0.64$, with relative age as a covariate, and individual and year as random effects; Table 2, Figure 3).

Laying date in the subsequent year was independent of whether the female was single- or double-brooded in the previous year ($F_{1,24} = 0.30$, $P = 0.59$, all single-brooders; $F_{1,16} = 0.43$, $P = 0.43$, excluding failed single-brooders) and was also independent of whether the previous year's second brood was a success or failure ($F_{1,1} = 6.56$, $P = 0.23$). Total annual productivity of birds in the following year did not relate to whether the female was single- or double-brooded in the preceding year (hurdle model, count portion, $\chi^2_{29, 28} = 2.00$, $P = 0.16$; 0/1 portion, $\chi^2_{29, 28} = 0.41$, $P = 0.52$; Table 2), even with failed single-brooders excluded (hurdle model, count portion, $\chi^2_{19, 18} = 1.19$, $P = 0.28$; 0/1 portion, $\chi^2_{19, 18} = 0.46$, $P = 0.50$; Table 2). Because the average number of breeding seasons for a bird on our site is 1.42 ± 1.31 years, this represented lifetime reproductive success for 64% of our birds. Similarly, successful and failed second brooders did not differ in their subsequent year's total breeding productivity (hurdle model, count portion $\chi^2_{15,14} = 0.59$, $P = 0.44$; 0/1 portion, $\chi^2_{15,14} < 0.01$, $P = 0.96$; Table 2).

DISCUSSION

We investigated the potential causes and consequences of double-brooding in European starlings, where we predicted that 'date' would have little effect on propensity to double-brood compared to individual quality due to the high degree of breeding synchrony in the population. Double-brooding effectively doubled annual fecundity in European starlings (based on 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-brooded. Furthermore, 39% of females that initiated a second clutch experienced total failure of their second brood, 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

productivity through double-brooding. As we predicted this variation in propensity for, and success of, double-brooding was independent of laying date, but was also independent of clutch size, egg mass, and relative age (putative measures of individual ‘quality’). However, double-brooding females had higher breeding productivity in their first broods, compared to all single-brooded females. Furthermore, double-brooded females had higher local return rate, and similar breeding productivity in the year after double-brooding compared with single-brooding females (even when failed single-brooders were excluded), i.e. there was no evidence of a cost of double-brooding.

Most studies have reported annual variation in frequency of double-brooding with an increase in incidence of double-broods during years with earlier lay dates (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). In some species this variation can be quite marked, e.g. in black redstarts (*Phoenicurus ochruros*) the proportion of females initiating more than one clutch per season varied from 84% to 42% over 10 years (Wegglar 2006). In contrast, we found no annual variation in the proportion of double-broods over three years, which is likely due to the small inter-annual variation in laying dates in European starlings (± 4 days; Williams et al. 2015). Similarly, neither frequency of double-brooding nor success of double-broods were related to relative laying date which is also consistent with the high level of breeding synchrony within-years in European starlings (Feare 1984); even though other life-history traits are related to date in this species (e.g. clutch size, Williams et al. 2015, and recruitment, Smith 2004). In other species, where an effect of date on double-brooding has been reported, the range of first egg dates is relatively large e.g. in the well-studied great tit (*Parus major*) the range of the first egg dates within years averages 27 days (n=59 years; M. Visser personal communication),

compared with only 12 days in our study population. Therefore, as we predicted egg-laying date, within the typical breeding window for first breeding attempts, is not a major determinant of double-brooding in European starlings.

In our study population females that double-brooded fledged almost twice as many chicks as single-brooded females, consistent with other studies showing that multiple brooding significantly increases total reproductive output (e.g. Holmes et al. 1992, Poirior et al. 2004, Carro et al. 2014, Hoffmann et al. 2015, Weggler 2006). However, we show that part of this increased productivity is due to a higher brood size at fledging in these female's *first* broods, not simply due to the additive effect of second brood productivity. One cause of this difference in first brood productivity was that single-brooded females had nearly a 46% total brood failure rate. Re-nesting after first brood failure does occasionally occur on our site. However, for over 157 records of single-brooders we have only 19 records of birds relaying after failing during the first brood (12%). Only 12 of these 19 nests (7.6%) were successful in fledging offspring, and none of these females attempted a second brood. This is likely due to the limited time window for breeding in our system; typically all second brood nests fledge by July 1st. This supports the idea that either a) these are low-quality females, and b) that date is a main driver of breeding success at least for low-quality birds (although females which second brood can clearly still be successful later in the season). Almost all breeding failures observed are due to nest abandonment and/or starvation of the chicks; predation is rare and in some years does not occur at all. It is likely that adults either make a decision to abandon in order to invest in personal maintenance, or perhaps are depredated themselves. We suspect, but cannot confirm, that most breeding failure at this stage is caused by predation of adults away from the nest. Some adults probably 'choose' to abandon, investing in self-maintenance, rather than continued reproduction.

This would be consistent with failed single-brooders being potentially lower quality individuals than successful single- or double-brooders because they are unable to maintain investment of resources necessary for successful reproduction. However our putative measures of individual quality (lay date, egg mass, and clutch size), relative age, and parental care (nest visit rate) were not related to the propensity to double-brood (cf. Geupel and Desante 1990, Holmes et al. 1992), which suggests that “quality” was related to other components of parental quality, e.g. genetic or physiological traits associated with parental care and rearing of offspring or, simply, that higher quality parents produce higher quality offspring which then have better nestling or fledgling survival.

Interestingly, the pattern of high total brood failure rate (46%) initially found among single-brooders reemerges in second broods: with 39% of females that initiated a second clutch failing to rear any second brood chicks. However these double-brooding females that failed in rearing their 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 equally high quality based on success of their first broods. Instead, perhaps a date-dependent decrease in environmental quality during the second brooding window, makes double-broods a “risky” investment (in doubling reproductive effort) with high failure rate, despite the proven ability of parents to successfully rear offspring during first broods. Consistent with this idea, even successful double-brooding females had lower brood size at fledging for their second breeding attempt compared to their first breeding attempt. There is existing evidence suggesting that the seasonal window for second brooding 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, this 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 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 predicted by life-history theory (Reznick 1985, Stearns 1992). Several other studies also show this lack of 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-brooded birds had lower survival in house martins (*Delichon urbica*, Bryant 1979) and European coots (*Fulica atra*, Brinkhof et al. 2002). In our population regardless of the success of first the brood, single-brooders had 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 versus search for new breeding grounds. It is possible that successful single-brooders, that decided not to pursue a second brood, may require additional self-maintenance to support their return the following year. Thus these single-brooders chose not to invest in a second brood unlikely to pay off. On the other hand, double-brooders do increase their reproductive effort by rearing a second clutch, but may do so *because* they can manage the consequences of the additional effort without compromising return rate and subsequent year 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 double their potential breeding productivity through double-brooding without apparently paying any of the costs we measured or experiencing simple trade-offs on our indices of survival and future fecundity the way that life history theory predicts (as has been reported elsewhere, Ardia 2005, Weladji et al. 2008, Hamel et al. 2009).

ACKNOWLEDGEMENTS

We would like to thank the many field assistants who helped to collect data over the 10 yrs of this project, with special thanks to Sophie Bourgeon, Melinda Fowler, Raime Fronstin, and Oliver Love. David J. Green provided valuable comments on the writing of and statistical analysis for this paper.

Funding Statement: This work was funded by a Natural Sciences and Engineering Council of Canada Discovery and Accelerator Grant to T.D.W. (Grant numbers 155395-2012- RGPIN and RGPAS/429387-2012). The funders did not have any input into the content of the manuscript nor require approval before submission.

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FIGURE CAPTIONS

Figure 1

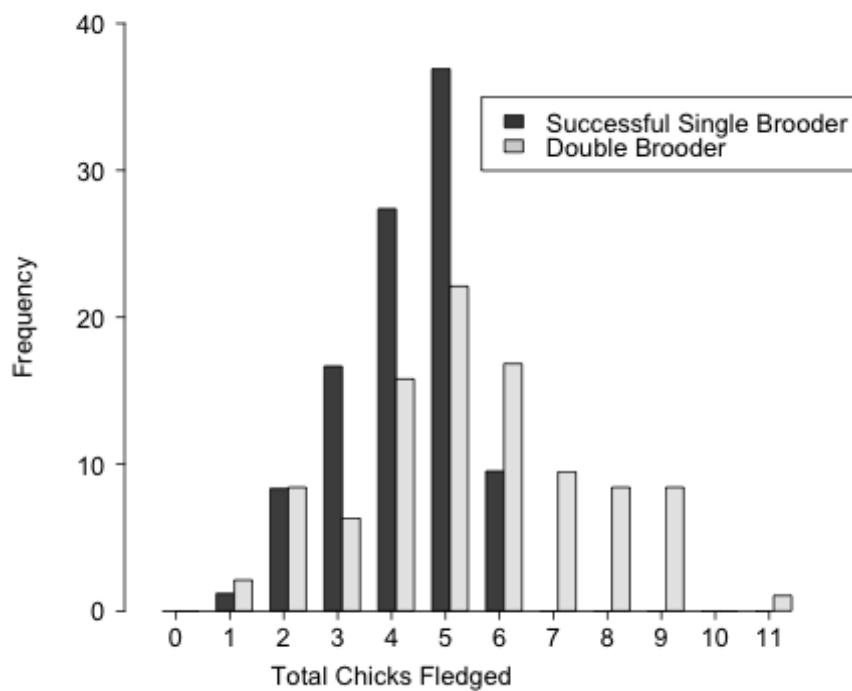


Figure 1. Total annual productivity, sum of offspring fledged from first and second, for the successful single-brooders and all double-brooders. Frequency reflects percent of successful single-brooders and all double-brooders respectively.

Figure 2

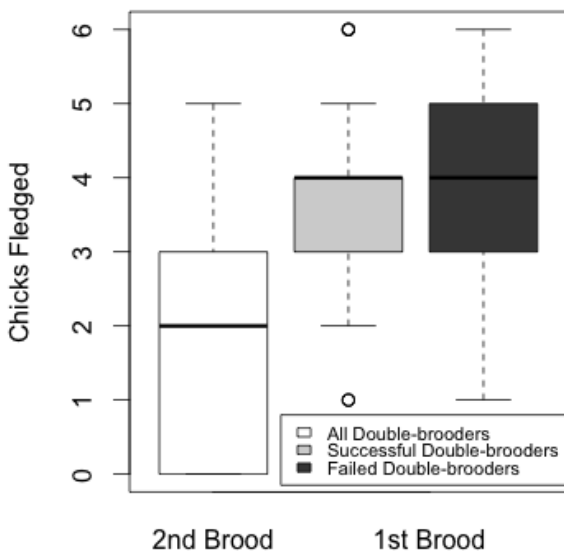


Figure 2. Productivity data for all double-brooders' 2nd brood; 1st brood productivity of successful double-brooders (>0 chicks fledged from second brood), and failed double-brooders (0 chicks fledged from second brood).

Figure 3

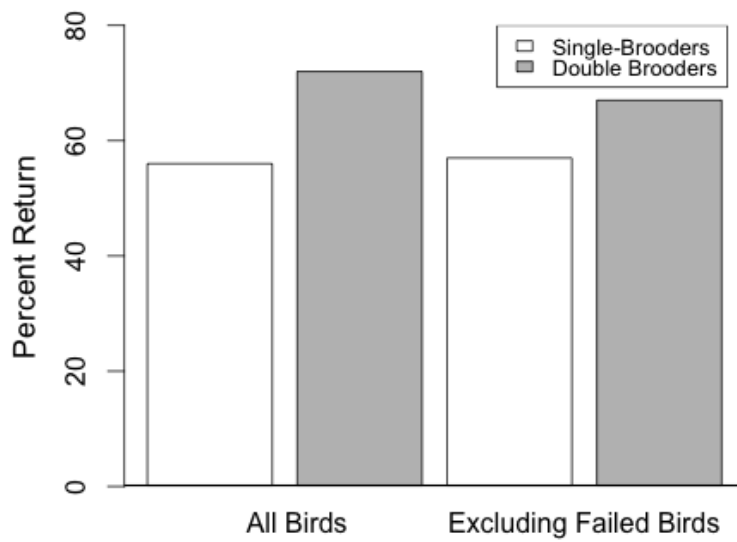


Figure 3. Total percent local return rates among all single-brooders and all double-brooders, successful single-brooders and successful double-brooders.

Table 1. Averages \pm standard deviation and significance of individual quality metrics between all single-brooders ($n = 157$) versus double-brooders ($n = 95$; P value¹), successful single-brooders ($n = 84$) versus double-brooders (P value²), and successful ($n = 53$) versus failed double-brooders ($n = 34$; P value³). Clutch size refers to the first brood only. Female provisioning rate is per chick every 30 minutes.

	All Single Brooders	P value ¹	Successful Single-brooders	P value ²	Double-brooders	Successful Double-brooders	Failed Double-brooders	P value ³
Relative Lay Date	0.00 ± 1.80	0.28	-0.06 ± 1.69	0.51	-0.25 ± 2.05	0.17 ± 1.48	-0.31 ± 1.81	0.14
Clutch Size	5.28 ± 0.86	0.61	5.30 ± 0.79	0.67	5.32 ± 0.70	5.22 ± 0.77	5.44 ± 0.61	0.26
Egg Size	7.08 ± 0.51	0.19	7.10 ± 0.49	0.34	7.13 ± 0.49	7.23 ± 0.48	6.98 ± 0.44	0.22
Relative Age	2.59 ± 1.28	0.07	2.63 ± 1.29	0.09	2.22 ± 1.33	2.28 ± 1.49	2.17 ± 1.15	0.47
Female Provisioning Rate	0.84 ± 0.55	0.09	0.85 ± 0.55	0.11	1.03 ± 0.66	1.10 ± 0.72	1.00 ± 0.53	0.92

Table 2. Mean values and 95% confidence intervals of productivities and “cost” metrics. *P* value¹ corresponds the comparison between all single and all double-brooders, *P* value² to the comparison between successful single and all double-brooders, and *P* value³ to the comparison between successful and failed double-brooders.

	All Single Brooders		<i>P</i> Value ¹	Successful Single-brooders		<i>P</i> Value ²	Double-brooders		Successful Double-brooders		Failed Double-brooders		<i>P</i> Value ³
	Mean	95% CI		Mean	95% CI		Mean	95% CI	Mean	95% CI	Mean	95% CI	
First Brood Productivity	2.84	2.51-3.17	<0.05	4.19	3.93-4.44	0.14	3.97	3.52-4.25	3.77	3.40-4.14	3.79	3.33-4.26	0.71
Total Annual Productivity	2.96	1.89-2.59	<0.0001	4.19	3.82-4.56	<0.0001	5.59	4.95-5.82	6.79	6.06-7.09	3.79	3.14-4.44	<0.0001
Local Return Rate	56%	-	<0.05	57%	-	0.08	71%	-	67%	-	81%	-	0.69
Subsequent Year Productivity	3.88	3.19-4.56	0.16	4.21	3.15-5.27	0.28	4.58	3.85-5.32	4.45	3.23-5.38	4.42	3.20-5.94	0.44
Subsequent Year Lay Date	0.19	-0.27-0.64	0.59	0.30	-0.31-0.91	0.43	-0.05	-0.48-0.39	-0.20	-0.43-1.11	0.44	-0.85-0.45	0.25