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Communication

Life-history innovation to climate change: can single-brooded migrant birds become multiple breeders?

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When climatic conditions change and become outside the range experienced in the past, species may show life-history innovations allowing them to adapt in new ways. We report such an innovation for pied flycatchers *Ficedula hypoleuca*. Decades of breeding biological studies on pied flycatchers have rarely reported multiple breeding in this long-distance migrant. In two populations, we found 12 recent incidents of females with second broods, all produced by extremely early laying females in warm springs. As such early first broods are a recent phenomenon, because laying dates have gradually advanced over time, this innovation now allows individual females to enhance their reproductive success considerably. If laying dates continue advancing, potentially more females may become multiple breeders and selection for early (and multiple) breeding phenotypes increases, which may accelerate adaptation to climatic change.

Keywords: climate change, life history, multiple breeding



Introduction

Seasonal reproduction has mostly evolved in response to seasonality in food supply (Perrins 1970, Daan et al. 1988). Whether species produce one or more clutches within a single year depends on the profitability of conditions, with more second broods occurring during a broad window of food availability for raising offspring (van Balen 1973, Verboven et al. 2001), when birds are well synchronized with food peaks, and/or when competitor density is low (Both et al. 2000). Other annual cycle stages like migration and/or moult likely have evolved to accommodate this best reproductive window for that population.

Climate change has resulted in many bird species changing their mean breeding phenology (Crick and Sparks 1999, Dunn and Winkler 2010), and extending the length of breeding seasons (Halupka and Halupka 2017). Resident species with multiple breeding have generally prolonged their breeding season during the last decades, whereas long-distance migrants that are single-brooded have reduced their breeding season length (Halupka and Halupka 2017). One of the outstanding questions is how birds will adapt when future environmental circumstances keep on changing to values outside the range that populations have experienced in their past history (Visser 2008).



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Is there a limit to plasticity, or do innovations occur that are yet considered unlikely within the ecology of that species?

In this paper, we address the question whether formerly single-brooded species can become multiple breeders if the circumstances change? We describe such a life-history innovation in two populations of the well-studied pied flycatcher *Ficedula hypoleuca*. As with many long-distance migrants, pied flycatchers are typically single-brooded (Glutz von Blotzheim et al. 1993). In fact, confirmed cases of double-brooding, i.e. producing a second brood after successfully fledging the first one (Table 1), are rare, despite at least ten-thousands nests having been studied intensively (Both et al. 2004). Interestingly, in the reported cases, the second broods were produced by the very early breeders and in early years, and often after a first brood not being very successful (Table 1). Here, we report 12 recent cases of females producing second broods in two populations, which were produced by extremely early laying females after first broods that had high success. We discuss whether this is a likely adaptation to earlier breeding that we will see increasing in the near future.

Methods

Study species and populations

The pied flycatcher is a long-distance migrant which resides in Europe between April and August (about 5 months), a period used for breeding and moulting. The rest of the year these small insectivorous birds reside in west Africa (about 6 months) or are migrating (about 1 month) (Ouweland and Both 2017). Pied flycatchers are most often single brooded, with biparental care. Most males are monogamous, but a proportion of males is polygynous, having broods with two females in different nest boxes often several hundred meters apart (Lundberg and Alatalo 1992).

We report cases of second broods from two study populations: Drenthe, the Netherlands (52°49N, 06°25E), and the north part of canton of Vaud, Switzerland (46°47N, 06°31E) (Ravussin et al. 2007). The two study populations belong to the earliest laying populations in Europe, and have both advanced laying dates since 1980 (Both et al. 2004). The Drenthe population has been studied since 2007, when we installed 1070 nest boxes in 12 study plots (10–75 ha) across a region of 40×20 km in the provinces of Drenthe and Friesland (Both et al. 2017), and increased the number of boxes with an additional 160 in 2017. The number of breeding pairs of pied flycatchers increased from 190 in 2007 to around 300 in 2010, and remained fairly stable since then. Habitats range from pure oak *Quercus robur* to pure coniferous (mostly Scots pine *Pinus sylvestris*) stands, with most sites showing a mixture of broad-leaved and coniferous trees. We compare breeding dates with a nearby population studied in similar habitat called Staphorst (ca 25 km to the south), for which laying dates were available from 1980–2002 (n = 5462 nests; Both et al. 2004).

In the north part of canton of Vaud, pied flycatcher first breeding attempts were observed in 1968 in nest boxes installed in the region of Grandson at the edge of lake Neuchâtel. The population study started in 1980 in Baulmes at the foot of the Jura mountains, and in 1986 at the north side of Lake Neuchâtel. The distance between these two areas is about 15 km. In Baulmes, nest boxes are mostly installed on the forest edges (mostly a mixture of broadleaved forest with beeches *Fagus sylvatica*, ashes *Fraxinus excelsior*, oaks and pines), in groves and hedges near pastures and in orchards. The banks of Lake Neuchâtel are composed of natural broadleaved riparian woods, with mainly alders *Alnus* sp., birches *Betula pendula* and ash trees with rich and varied undergrowth. Some nest boxes are on isolated trees in large parks at the lake side. Reports of second broods in Vaud were partly described by Ravussin et al. (2007).

Nest boxes were checked at least once a week, and laying dates of the first egg were back-calculated assuming one egg was laid every day. Females were mostly caught when incubating, and males and uncaught females during nestling feeding. All individuals were ringed with aluminium rings, as were the nestlings, that were also weighed at an age of 12 d. Fledging occurs around day 14–17. We define second broods as belonging to females that had successfully fledged young in an earlier brood in the same year. We aimed also to capture the males of these multiple breeding females. When comparing reproductive success of multiple breeding females with the rest of the population, we provide the mean number of fledglings for all broods between 2007 and 2017 for both populations, and separately for the females that successfully fledged a first brood.

Results

In Drenthe, we found five cases of second broods out of 3570 broods (2007–2018), and in Vaud we observed six second broods (out of 1372; Table 1; 1980–2018). In Drenthe there was one more possible second brood, although we are not absolutely sure whether the chicks of the first attempt were predated between day 12 and fledging. We do consider this likely to be a second brood because laying of the second brood was initiated 17 d after hatching of the first brood, and hence the female must have started preparing this when the chicks were still alive in the nest at day 12. In two of the 12 cases, the first brood performed badly, with only one and three chicks fledging (Table 1). In all other cases, these first broods fledged normal numbers of young, which had a normal weight at day 12 (Table 1, compare with mean over all broods 2007–2017: 13.91, SD 1.07; n = 12 926 chicks in Drenthe). Therefore, we regard the occurrence of these second broods in most cases not as a best-of-a-bad-job strategy after producing poorly during the first breeding attempt. Indeed, the three Dutch second broods in 2017 produced 13 fledglings, of which one (male) recruit was observed as breeder in 2018 (average first year recruitment rate is 4%).

Table 1. All reported cases of second broods by the same individual pied flycatcher female after successfully fledging a first brood. Data described in this paper are included, as well as all literature data and some unpublished personal communication. LD=laying date first egg; HD=hatch date first chick; CS=clutch size, # Fledg = number of fledged offspring. Weight = mean day 12 weight offspring (g). Interval = days between hatching first and laying second clutch, Distance = meters between boxes (in two cases distance is unknown, but it was known to be a different nest box (Diff NB). All dates are in days since 31 March. Campbell suggested more second broods, but only gave proof for one as female identity was known. Early years were defined as being within the 10% earliest years in longer term studies, or on study plots in nearby areas. Blanks are unknown.

Source	Area	Year	First brood							Second brood							Comparison		
			LD	HD	CS	# Fledg	Weight	LD	HD	CS	# Fledg	Weight	Total fledglings	Males	Interval	Distance	Phenology		
This study	Drenthe, NL	2010	30	52	7	1	14.6	63	81	5	3	4	14.6	11	32	Late year			
This study	Drenthe, NL	2011	24	43	7	7	13.6	60	60	5	0	4	14.6	17	79	Early year			
This study	Drenthe, NL	2017	23	44	7	7	14.5	59	76	5	4	11	14.5	15	450	Early year			
This study	Drenthe, NL	2017	22	42	7	7	58	72	4	4	4	11	14.2	16	643	Early year			
This study	Drenthe, NL	2017	23	42	7	7	13.9	63	80	5	5	12	13.7	21	137	Early year			
This study	Drenthe, NL	2018	31	52	7	6	12.6	67	94	4	4	10	14.1	15	132	Early year			
This study	Baulmes, CH	2000	33	53	7	7	13.0	72	4	4	11	11	13.5	19	400	Early year			
This study	Bonvillars, CH	2006	32	50	6	6	15.0	75	4	0	6	6	14.0	25	910	Early year			
This study	Baulmes, CH	2006	29	50	7	7	12.9	71	4	3	10	10	13.9	21	100	Early year			
This study	Onnens, CH	2007	31	51	6	5	14.7	73	5	1	6	6	14.6	22	Intermediate				
This study	Corcelles-près-Concise, CH	2011	29	48	6	3	15.7	68	4	4	7	7	15.4	20	140	Early year			
This study	Corcelles-près-Concise, CH	2011	28	48	7	7	15.5	55	5	3	7	7	15.3	6	32	Early year			
Campbell (1950)	Forest of Dean, UK	1948	28	49	8	8	86	55	5	3	11	11	86	20	Diff NB	Early year			
Campbell (pers. comm.)	Forest of Dean, UK	1951	46	66	7	7	79	86	5	0	7	7	79	27	Diff NB	Late year			
Likhachev (1955)	Moscow Region, RU	1954	42	62	7	4	66	83	4	4	8	8	66	22	0	Early nest			
Harms (1964)	Harburg, DE	1961	25	44	7	7	79	66	83	4	4	11	79	27	0	Early year			
Anorova (1976)	Moscow Region, RU	1968	42	62	7	6	76	76	2	0	6	6	76	19	0	Early year			
Lander (pers. comm.)	Forest of Dean, UK	1994	37	57	7	6	73	73	6	6	6	6	73	14	290	Intermediate			
Burgess (pers. comm.)	East Dartmoor, UK	2000	40	59	6	4	68	68	4	0	5	5	68	17	403	Early year			
Burgess (pers. comm.)	East Dartmoor, UK	2007	31	51	7	5	88	88	4	1	5	5	88	25	0	Early year			
Kuranov (2008)	Tomsk, RU	2007	40	63	9	4	76	76	4	4	7	7	76	22	0	Early year			
Mazgajski and Dubiec (2011)	Poland	2010	35	54	6	3	74	88	5	4	10	10	74	23	210	Early year			
Briggs (pers. comm.)	Lune Valley, UK	2011	32	51	6	6	74	88	5	4	4	4	74	23	210	Early year			

Females that produced second broods were often among the earliest laying females of that year, and we only found second broods in years with an early average breeding phenology (Fig. 1, Table 1). To place this timing into perspective, in Drenthe, four double-breeding females started laying before 25 April, whereas between 2007 and 2018 only 1.3% of the clutches started before this date. In the period 1980–1990, only 0.18% of clutches were initiated this early, and for 1991–2000 it was 0.16%. Of the 47 females that started laying before 25 April (2007–2018) that fledged at least one chick, 9% produced a second brood. Also in Vaud multiple breeding females were in the early tail of the laying distribution, all starting before 4 May. In 1980–1990 only a single female was observed to lay this early (0.4%), whereas

between 2003 and 2018 12% of females ($n=611$) started laying before 4 May.

Second broods were started in the very end-tail of the laying date distribution (latest 1.3% in Drenthe, 2.6% for Vaud). Interestingly, in the past decades this tail has not shifted to a large extent (Drenthe: 2.3% in 1980s, 2.0% in 1990s; Vaud: 2.5%, 3.9% resp.). One of the possible penalties of laying so late is the increased overlap between caring for the young and moulting the flight feathers (Hemborg and Lundberg 1998), which need to be replaced before the birds depart for Africa around early August (Ouweland and Both 2017). Indeed, we found that five out of five females scored for moult during incubation of their second brood started moulting their primaries. The sixth female with a second

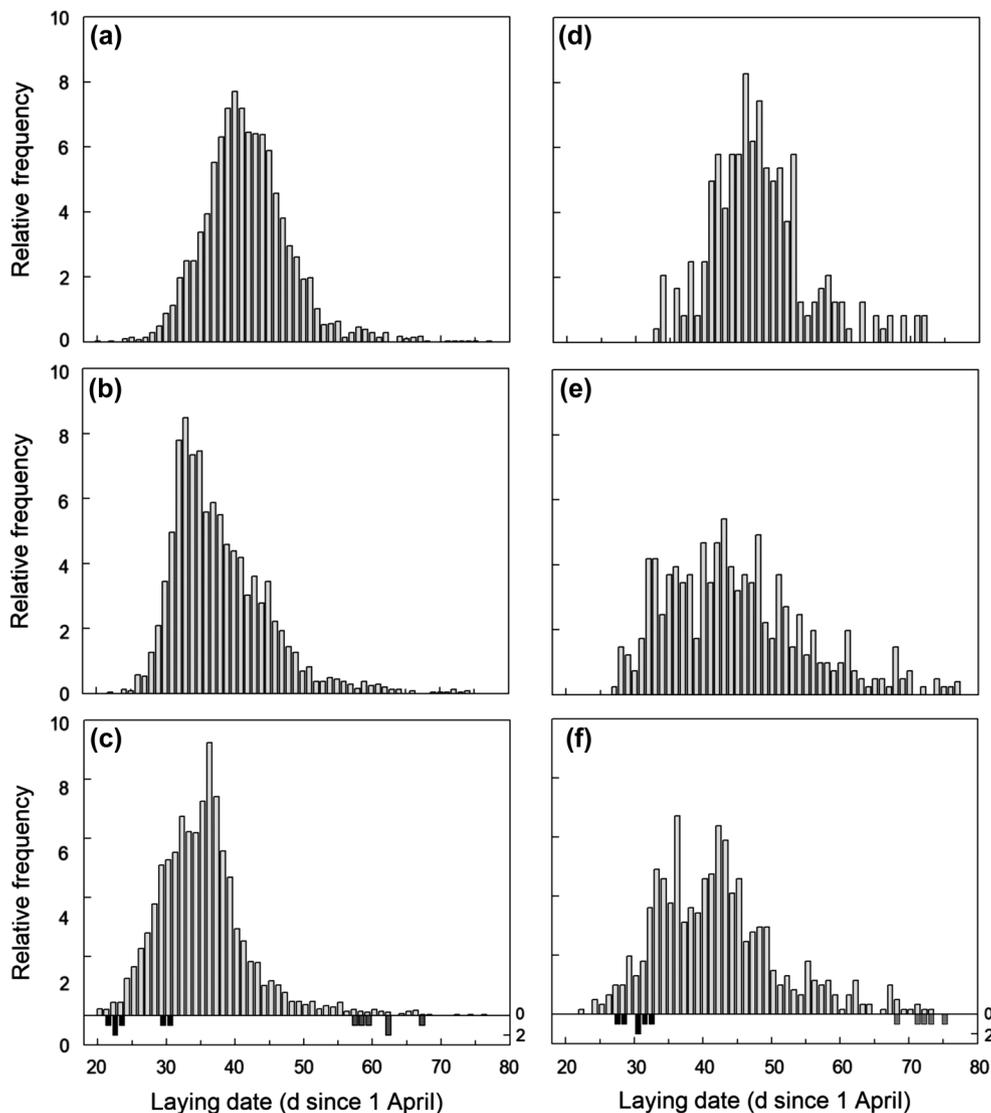


Figure 1. Frequency distribution of laying dates in a Dutch and a Swiss pied flycatcher population for different time periods (1980–2018). Black bars below zero are the laying dates of females starting a second brood later in the season. Grey bars are the laying dates of the second broods. Scales are different for second broods (and given at the right y-axes), as otherwise their frequencies are invisible. (a) Staphorst (NL): 1980–1990; (b) Staphorst (NL) 1991–2002, (c) Drenthe (NL): 2007–2018; (d) Vaud (CH) 1980–1990; (e) Vaud (CH): 1991–2002; (f) Vaud (CH): 2003–2018.

brood was caught during egg-laying, and was not moulting. In the Drenthe population moult is seldom observed in females caught before 10 June, and the general end of the breeding season coincides with this start of female moult. Although sample sizes are low, we have no indication that female return rates were lower for double breeding females in the Swiss population, as 50% of them returned to the following year, which is comparable to the overall return rate (Ravussin et al. 2007). One out of the three females that produced a second brood in Drenthe in 2017 returned as breeder in 2018, again comparable to the overall female return rate (which was 0.26). It is noteworthy that one Swiss female produced second broods in two subsequent years.

In all but one case in which both male identities were known ($n=9$, Table 1), the second brood was produced with a different male at some distance from the original nest (up to 900 m), and hence the observed multiple breeding can be regarded as sequential polyandry. The only case where the original pair remained together was after fledging only one chick out of seven eggs, and the female started laying in a neighbouring box at the time the chick was only 11 d old. In the other cases the interval between hatching of the first brood and start of laying of the second brood was 15–25 d, and was 5 d longer in Vaud than in Drenthe (21.4 (SE:1.0) versus 16.8 (1.1), KW = 4.42, $p=0.04$). As nestlings fledge around day 15, in most Dutch cases the female must have started nest building and growing follicles before the chicks left the nest, and females unlikely participated in post-fledging care, or even abandoned the nest prior to fledging (at least observed in the case in 2018).

Second broods varied in success, with 3 out of 11 failing to fledge offspring, whereas most fledged between 3 and 5 young in good condition, with fledglings being of similar mean mass as the first broods (Table 1). Total annual fledging production of these double breeding females was 9.6 in Drenthe, which is considerably larger than for other nests that did fledge nestlings (i.e. the group that could produce a second brood in our definition): 5.64 ($n=2335$), or for all broods including failures (4.40, $n=2900$). For Vaud this was 7.8 for double breeders, and for single breeders this was 4.78 for nests that fledged at least one chick ($n=378$), and 3.62 for all broods ($n=500$).

Discussion

In two pied flycatchers populations that advanced laying dates in response to climate change, we found early laying females to produce second broods in recent warm years after producing a successful first brood. This double breeding strategy strongly increased annual reproductive output without noticeable survival consequences. As laying date has a genetic basis (heritability estimate from a different Dutch population was 33%; Visser et al. 2015), this new breeding strategy may become strongly favoured in years with warmer springs, resulting in a positive feedback in evolutionary change.

Multiple breeding in pied flycatchers seems not a totally recent innovation, as incidental cases were reported between 1948 and 1968 (Table 1). Information from these older reports is often incomplete, but Campbell (1950) considered second broods more common in 1948–1949 based on the laying date variation, but only proved one on the basis of a ringed female. These were warm springs with early laying dates (Lack 1966), and at least shows that multiple breeding has been part of the life history option set of pied flycatchers under profitable conditions. The apparent lack of reported second broods from 1970 to 2000, and the subsequent increase (16 out of 23 of all cases were reported since 2006) may hence be a response to long-term temperature changes. It is interesting to note that this innovation has not arisen locally, but observed in very low frequencies over most of the southern half of the breeding range (Table 1).

The observed females with second broods all moved to a different nest box, up to 900 m from their first nest, and hence it is possible that we may have missed second broods of local females that moved out of our study area, or had successfully bred somewhere else and entered the area for a second brood. We cannot rule out this possibility, although the average distance between subsequent nests was mostly less than 400 m. Within years we observed females arriving over an extended period of more than 30 d, and hence late broods could be late arriving (mostly young?) individuals (Both et al. 2016).

We have no idea whether second broods can become common in the future if laying dates keep on advancing, or that conditions must be special for them to occur. In our Drenthe population we only had several cases of double breeding in 2017, a year with extremely early breeders, but also with a relatively late caterpillar peak (22 May, unpubl.), and double breeding females fledged their first brood just around the caterpillar peak. It also requires having sufficient numbers of unpaired (or failed) males still advertising late in the season (as is observed in almost all years, Both et al. 2017), as multiple breeders were sequential polyandrous females. It is interesting that a species with a well-known mixed breeding strategy in males, with polygyny occurring frequently (Lundberg and Alatalo 1992), also has females that occasionally are polyandrous. The mean number of fledglings in polyandrous females (9.6) is similar to that of polygynous males in the Drenthe population (9.1, $n=81$).

Whether multiple breeding is a profitable strategy depends on how it fits within other annual cycle stages. Flycatchers have a complete moult prior to fall migration (Hemborg et al. 2001) lasting about 45 d for primary moult (Ginn and Melville 1983, de la Hera et al. 2010). Their autumn schedule seems tight, as successful breeders in the Netherlands have their medium departure on 5 August, (females, $n=5$) and 3 August (males, $n=19$, range: 18 July–14 August). Departure is on average 53 d after fledging (assuming this occurs when chicks are 15 d old), (data from: Ouweland et al. 2016, Ouweland and Both 2017), which just fits the 45 d needed for a complete primary moult. Females normally start moulting around the date when their chicks fledge, and moult seems causally related to hatching date in females, but not males

(Hemborg and Lundberg 1998). We observed moult in all female second breeders already during incubation, suggesting that these females indeed started moult just when their first broods fledged. Whether moult-breeding overlap is actually detrimental to the chicks or future survival of females is unclear, as it often covaries with hatching date. In general it seems that fitness costs to females are small, although some studies show that moulting males reduce their share in nestling feeding, and thereby putting the costs to the female (Tomotani et al. 2018).

The observed pattern that single-brooded migrant birds shorten their breeding season (Halupka and Halupka 2017) does not seem to account for our pied flycatchers, and we suggest that species cannot easily be classified into a single life-history category. Although, the first brood of pied flycatchers has been suggested to be too late for the main food peak as a result of global warming (Both et al. 2009, Samplonius et al. 2016), the potential success of second broods requires knowledge also about the broadness of the food peak, which may actually consist of different prey species peaking in succession. Little knowledge has been gathered how the broadness of food peaks is affected by climate change. Our rather anecdotal observations show that populations encountering conditions outside the range for which we have observed them in the recent past, can surprise us with adaptations that we considered unlikely to occur. How important such innovations will be in this rapidly changing world, is presently unknown, and other species may actually be highly constrained in adjustments when conditions change too much outside their former range, or may start behaving maladaptively.

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