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1 Manuscript IBIS-2014-OP-039 "Following a common rule: strategic allocation to replacement

2 clutches in Tree Swallows *Tachycineta bicolor*"

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4 Running head: *Seasonal clutch size decline in Tree Swallows*

5

6 **Differences in size between first and replacement clutches match the seasonal decline in**

7 **single clutches in Tree Swallows *Tachycineta bicolor***

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19 The seasonal decline in clutch size in birds can be a response to the environmentally conditioned

20 decrease in prospects for offspring or a consequence of a lower physical ability of late-breeding

21 females. To find out which of the explanations apply in Tree Swallows *Tachycineta bicolor*, we

22 tested whether replacement clutch size in this species is affected by individual female's ability to

23 lay a certain number of eggs. To do this, we measured the decline of clutch size as a function of

1   laying date between first and replacement clutches in individuals that re-nested following natural

2   failure, and compared this with the rate of decline in clutch size with laying date for Tree

3   Swallows that laid only a single clutch in that season. Additionally, we tested whether the clutch

4   size and the rate of its seasonal decline varied across years. We accounted for the truncated and

5   underdispersed nature of clutch size data, taking a Bayesian approach in the analysis. We found

6   little variation in the rate of clutch size decline across years at our breeding site. Accounting for

7   this seasonal decline in clutch size, mean clutch size was similar between single-time breeding

8   females and those that laid replacement clutches, implying that the number of eggs laid on the

9   second attempt by female Tree Swallows is determined by laying date, rather than by the

10   female's physical ability to produce a clutch of a certain size.

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1   Many birds show a seasonal decline in clutch size. There have been many attempts to explain

2   this phenomenon (Lack, 1947; Klomp, 1970; Drent & Daan, 1980). For example, the seasonal

3   decline may be a result of high quality females laying large clutches early in the season and low

4   quality females laying small clutches later. Alternatively, it may reflect a strategic response by

5   individual females who perceive breeding conditions to become less favourable as the season

6   progresses and thus lay smaller clutches. Most studies to date have found that both processes are

7   involved (Verhulst & Nilsson, 2008), with laying date most closely correlated with female

8   quality, and seasonal declines in clutch size reflecting the decline in expected breeding success

9   (Stearns, 1992; Hansson *et al.*, 2000).   However, strategies of reproductive investment may

10   vary between species as a result of differences in both life history and environmental conditions

11   they experience (Dhondt *et al.*, 2002; Goodenough *et al.*, 2009; Westneat *et al.*, 2009). Here we

12   study a strategy of allocation to breeding via regulation of clutch size in the Tree Swallow

13   *Tachycineta bicolor*. This migrant passerine is widely distributed throughout North America and

14   meets a wide spectrum of environments across its range (Winkler *et al.*, 2011). Tree Swallows

15   nest in cavities, which implies that the same individuals may experience various circumstances

16   between years, depending not only on phenological conditions, but also on the luck of finding a

17   nesting territory. They are socially monogamous, and in north-eastern North America each pair

18   usually only rears a single brood per season. Typical for a single-brooded species, clutch size in

19   the Tree Swallow shows a linear decline over the course of the season (Dhondt *et al.*, 2002;

20   Winkler *et al.*, 2014).

21   Fledgling production also decreases with laying date in tree swallows, and, in a

22   population nesting in Canada, it has been found that this trend is better explained by

23   deterioration of environment rather than by lower quality of late breeders (Dawson, 2008b).

24   However, two-year and older females are known to lay earlier and produce larger clutches than

25   young birds. Also, given relatively low annual survival rate of tree swallows (Winkler *et al.*,

26   2011), they may be expected to maximize investment to current reproduction, whenever it is

1   possible. Therefore, it remains unclear, whether the smaller number of eggs laid by late breeders

2   is a response to the environmentally conditioned decrease in prospects for offspring or just a

3   consequence of environmentally or internally caused lower physical ability of late-breeding

4   females to lay clutches of early-season size.

5   In this study, we tried to answer this question by unraveling whether female's physical

6   ability to lay more eggs affects the size of replacement clutches in Tree Swallows. For this, we

7   used data from a long-term study of a nestbox population of Tree Swallows in Ithaca, New York,

8   USA (centered on 42°29' N, 76°27' W). Most of the birds breeding at this site were ringed, and

9   a large number of the marked females initiated a replacement clutch following an initial failed

10   breeding attempt. Re-nesting females face the same environmental circumstances as

11   concurrently nesting, first-time breeders but may have additional energetic constraints resulting

12   from resources invested in their previous attempt. On the other hand, birds which re-nest may be

13   of higher quality than their contemporaries breeding for the first time, and thus may be able to

14   produce a clutch of the same size or even larger (Winkler & Allen, 1996; Bowlin & Winkler,

15   2004; Verhulst & Nilsson, 2008).

16   We tested whether the difference in size between the first and replacement clutches of

17   females that re-nested (hereafter, individual decline in clutch size) matched the seasonal rate of

18   decline in the sample including first clutches of re-nesting females and clutches of females that

19   nested once in a season (hereafter, population decline in clutch size). As such, we strove to

20   distinguish among the following possibilities (Hansson *et al.*, 2000; Verhulst & Nilsson, 2008):

21   (1) a carry-over cost from the resources invested in the first clutch affects individual decline of

22   clutch size in re-nesting females (which predicts that the average individual decline in clutch size

23   among re-nesting females is steeper than the population decline), (2) re-nesting females lay

24   larger clutches because they are of higher quality than late-nesting single-time breeders (which

25   predicts that the average individual decline in clutch size among re-nesting females is shallower

3

1   than the population decline) and (3) both groups regulate their clutch size in response to the same

2   seasonal deterioration of breeding prospects (which predicts that the gradients of seasonal

3   decline in clutch size for females which nest once and for those which re-nest, are

4   indistinguishable). We have also considered the possibility that Tree Swallows adjust the rate of

5   decline in clutch size in response to annual variation in environmental conditions.

6   **METHODS**

7   The nestbox population of Tree Swallows in Ithaca has been continuously monitored since 1986.

8   However, for the current analysis we only used data from 2002 - 2010 as the data collection

9   protocol during this period remained the most consistent. During this period there were between

10 500 and 600 nestboxes present at four main study areas of which between 280 and 420 were

11 occupied during any given year. The nestboxes were mounted on metal poles about 1.5m above

12 the ground or water and had an internal diameter of 12.7 x 12.7 x 25cm (L x W x H) and a 3.5cm

13 diameter entrance hole center about 5 cm below the top of the front face. Nestboxes were

14 checked every other day during the pre-laying, incubation and nestling periods, with daily

15 checks around projected hatching dates and often during the laying period. Only nests with

16 complete, incubated clutches of at least three eggs were used in the analysis. Clutch completion

17 was assumed to occur on the date that a clutch first gained a size that did not change on at least

18 two successive nest checks. Clutches were only deemed to be replacement clutches if they were

19 produced after the first clutch had been lost or abandoned through presumably natural

20 circumstances, as opposed to being deserted because of an experimental manipulation or unusual

21 disturbance to the laying female. Females were trapped on the nest from mid-incubation

22 onwards, fitted with individual metal rings or re-identified. Replacement clutches were identified

23 by the recapture of a ringed female who had been associated with a previous nest that was

24 known to have failed. For further details of the study site and general field methods see Winkler

25 & Allen (1996).

1   Of the 2328 first clutches produced over the eight years of the study, 543 (30%) failed,

2   and 170 of the failed females laid replacement clutches, with 10 females producing replacement

3   clutches in more than one season. Accounting for individual random effects in the model would

4   have over-complicated the analysis, as in female Tree Swallows, clutch size changes non-

5   linearly throughout life (D. W. Winkler, *unpubl.*). Therefore, between-year individual random

6   effect on clutch size cannot be expected to randomly vary around certain mean value, but has to

7   be modelled, depending on an individual's age. Instead of introducing individual random effects

8   in the model, we avoided pseudoreplication in the data by randomly sampling only one (first or

9   single) nesting attempt per female, coupled with a re-nesting attempt in the same year if one was

10   made. Additionally, we excluded all nests manipulated in other experiments at or before the

11   laying stage. This reduced the sample size to 914 females who made single attempts and 122

12   females who produced both a first and replacement clutch (the data are available as Suppl. S1

13   and also at https://raw.githubusercontent.com/eldarrak/second_clutch/master/raw_data.csv).

14   We tested whether the rate of decline in clutch size within re-nesting individuals

15   (individual decline) differed from the seasonal rate of decline of first clutches, observed among

16   both single-time breeders and re-nesters. Additionally, we tested for variation in the rate of

17   seasonal clutch size decline across years. R script with analysis code is available as Suppl. S2

18   and also at https://github.com/eldarrak/second_clutch/blob/master/S2.rmd). A challenge we met

19   was to introduce the individual decline, i. e. the slope between first and second clutches of the

20   same individual, in a model, since classical frequentist regression allows the comparison of mean

21   slopes in clutch size either between the populations of single-time breeders and re-nesters (with

22   first and second clutches mixed in one sample and providing an averaged estimate for these two

23   clutch types) or between the three types of clutches but without connection between first and

24   second clutches of the same individual (see Suppl. S3 for illustration). This forced us to use a

25   Bayesian approach in the following model:

5

$$\log(Clutch_{ij}) \sim Intercept + InterceptYear_i + InterceptDoubleBreeders$$
$$\times DoubleBreeders_j + (Slope + SlopeYear_i) \times DayFirst_{ij}$$
$$+ (Slope + SlopeYear_i + SlopeSecondClutch) \times DayDiff_{ij}$$

$$InterceptYear_i \in Norm(0, \delta^2_{intercept})$$

$$SlopeYear_i \in Norm(0, \delta^2_{slope})$$

1 In the model, the response variable $\log(Clutch)$ for each year (i) and individual (j) changes

2 linearly with laying date. *Intercept* and *Slope* refer to population mean clutch size and the rate

3 of its decline with laying date, correspondingly. $InterceptYear_i$ and $SlopeYear_i$ are random

4 intercept and slope, accounting for variation in clutch size and the rate of its decline with date

5 across years.

6   The laying date was centred on its mean and introduced in the model as $DayFirst_{ij}$ for

7 first clutches and $DayFirst_{ij} + Daydiff_{ij}$ for replacement clutches., $Daydiff_{ij}$ is the difference in

8 laying dates between the first and replacement clutches of the same individual for replacement

9 clutches (set at zero for first clutches). The term

10 $(Slope + SlopeYear_i + SlopeSecondClutch) \times DayDiff_{ij}$ therefore also has non-zero value

11 only for replacement clutches. In these cases the potential difference in the rate of individual

12 seasonal decline in clutch size from the population decline could be captured by parameter

13 $SlopeSecondClutch$: a revealed by variable selection probability of $SlopeSecondClutch$ being

14 different from zero is also a probability of difference between the population and individual

15 slopes, by the value of $SlopeSecondClutch$ estimated in the model.

16   To test whether mean clutch size differed between those females that nested once in a

17 season and those that laid a replacement clutch, a term $InterceptDoubleBreeders \times$

18 $DoubleBreeders_j$ was introduced. The parameter $DoubleBreeders_j$ was assigned 0 for

19 clutches of single-time breeders and 1 for first and replacement clutches of re-nesters. In the

1   latter case, the term *InterceptDoubleBreeders* × *DoubleBreeders$_j$* had non-zero value, and

2   probability of difference between mean clutch sizes of single-time breeders and re-nesters by this

3   estimated value could be evaluated by eliminating this term during variable selection.

4   Hypothesis testing was performed through Bayesian variable selection with Reversible

5   Jump MCMC (RJMCMC; (Green, 1995), following the implementation of (Gimenez *et al.*,

6   2009). With this method, alternative models with different sets of variables are introduced by

7   using additional binary parameters for each variable of interest (*w*-parameters in Suppl. 2). A

8   variable is present in the model, when its *w* (presence/absence) parameter is 1. RJMCMC

9   extends MCMC by allowing transition between different sets of variables, searching for the

10   optimal set (see (O'Hara & Sillanpää, 2009) for review and e.g. (Gimenez *et al.*, 2009) or

11   (Rakhimberdiev *et al.*, 2015) for practical application). Posterior probability for a variable is

12   revealed from the posterior distribution of its *w*-parameter, e.g. if the posterior distribution

13   comprises 50 1's and 950 0's, the posterior probability of the variable validated is 50/1000 =

14   0.05. We coded our model in BUGS language for JAGS MCMC software (Plummer, 2003) and

15   ran it from R (R Development Core Team, 2015) through the R2jags package (Su & Masanao,

16   2015).

17   Because in our case the distribution of clutch size data was truncated and underdispersed

18   (e. g. 3 - 8), we benefited from the flexibility of the BUGS language, which allows custom

19   truncation of error distribution. The latter also copes with potential drawbacks of

20   underdispersion If not accounted for, truncation and underdisperion of the response variable may

21   impose bias in a model outcome (Zuur *et al.*, 2012). The model was first verified with

22   simulations and then ran on the data. Convergence of MCMC was assessed with the Gelman and

23   Rubin statistic (Gelman, 1996).

24

25

7

1   **RESULTS**

2   Posterior mean values of variables with standard deviations and posterior probabilities are

3   presented in Table 1. As revealed from the variable selection in our model, probability that either

4   clutch size ($InterceptDoubleBreeders$) or its rate of seasonal decline ($SlopeSecondClutch$)

5   differed between re-nesting females and single-time breeders, was low (posterior probability =

6   0.003 for both parameters). This indicates that the gradients of seasonal decline in clutch size for

7   females which nest once and for those which re-nest, are indistinguishable and that re-nesting

8   females lay both, first and replacement clutches of a similar size to those laid by females that

9   nested once in a season, on the same date (Fig. 1). Therefore, our results support the third of the

10   three alternatives laid out in the Introduction, that both groups regulate their clutch size in

11   response to the same seasonal deterioration of breeding prospects.

12   In the selection procedure on random variables, importance weights were obtained for

13   variance of parameters. In our model, posterior probabilities of random effects of year on the

14   clutch size, $\delta^2_{intercept}$ and δ^2_{slope} , were 0.041 and 0.002, correspondingly, pointing at low

15   probabilities of variation in average clutch size and its rate of decline across years. This rejects

16   the hypothesis that Tree Swallows adjust the rate of decline in clutch size in response to annual

17   variation in environmental conditions.

18

19   **DISCUSSION**

20   In this study of Tree Swallows, we found little variation in mean clutch size and its rate of

21   decline across years. Hence, consistent with previous studies (Winkler & Allen, 1996; Winkler *et*

22   *al.*, 2002; Dawson, 2008b), it is the laying date that determines the number of eggs produced by

23   laying Tree Swallows. Our studies show that females who re-nested after a failed first attempt

24   laid both first and replacement clutches of a similar size to those of females laying only once in

1   the season on the same date. This suggests that the number of eggs laid on the second attempt

2   was also determined by laying date, rather than by female's physical ability to lay a certain

3   number of eggs.

4   Conditions important for reproductive success often decline over the course of a breeding

5   season and date can therefore be a predictor of offspring prospects (Lack, 1947; Verhulst &

6   Nilsson, 2008). To keep track of dates, birds use the rate of change in day length, as the most

7   consistent cue for timekeeping (Bradshaw & Holzapfel, 2007; Dawson, 2008a). In fact,

8   photoperiod triggers and facilitates certain stages of an annual cycle, and particularly gonadal

9   growth and regression (Gwinner, 1986; Chandola-Saklani *et al.*, 2004; Dawson, 2008a), so that

10 the rate of the physiological processes usually correlates with the rate of change in day length

11 (Dawson, 2008a). This is consistent with the results of a study across the entire *Tachycineta*

12 genus which demonstrated that the slope of the decline in clutch size with laying date varies

13 across the Western Hemisphere, being less steeply negative in populations breeding closer to the

14 equator (Winkler *et al.*, 2014). A similar pattern was also found in the House Wren *Troglodytes*

15 *aedon*, another widely distributed, single-brooded passerine (Young, 1994). It is possible that

16 this large-scale trend in the slope of seasonal clutch size decline from north to south may be a

17 consequence of the latitudinal trends in photoperiod, where the amplitude of day length change

18 correlates with distance to the equator (Hut *et al.*, 2013).

19   However, across the large range of the Tree Swallow, the rate of seasonal clutch size

20 decline in this species varies little, and remains rather consistent between years (Winkler *et al.*,

21 2002). It is also similar between first-year and older females (Winkler & Allen, 1996), and is not

22 affected by variation in local food abundance (Winkler *et al.*, 2014). Such consistency provides

23 further support for the possibility that the rate of seasonal decline in clutch size may be

24 facilitated by the seasonal dynamics of photoperiod.

9

1   Considering that laying date varies considerably, conditioned by phenology and

2 individual's age (Winkler & Allen, 1996), we, therefore, suggest that there is a fixed

3 (photoperiodically determined) temporal window, during which swallows are able to lay eggs,

4 and the number of eggs that can potentially be laid decreases with a certain rate, likely facilitated

5 by photoperiodically mediated changes in circulating plasma hormones (Sockman *et al.*, 2006;

6 Dawson, 2008a). Environmental factors, and particularly ambient temperature (Dunn & Winkler,

7 1999) trigger laying within this window, and in cold springs laying occurs later so that smaller

8 clutches are produced. This simple adjusting mechanism may be insufficient to meet the variety

9 of environments experienced by Tree Swallows, given their wide breeding range (Winkler *et al.*,

10 2002, 2011; Hahn & MacDougall-Shackleton, 2008), and hence there may be additional fine-

11 tuning of reproductive investment in response to variable conditions, for example through

12 differential allocation of resources to individual eggs (Ardia *et al.*, 2006; Whittingham *et al.*,

13 2007; Liljesthröm, 2012) or nestlings (Hussell, 1988; Leonard & Horn, 1998).

14   In our study of Tree Swallows, there was no evidence that energetic expenditure on the

15 previous breeding attempt imposed a limiting effect on the number of eggs in replacement

16 clutches. This is not a surprising result, because swallows are income breeders that can quickly

17 compensate for prior energetic expenditures (Winkler & Allen, 1996; Dawson, 2008b) and have

18 a relatively low annual survival (ca 50 %, (Winkler *et al.*, 2011). Therefore, they would be

19 expected to prioritise investment into current over future reproduction. However, re-nesting Tree

20 Swallows lay the same number of eggs in replacement clutches that would be expected for birds

21 laying at the same date for the first time. These swallows vary in when they lay and how much

22 they put into the rearing of offspring (Ardia, 2005a; b; Winkler *et al.*, 2014), but these

23 adjustments in effort are made against the backdrop of a remarkably regular seasonal decline in

24 clutch size.

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1   Table 1. Posterior values (estimated mean and SD) of the variables from two-truncated Poisson

2   model. Posterior probabilities (a measure of variable importance) are obtained from Bayesian

3   variable selection (RJMCMC).

Variable	Mean	SD	Posterior probability of presence in the optimal model
Intercept log(clutch size) for single-time breeders	1.712	0.016	
InterceptDoubleBreeders difference in clutch size between single-time breeders and re-nesters (log scale)	0.001	0.040	0.003
Slope rate of decline in size of first and single clutches	-0.006	0.002	
SlopeSecondClutch difference in the rate of decline between replacement and first/single	-0.001	0.003	0.003

clutches			
$\delta^2_{intercept}$ random effect of year on the clutch size	0.015	0.012	0.041
δ^2_{slope} random effect of year on the rate of seasonal clutch size decline	0.001	0.001	0.002

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1   Figure captions

2

3   Figure 1. Modelled clutch size decline across season in Tree Swallows nesting in Ithaca, New

4   York, predicted from the Bayesian model (see text, Table1). Population decline is shown as

5   median (heavy black line) with 95% credible interval (dark shading) and individual decline

6   (white lines and lighter shading). The dots represent clutch size values from re-nesting (dark-

7   grey circles for first clutches and light-grey circles for replacement clutches) and single-time

8   breeding birds (small black dots), used for the prediction. Note that small random jitter was

9   added to the original data for plotting.