Causes and consequences of within-population variation in inter-brood interval of a migratory songbird

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Many birds produce two broods each year and exhibit significant intra-population variation in the length of time between the hatching of first and second broods (the inter-brood interval). Why within-population variation in inter-brood interval occurs and whether longer inter-brood intervals influence second-brood survival remain key questions in understanding the benefits of producing a second brood. We examined the causes and consequences of variation in inter-brood interval in a wild population of migratory Savannah Sparrows *Passerculus sandwichensis* breeding on Kent Island, New Brunswick, Canada. Using a 29-year dataset, we show that females tended to have short inter-brood intervals when their first nest was initiated later in the season, when they had a low number of first-brood fledglings to care for, or when they had higher lifetime recruitment (suggesting that they were of higher quality). Males with the shortest and longest inter-brood intervals had low feeding rates. Finally, structural equation modelling provided evidence that longer inter-brood intervals led to later second-brood hatch dates, which in turn led to smaller clutch sizes and fewer recruits. Our results suggest that the length of time between broods is a key factor predicting the first-year survival of second-brood offspring. These long-term data reveal that inter-brood interval reflects the timing of breeding and variation in female quality and that it influences offspring survival and, likely, fitness.

Keywords: fecundity, individual quality, interbrood interval, inter-clutch interval, Savannah Sparrow.

Pairs of birds that rear two broods within a breeding season, termed 'double-brooding', often experience lower recruitment rates for second-brood than first-brood offspring (Morrison 1998, Dietrich *et al.* 2003, Schmoll *et al.* 2003, Hodges

et al. 2015). Second-brood offspring may be less likely to recruit because optimal conditions for rearing young decline across the breeding season (Winkler *et al.* 2014, Meltofte *et al.* 2021, Sutton & Freeman 2023), resulting in second-brood nestlings that are in poorer condition compared with first-brood nestlings (Aguon & Conant 1994, Antonov & Atanasova 2003, Cornell & Williams 2017). By initiating second broods earlier in the year, offspring of migratory species have more time to reach independence, moult and build up energy reserves before migration and overwintering. Hence, initiating a second brood as early as possible may maximize the fitness potential of that

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brood (Verboven & Visser 1998, Zabala *et al.* 2020). Despite the expected benefits of rearing second-brood offspring earlier in the season, substantial intra-population variation in the length of time between the hatching of first and second broods (the 'inter-brood interval') is observed in wild songbird populations (Weggler 2006, Grüebler & Naef-Daenzer 2010, O'Brien & Dawson 2013). Why within-population variation in inter-brood interval occurs and whether longer inter-brood intervals influence survival of second broods remain key questions in understanding lower recruitment of second-brood offspring.

Previous studies investigating the causes of intra-population variation in inter-brood intervals have predominantly explored the influence of timing of the first brood (Smith *et al.* 1987, Weggler 2006, O'Brien & Dawson 2013), the number of first-brood fledglings (Smith & Roff 1980, McGillivray 1983, Smith *et al.* 1987, Verboven & Verhulst 1996, Mariette *et al.* 2015, McDermott *et al.* 2023) and resource availability (Eden *et al.* 1988, Verboven *et al.* 2001, Teglhøj 2017). Multiple studies have demonstrated that fledging a first brood later in the season was associated with a shorter inter-brood interval (Smith *et al.* 1987, Weggler 2006, O'Brien & Dawson 2013; but see Verboven & Verhulst 1996), which may reflect constraints on timing related to changing food availability across the breeding season or the impending autumn migration. Additionally, several studies have demonstrated that having a higher number of first-brood fledglings is associated with a longer inter-brood interval (Smith & Roff 1980, McGillivray 1983, Smith *et al.* 1987, Verboven & Verhulst 1996, Mariette *et al.* 2015, McDermott *et al.* 2023). Given that successfully raising young to independence takes significant time and energy (Drent & Daan 1980), the ability of parents to begin a second brood soon after the first may depend on the parents' physiological capacity for reproduction and brood rearing. Having many first-brood fledglings would further increase the energetic demands of brood rearing and parents may need more time to recuperate the energy required to initiate a second brood. The ability of parents to quickly begin a second brood after a first has also been positively related to resource availability (Eden *et al.* 1988, Verboven *et al.* 2001, Teglhøj 2017), which further supports the idea that variation in inter-brood intervals could be driven by the capacity of parents to care for multiple broods sequentially or, in some cases, simultaneously.

Weather conditions, population density and parental quality could also potentially influence intra-population variation in inter-brood interval. Given that poor weather can create unfavourable breeding conditions (Martin *et al.* 2017, Nägeli *et al.* 2022, Taff & Shipley 2023), inclement weather following the fledging of the first brood could delay initiation of a second. Alternatively, inclement weather following the fledging of the first brood could expedite parents' initiation of a second if poor weather conditions led to first-brood fledgling mortality. Population density could impact inter-brood intervals because higher densities can increase interference competition (Lewis *et al.* 2001). Under scenarios of higher competition, parents may take longer to acquire the energy reserves necessary to rear a second brood. Finally, higher quality individuals could have shorter inter-brood intervals if they have accumulated more resources to invest in consecutive reproductive attempts (van Noordwijk & de Jong 1986). None of these factors have been explicitly examined to explain variation in inter-brood interval.

The latency between first and second broods could have important fitness consequences (Verhulst *et al.* 1997, Naef-Daenzer *et al.* 2011). Rearing two broods in one season often requires parents to initiate the second brood before parental care of the first brood ends (Smith *et al.* 1989, Dowding *et al.* 1999, Wheelwright *et al.* 2003, Grüebler & Naef-Daenzer 2010, Boyarski *et al.* 2020), which can increase the energetic demands on parents. Overlap between broods could compromise parents' self-maintenance or survival if they exhaust energetic resources on brood care (Verhulst & Nilsson 2008). Moreover, brood overlap could affect parental investment in each brood. Studies have shown that double-brooded parents reduced feeding frequency or the duration of the post-fledging care period to first-brood fledglings when second broods were initiated (Verhulst *et al.* 1997, Naef-Daenzer *et al.* 2011). Male parents also reduce their feeding rates to second-brood nestlings compared with first-brood nestlings (Evans Ogden & Stutchbury 1996, Kuitunen *et al.* 1996, Slagsvold & Rohwer 2000). Males may provide more post-fledging care to first broods so that females can invest in second-brood initiation (Wheelwright *et al.* 2003). Whether reduced nestling feeding rates during second broods are caused by males

having to divide time and resources between first-brood fledglings and second-brood nestlings remains to be determined.

Two studies, both of Barn Swallows *Hirundo rustica*, have examined the behavioural and fitness consequences of variation in inter-brood interval. In the first, second-brood nestling feeding rates by males were not related to the duration of the inter-brood interval (Møller 1991). However, although there was overlap between first-brood post-fledging care period and the female's second fertile period, it was unclear whether there was overlap between the post-fledging care of the first brood and the nestling period of the second brood (Møller 1991). A second study demonstrated that pairs with longer inter-brood intervals produced more fledglings than those with shorter inter-brood intervals (Møller 2007). However, how inter-brood interval influences the recruitment of first- and second-brood offspring has not been examined before.

Given the potential impact of inter-brood interval on offspring fitness, exploring the causes and consequences of within-population variation in inter-brood interval in wild populations could provide insights into why many songbird species exhibit high variability in inter-brood intervals. One species with substantial overlap between broods and variation in inter-brood interval is the Savannah Sparrow *Passerculus sandwichensis* (Wheelwright *et al.* 1992, 2003). Savannah Sparrows are migratory, grassland songbirds (Wheelwright & Rising 2020). They are facultatively double-brooded, with intervals between the hatching of successive broods ranging from 27 to 37 days (Wheelwright & Rising 2020). As open-cup nesters with brief nestling periods (approximately 9–11 days; Wheelwright & Rising 2020) and a post-fledgling parental care period lasting up to 26 days after fledging (Wheelwright *et al.* 2003), Savannah Sparrows provide an excellent opportunity for studying breeding success and parental care.

We investigated the factors influencing inter-brood interval and the impact of inter-brood interval on fitness using 29 years of breeding data from a wild population of Savannah Sparrows and addressed the following questions. (1) What influences variation in inter-brood intervals within a population? (2) Are male feeding rates during the second brood influenced by inter-brood intervals? (3) Does inter-brood interval influence female fitness? We explored hypotheses that attempted to answer these questions and used generalized linear mixed models (GLMMs; questions 1 and 2) and structural equation modelling (SEM; question 3) to test predictions from these hypotheses (Table 1).

METHODS

Study system and field methods

Savannah Sparrows (Fig. S1) were studied in a 10-ha plot located in the centre of Kent Island, New Brunswick, Canada (44.58254°N, 66.75604°W), an 80-ha island in the Bay of Fundy, where individually marked Savannah Sparrows have been studied since 1987 (Woodworth *et al.* 2017a, Burant *et al.* 2022). In late April and early May, males establish their territories across old field habitat composed primarily of Blueberry *Vaccinium angustifolium*, Fireweed *Chamaenerion angustifolium*, Goldenrod *Solidago rusa*, Raspberry *Rubus idaeus* and several species of grasses (Woodworth *et al.* 2016, Dobney *et al.* 2023, Suarez Sharma *et al.* 2024). All pairs attempt to rear at least one brood to fledging, with re-nesting occurring up to four times if the previous nest fails. If the first brood fledges early in the season, pairs may attempt a second brood (Woodworth *et al.* 2017a), with mate-switching sometimes occurring between broods (H.A.S., D.R.N., S.D.M., G.W.M., pers. obs.). On average, 28% of pairs successfully double-brooded between 1987 and 2022 (range 4–63% per year, Spina *et al.* 2025b). Females that did not attempt a second brood produced an average of three fledglings per year (range two to four per year), with 14% of females failing to fledge any offspring (Spina *et al.* 2025b dataset). Females that attempted to double-brood produced an average of seven fledglings per year (range four to eight per year), with 10% of females failing to fledge any offspring from the second brood (Spina *et al.* 2025b dataset). Males may be polygynous or monogamous (Wheelwright *et al.* 1992). A 30-year study on this population demonstrated that on average, 67% (range 28–100%) of females were monogamously mated, 14% (range 0–34%) were the primary female of a polygynous male (i.e. the first female the male paired with that season) and 19% (range 0–46%) were a secondary female of a polygynous male (i.e. any subsequent female the male paired

Table 1. Hypotheses and predictions associated with questions related to the causes and consequences of within-population variation in inter-brood intervals.

Questions	Hypotheses	Predictions
1) What influences variation in inter-brood intervals within a population?	Females whose first broods are later than the average will have less time remaining to rear a second brood and, therefore, shorter inter-brood intervals (later in season > shorter intervals)	Inter-brood interval will be negatively related to first-brood fledge date
	Given limited resources for breeding, the amount of investment in the first brood will have a positive effect on inter-brood interval (more investment > longer intervals)	Inter-brood interval will be positively related to the number of first-brood fledglings
	If resource acquisition for breeding is dependent upon female quality, female quality will have a negative effect on inter-brood interval (higher quality > shorter intervals)	Inter-brood interval will be negatively related to female age (i.e. a proxy for experience) and lifetime recruitment
	Given that inclement weather can create unfavourable breeding conditions, inclement weather following the fledging of the first brood could delay the initiation of a second brood (poor weather > longer intervals)	Inter-brood intervals will be negatively associated with temperatures and positively associated with precipitation
	Given that inclement weather following the fledging of the first brood could lead to higher-than-average juvenile mortality, having fewer fledglings to care for could result in a shorter inter-brood interval (poor weather > shorter inter-brood intervals)	Inter-brood intervals will be positively associated with temperatures and negatively associated with precipitation
	Given that higher densities can increase interference competition, parents may take longer to acquire energy reserves necessary to rear a second brood when densities are high (higher density > longer inter-brood intervals)	Inter-brood intervals will be positively related to the number of adults in the study site that season
2) Are male feeding rates during the second brood influenced by inter-brood intervals?	Given the time and energy required to rear two broods in quick succession, if the first-brood post-fledging period and the second-brood nestling period overlap, male feeding rates during the second brood will be positively affected by the inter-brood interval (longer inter-brood intervals > higher male feeding rate of second brood). Male feeding rates, rather than female feeding rates, would be affected by the inter-brood interval because males may take on more first-brood post-fledgling care when the female initiates the second brood	Inter-brood intervals will be positively associated with nestling feeding rates by males during the second brood
3) Does inter-brood interval influence female fitness?	Given the time and energy required to rear two broods in quick succession, short inter-brood intervals cost females in terms of subsequent survival and the survival of young from the first brood (shorter inter-brood intervals > reduced female and offspring survival).	Inter-brood intervals will be positively associated with apparent survival of females and first-brood recruitment.
	Given that clutch sizes in migratory songbirds tend to decrease as the breeding season progresses, shorter inter-brood intervals increase the number of fledglings produced because eggs were laid earlier in the season (shorter inter-brood intervals > higher second-brood fledgling production)	Second-brood lay date will be positively related to inter-brood interval and number of fledglings will be negatively related to second-brood lay date. These two relationships result in a negative indirect effect of inter-brood interval on the number of young fledged
	Given that the offspring survival in migratory songbirds tends to decrease as the breeding season progresses, shorter inter-brood intervals increase the probability that young from second broods will recruit because they are born earlier in the season (shorter inter-brood intervals > higher second-brood offspring recruitment)	Second-brood lay date will be positively related to inter-brood interval and probability of recruitment will be negatively related to second-brood lay date. These two relationships result in a negative indirect effect of inter-brood interval on recruitment

with that season; Mueller *et al.* 2025a). Extra-pair mating is common, with an estimated 34% of young arising from extra-pair fertilizations (Freeman-Gallant 1997). Laying is initiated between May and July. Offspring rely on parental provisioning for the first 3 weeks of life until they develop the ability to forage approximately 24 days after hatching (Wheelwright & Templeton 2003). Parents may continue provisioning first-brood fledglings until 35 days after hatching (Wheelwright *et al.* 2003). On Kent Island, Savannah Sparrows forage in open fields, the intertidal zone and in conifers, providing nestlings with diverse invertebrate prey (Wheelwright *et al.* 1992). Adults and juveniles moult in August and September (Wheelwright & Rising 2020) and spend the non-breeding period in the South Atlantic United States (Woodworth *et al.* 2016). Individuals breeding on Kent Island demonstrate a high degree of site philopatry, with returning nestlings typically establishing territories within approximately 200 m of their natal site and adults dispersing an average of 40 m between successive seasons (Hensel *et al.* 2022, Wheelwright & Mauck 1998). Recruitment rates of nestlings banded the previous season on Kent Island were 17% and 10% for first- and second-brood offspring of double-brooded parents, respectively (Spina *et al.* 2025b), compared with an annual adult male return rate of 48% (Woodworth *et al.* 2017a). Mean (sd) longevity of adult males (individuals banded on Kent Island between 1987 and 2022 that survived one or more years; $n = 1046$) and females ($n = 1235$) was 1.7 ± 1.2 years and 1.7 ± 1.1 years, respectively (H.A.S., unpubl. data), though some individuals can live up to 8 years (Wheelwright & Rising 2020; Hensel *et al.* 2022).

The breeding behaviour of Savannah Sparrows was monitored from 1987 to 2022 (excluding 2005–07 and 2020). Upon their return from migration, unbanded adults were captured using mist-nets and given a unique combination of a U.S. Fish and Wildlife Service/Canadian Wildlife Service aluminium leg band and three coloured leg bands, and all previously banded adults in the study area were resighted to determine recruitment (for yearlings) or apparent survival (for older birds). Adults were also resighted in 2023 to determine recruitment and apparent survival. With a high degree of site fidelity in our population, previously unbanded birds are generally assumed to be second-year birds (Suarez Sharma *et al.* 2024) and age estimations are supported by tail feather shape assessment (Pyle 2022). In the first year after any year when monitoring was not conducted, the age of unbanded birds was determined by tail feather shape. Mating pairs were determined by observing social interactions and nesting behaviour. Nests (Fig. S2) were primarily located by observing female behaviours (e.g. observing a female return to the same location multiple times).

In 2021 and 2022, a subset of nests within the study site were protected with predator exclosures (Spina *et al.* 2025a, 2025b) and all nests from these years that fit the inclusion criteria for this study (see data filtering steps below in Data analysis) were protected. High levels of predation on Kent Island have historically limited the number of pairs attempting to double-brood (Dixon 1978) because once a pair renests due to a failed nest, they typically do not have enough time remaining in the season to successfully fledge young from the renest and attempt a second brood (Woodworth *et al.* 2017a). Given that only 2% of females that had their first nest attempt predated double-brooded (Woodworth *et al.* 2017a), we did not expect the use of predator exclosures to impact inter-brood intervals. Modelling inter-brood interval by exclosure use (two-level factor, $0 =$ no exclosure, $1 =$ exclosure) while including a random effect of year revealed no effect of exclosures on inter-brood interval ($\beta = 0.85$, $z = 0.42$, 95% CI $= -3.08$ to 4.79; Fig. 1).

Nests were monitored every other day for hatching. Hatching occurs over a 24- to 36-h period (Wheelwright & Rising 2020). If the clutch was not fully hatched on the day the nest was checked, hatch date was assigned to that day. If the clutch was fully hatched, then hatch date was assigned to the previous day. After the fledging of the first brood, pairs were monitored every 1–2 days to observe whether they initiated a second brood. Following the fledging of the first brood, many pairs left their territory to follow fledglings as they began wandering but then returned to initiate their second brood (H.A.S., D.R.N., S.D.M., G.W.M., pers. obs.). Pairs rarely have second broods outside the original breeding territory. Hence, through careful monitoring of pairs on their territories following the fledging of the first brood, it is unlikely that any second broods were missed.
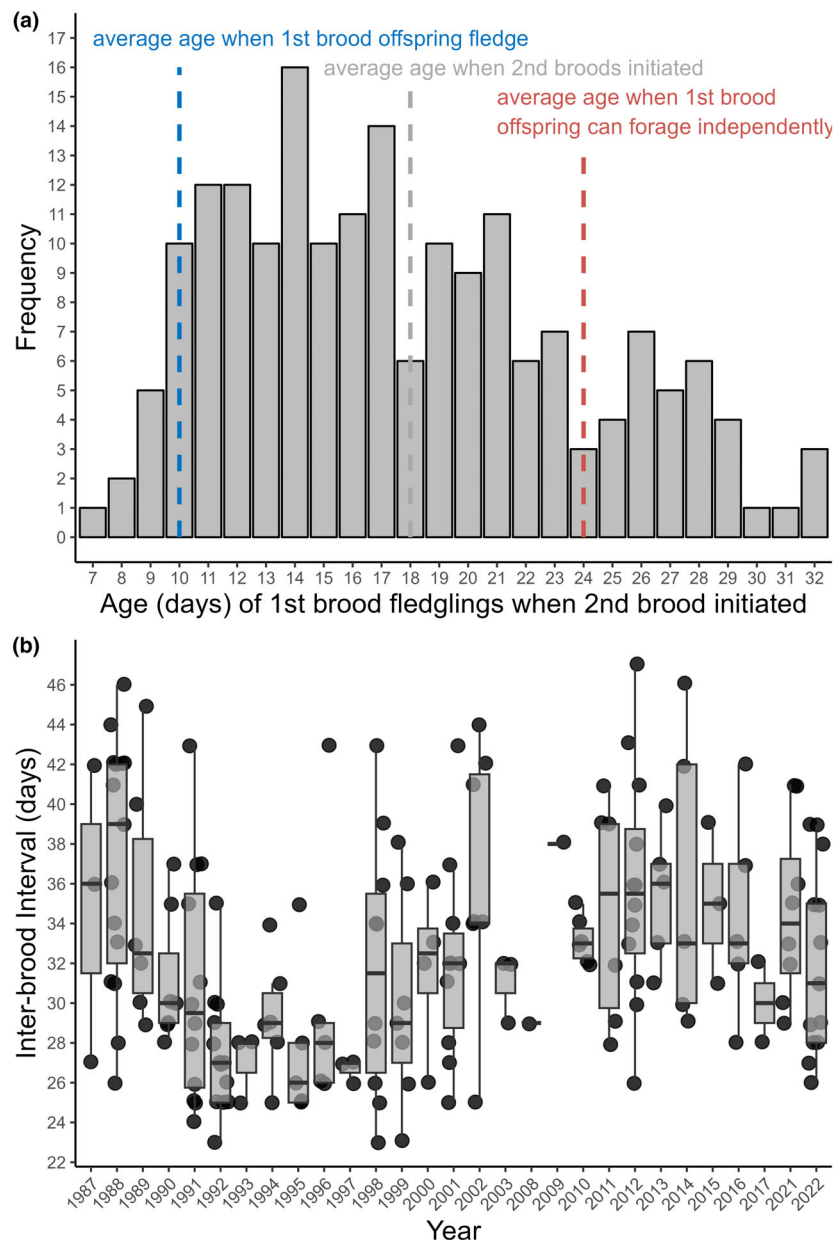
Figure 1. (a) Frequency distribution of first-brood Savannah Sparrow ages at the time pairs initiated the second brood. Second clutch initiation dates (first egg dates) from 1987 to 2022 ranged from before the fledging of the first brood (~9–11 days post-hatch) to before the time that parents were last observed providing post-fledging care to the first brood (35 days post-hatch). Blue line represents the average age that first-brood offspring fledge (range 9–11 days post-hatch). Red line represents the average age when first-brood offspring can forage independently. Grey line represents the average age of first-brood offspring when second broods are initiated (18 days post-hatch). (b) Annual variation in inter-brood intervals. Inter-brood intervals were variable across years. There was no evidence that use of exclosures (2021 and 2022) impacted inter-brood intervals. Some years are excluded because of the absence of monitoring (2005–07, 2020) or because all females in those years were excluded from analyses (2004, 2018, 2019; see Data organization and statistics for details). The boxes show the 25th to 75th centile of data, with the mean shown by the thicker black bar. Error bars represent 1.5 × interquartile range. Each dot represents a breeding pair in the dataset. Any observed colour difference in the dots comes from the boxplot overlay (i.e. all dots are black).

For our analysis, we defined 'recruitment' and 'apparent survival' as return the following breeding season. Given the strong natal and breeding philopatry in this population (Wheelwright & Mauck 1998, Hensel *et al.* 2022), dispersal far beyond our study site was unlikely (only one to four dispersed yearlings are found during annual censuses outside the study area on Kent Island or on neighbouring islands; Mueller *et al.* 2025b). In a recent study of our population, only 35 of 4870 individuals (0.7%) were not detected as yearlings but were detected in a subsequent year (Mueller *et al.* 2025b). Hence, we assumed that individuals not observed on our study site in any following year had died rather than dispersed.

Nest watches

From May to August 2022, we studied parental behaviour during the nestling stage in a subset of monogamous double-brooded pairs ($n = 14$). Nest watches were conducted to assess parental feeding behaviour during the nestling stage of second broods. Three and six days after hatching (Fig. S3), a camera (Campark, X30 True 4K Ultra HD Action Camera) was deployed for approximately 1 h between 8:00 AM and 12:00 PM to record parental visits to the nest (see Video S1 for example footage). Six days after hatching was selected because, within the nestling stage, it is the day for which parental feeding rates and mass gain are the greatest in Savannah Sparrows (Wheelwright *et al.* 1992). Three days after hatching was selected as an intermediate day between hatching and day 6. In songbirds, 1- to 2-h monitoring periods have been shown to be as effective at estimating parental feeding rates as 6- to 7-h monitoring periods (Wheelwright *et al.* 1992, García-Navas & Sanz 2012, Pagani-Núñez & Senar 2013). Parents were recorded returning to normal feeding behaviour within minutes of positioning the camera at the nest and did not seem alarmed by its presence (S.L.D., H.A.S., D.R.N., pers. obs.). Cameras were positioned approximately 15–30 cm in front of the nest entrance to provide an optimal view of the coloured bands of the parents. Nestlings were counted at the time of camera deployment to confirm brood size. We conducted nest watches during days with no rain. All nests ($n = 14$) were recorded at least once during each brood, with most nests recorded twice ($n = 12$ nests recorded both 3 and 6 days after hatching, and one nest each, 3 days or 6 days after hatching).

Data analysis

To explore the causes and consequences of within-population variation in inter-brood interval, our analyses included all adult females for which a complete within-season breeding history was obtained (see Woodworth *et al.* 2017a for individual exclusion criteria). We also only included females that were mated to a monogamous male and that attempted double-brooding in the focal year. We included females breeding between the years of 1987 and 2022 (excluding the years when monitoring did not occur: 2005–07 and 2020). We removed females sampled in 2004 and 2019 as survival and future breeding success could not be assessed because of the absence of monitoring in the subsequent years. No females that attempted double-brooding in 2018 fit our inclusion criteria. Hence, our full dataset included 29 years of data ($n = 186$ observations). We conducted analysis in R v4.2 (R Core Team 2023). For all analyses, we used GLMMs (glmmTMB Package; Brooks *et al.* 2017) and assessed model fit using the DHARMa package (DHARMa function: *simulateResiduals*; Hartig 2022). In all models, inter-brood interval was assigned as a continuous variable and was measured as the difference in days between the hatching day of the second and first broods. All reported means are presented as ± standard deviation (sd).

Analysis 1: factors influencing inter-brood interval
To assess factors predicted to influence inter-brood interval (Table 1), particularly female quality via lifetime recruitment, we further subset the dataset to only include females for which we had a record of their lifetime breeding history (i.e. breeding records for each year they were known to be alive within 1987–2022; $n = 137$ observations). This included removing females that potentially bred in the years when monitoring did not occur (2005–07 and 2020). We also excluded females breeding in 2008 that were aged as after-second-year (hatched between 2005/06) because we would have missed one or more years of breeding data from these females. Additionally, we removed females that were observed breeding in 2023 because we would not yet know their complete lifetime reproductive success.

To investigate which factors influenced inter-brood interval, we built a global GLMM with all predictor variables hypothesized to impact inter-brood interval (Table 2): estimated first-brood fledge date, the number of first-brood fledglings, age (second year versus after second year), lifetime recruitment, annual density, mean temperature after first-brood fledging and mean precipitation after first-brood fledging (see Table 3 variable descriptions). Weather data were obtained from an Environment and Climate Change Canada weather station at the airport in Saint John, New

Table 2. Global models, top models, sample sizes and years of data for Analysis 1, Analysis 2 and Analysis 3.

Global model	Top model	Sample size	Years of data
Analysis 1: inter-brood interval ~ first-brood fledge date + number of first-brood fledglings + age + lifetime recruitment + annual density + mean temperature post-first-brood fledging + total precipitation post-first-brood fledging + (1|ID) + (1|year)	Inter-brood interval ~ first-brood fledge date + number of first-brood fledglings + lifetime recruitment + (1|ID) + (1|year)	137	27
Analysis 2: Male feeding rate ~ inter-brood interval + (inter-brood interval)^2 + nestling age + time of day + mate's feeding rate + brood size + (1|ID)	Male feeding rate ~ inter-brood interval + (inter-brood interval)^2 + mate's feeding rate + (1|ID)	14	1
Analysis 3 (paths in global model): Path 1: second-brood lay date ~ inter-brood interval + (1|ID) + (1|year) Path 2: second-brood clutch size ~ second-brood lay date +(1|ID) + (1|year) Path 3: second-brood fledglings produced ~ clutch size + (1|ID) + (1|year) Path 4: second-brood recruits ~ second-brood fledglings + second-brood lay date (1|ID) + (1|year) Path 5: first-brood recruits ~ inter-brood interval + (1|ID) + (1|year) Path 6: female survival ~ inter-brood interval + (1|year)	(Paths remaining after removing non-significant paths): Path 1: second-brood lay date ~ inter-brood interval + (1|ID) + (1|year) Path 2: second-brood clutch size ~ second-brood lay date +(1|ID) + (1|year) Path 3: second-brood fledglings produced ~ clutch size + (1|ID) + (1|year) Path 4: second-brood recruits ~ second-brood fledglings + second-brood lay date (1|ID) + (1|year)	186	29

Table 3. Descriptions of factors hypothesized to influence inter-brood intervals in Analysis 1.

Predictor variable	Description
First-brood fledge date	The estimated ordinal date that the first-brood fledged (day 1 = 1 January). First-brood fledge date was calculated as the hatch date of the first brood plus 10 days (fledge dates range from ~9 to 11 days)
Number of first-brood fledglings	The number of first-brood offspring that were banded 7 days after hatching. Nests are not visited after banding to prevent premature fledging, so all banded nestlings are assumed to have fledged
Age	Two-level factor: 1 = females 1 year of age (second-year females), and 2 = females 2 years of age or older (after-second-year females)
Lifetime recruitment	The total number of offspring produced across the individual's lifespan that became breeders on Kent Island
Annual density	The peak number of breeding adults of both sexes in the study area in each year (study area size remained constant over the length of the study)
Mean temperature post-first-brood fledging	The average temperature (°C) recorded for the first 7 days following the fledging of the first brood. Mean temperature was calculated for each brood and so was unique to each brood with a different fledge date
Total precipitation post-first-brood fledging	The total precipitation (cm) recorded for the first 7 days following the fledging of the first brood. Total precipitation was calculated for each brood and so was unique to each brood with a different fledge date

Brunswick, Canada (45.32°N, 65.89°W), approximately 110 km northeast of Kent Island (Woodworth *et al.* 2017b, Burant *et al.* 2022). Mean temperature and total precipitation were calculated for each first brood for the 7 days following fledging. Given that nests were not checked after nestlings were banded (7 days after hatching) to prevent premature fledging, first-brood fledging dates were estimated to be 10 days after hatching. To make intercepts and estimates more comparable, all predictor variables were grand-mean centred before analysis. Inter-brood interval was modelled with a Poisson distribution. In all models, we also included a random effect of female identity to account for repeated sampling of females in multiple years and a random effect for year to account for environmental variation across years that could impact metrics of fitness. For this analysis, and for Analysis 2 below, we dredged the full model (MuMIn function: *dredge*; Bartoń 2023) to analyse all possible model combinations, including the null model, and reported statistics for predictor variables in the top model, represented as having an Akaike Information Criterion for small sample sizes (AICc) value at least 2 units lower than the next best model (Burnham & Anderson 2002). We calculated 95% confidence intervals using the function *confint* and we report the lower (2.5%) and upper (97.5%) limits for each parameter. We considered predictors to be important when the lower and upper confidence limits did not overlap zero (Payton *et al.* 2003).

Analysis 2: influence of inter-brood interval on male feeding behaviour

To explore whether inter-brood interval influenced male feeding behaviour during second broods, we first examined whether first- and second-brood parental feeding periods overlapped in a subset of double-brooded pairs in 2022 for which feeding behaviour was recorded ($n = 14$). Due to the use of predator exclosures (Spina *et al.* 2025a, 2025b), all first broods were the parents' first nest attempt that season and all second broods were reared after the successful fledging of the parents' first nest attempt. We examined two levels of overlap based on past observations of the post-fledging period in Kent Island Savannah Sparrows (Wheelwright & Templeton 2003). To assess definite brood overlap, we determined whether 3 or 6 days after hatching of the second brood overlapped with the

period between the hatching of the first brood and the time first-brood fledglings can forage independently (approximately 24 days after hatching; Wheelwright & Templeton 2003). To assess potential brood overlap, we determined whether 3 or 6 days after hatching of the second brood overlapped with the period between the hatching of the first brood and the maximum length of the first brood post-fledging care period (approximately 35 days after hatching; Wheelwright *et al.* 2003).

We then explored the prediction that shorter inter-brood intervals would be associated with reduced nestling feeding rate by males during second broods (Table 1). We modelled feeding rate per nest as a function of inter-brood interval using our 2022 video recording dataset (Table 2). Feeding rate per nest was calculated as the number of food deliveries brought to the nest per hour. A delivery often consisted of one food item. However, sometimes parents delivered multiple food items in the same visit. Given that the feeding rate data were continuous, positively skewed data that included zeros (if the male did not visit the nest at all), feeding rate per nest was modelled with a Tweedie distribution and log link function (Bonat & Kokonendji 2017). We also included a quadratic term for inter-brood interval in this model after preliminary data exploration. We additionally included predictor variables that we hypothesized could influence feeding rates by males (nestling age, time of day, mate's feeding rate and brood size). To account for the possibility that parental feeding rates may increase as nestlings grow, we included nestling age as a two-level factor (0 = nestlings were 3 days old, 1 = nestlings were 6 days old). To account for variation in the timing of nest watches, time of day was included as a continuous predictor. To account for the possibility that parents may alter their feeding rates depending on their mate's contribution (Freeman-Gallant 1998), we included mate's feeding rate per nest as a continuous predictor. To account for the possibility that parents may alter their feeding rate depending on brood size, we included brood size at the time of feeding as a continuous variable. Male identity (factor) was included as a random effect to account for repeated observations of individuals 3 and 6 days after brood hatching. All continuous predictor variables were grand-mean centred before analysis.

Analysis 3: influence of inter-brood interval on metrics of fitness

To test potential direct and indirect effects of inter-brood interval on metrics of fitness (Table 1), we used SEM (piecewiseSEM Package; Lefcheck 2016). We built a global model that contained a series of paths representing all hypothesized relationships (Table 2). We hypothesized that if longer inter-brood intervals resulted in second broods being initiated later in the season, then clutch size, fledging success and survival of second-brood offspring would be reduced (Table 1). Longer inter-brood intervals were also predicted to be associated with higher probabilities of first-brood recruitment and female apparent survival rates (Table 1). Hence, our paths included direct effects of inter-brood interval on female apparent survival (two-level factor; 0 = the female did not return the next breeding season, and 1 = the female did return the following breeding season), the number of first-brood recruits (continuous variable representing the number of first-brood offspring that returned to breed the following year), and the second-brood lay date (the ordinal date that the first egg was laid for the second brood, estimated as the hatch date minus the length of the incubation period, 12 days, and one additional day for each egg that was laid up to the penultimate egg), direct effects of second-brood lay date on second-brood clutch size (the number of eggs laid in the second brood) and the number of second-brood recruits (continuous variable representing the number of second-brood offspring that returned as breeders the following year), a direct effect of second-brood clutch size on the number of second-brood fledglings (continuous variable representing the number of fledglings produced during the second brood), and a direct effect of the number of second-brood fledglings on the number of second-brood recruits (Fig. 5a). The paths in our global model were GLMMs. All models included a random effect of female identity to account for repeated sampling of females in multiple years and a random effect for year to account for environmental variation across years that could impact metrics of fitness. All continuous variables were grand-mean centred before analysis. After centring, all response variables were modelled with a Gaussian distribution, except apparent survival, which was modelled with a binomial distribution. Model fit of the SEM was assessed by computing a Fischer C statistic (Lefcheck 2016), with $P > 0.05$ indicating good model fit. We included paths in the top model that the global model demonstrated evidence for ($P < 0.05$). We reported standardized estimates (β) from the top model.

We calculated the total effect (TE) of inter-brood interval on the number of second-brood young fledged and the number of second-brood young recruited. TE is calculated as the sum of direct and indirect effects (Bart & Earnst 1999, Norris *et al.* 2004). Given that effects of inter-brood interval on reproductive success were hypothesized to occur via indirect effects on second-brood lay date (Table 1), we did not model direct effects of inter-brood interval on reproductive success within SEM analysis. As a result, the TE equated solely with the indirect effects. Our final SEM model had one indirect pathway linking inter-brood interval and the number of second-brood young fledged, and one indirect pathway linking inter-brood interval and the number of second-brood young recruited. Hence, for each indirect pathway, indirect effects were calculated by multiplying the standardized estimates linking these variables (Norris *et al.* 2004). We then predicted the reproductive consequences of increasing inter-brood intervals using the TE values and sd for each variable (i.e. sd(Inter-brood Interval) = sd (young fledged) × TE; Bart & Earnst 1999, Norris *et al.* 2004).

Language of evidence

Abandoning the use of binary (significant versus non-significant) statements when reporting statistical results has been suggested (Wasserstein *et al.* 2019, Courtenay 2024). Hence, we report results using the language of evidence, as suggested by Muff *et al.* (2022), which focuses on reporting relationships while avoiding reliance on an arbitrary *P*-value cut-off. Use of the language of evidence also facilitates understanding by describing the strength of relationships as a gradient (Muff *et al.* 2022). We report no evidence that predictors are important when $P > 0.10$, weak evidence when $0.10 > P > 0.05$, moderate evidence when $0.05 > P > 0.01$, and strong evidence when $P < 0.01$.

RESULTS

Savannah Sparrow inter-brood intervals ranged from 23 to 47 days ($n = 186$ females; mean ± sd,

32.6 ± 5.7 days). Correspondingly, the estimated ages of first-brood fledglings at the time of second-brood initiation (the day the first egg was laid) ranged from 7 to 32 days post-hatch (Fig. 1; mean ± sd, 17.7 ± 6.0 days post-hatch).

Factors influencing inter-brood interval

There was one top model that best predicted inter-brood interval (all other models ΔAICc > 2). This model suggested that inter-brood interval was shorter when first-brood offspring fledged later in the season (β = −0.01, z = −2.52, 95% CI −0.01 to −0.002; Fig. 2), when there were fewer first-brood fledglings (β = 0.05, z = 3.01, 95% CI 0.02–0.09; Fig. 2), and when females had higher lifetime recruitment (β = −0.02, z = −2.23, 95% CI −0.04 to −0.002; Fig. 2).

Influence of inter-brood interval on male feeding behaviour

In the subset of double-brooded pairs for which we sampled feeding rates by males during second broods (n = 14), inter-brood intervals ranged from 27 to 43 days (mean ± sd, 34 ± 5 days). Brood sizes ranged from one to five nestlings (mean ± sd, 3 ± 1). The start time of feeding rate data collection ranged from 8:03 AM to 12:09 PM (mean ± sd, 9:47 AM ±56 min). All observations (n = 26) of parental feeding occurred after the time that first-brood fledglings could forage independently, which means that there were no confirmed cases of definite brood overlap in this dataset (Fig. 3). However, 10 observations of second-brood parental feeding behaviour occurred during the period that parents could still have been feeding first-brood fledglings (before 36 days after hatching; Fig. 3). During second broods, feeding rates by males were 4.1 ± 2.8 sd deliveries/h and feeding rates by females were 6.3 ± 2.8 sd deliveries/h. Feeding rates by males were higher but more variable when nestlings were 6 days old than when they were 3 days old (feeding rates day-3: 3.1 ± 2.0 sd deliveries/h; feeding rates day-6: 5.1 ± 3.3 sd deliveries/h). There was one top model that best predicted feeding rates by males during second broods and this included linear and quadratic functions of inter-brood interval (inter-brood interval: β = −0.08, z = −2.70, 95% CI −0.14 to −0.02; (inter-brood interval)^2: β = −0.03, z = −3.29, 95% CI = −0.04 to −0.01; Tweedie family dispersion
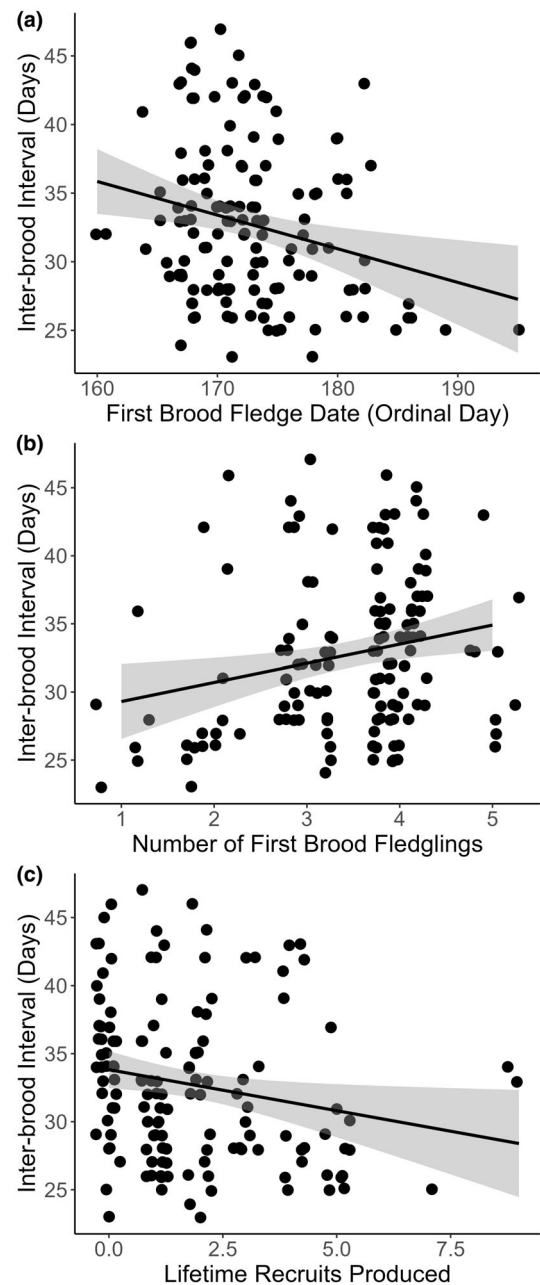

Figure 2. Factors influencing inter-brood intervals in monogamous, double-brooded Savannah Sparrows. Inter-brood intervals were shorter (a) when first broods fledged later in the season, (b) when the number of first-brood fledglings was lower and (c) when females had higher lifetime recruitment. Points are jittered along the x-axis (width = 0.3) and y-axis (height = 0.1). The grey band around the regression line represents the 95% confidence interval.

parameter = 0.80) and the mate's feeding rate per nest. There was an inverted U-shaped relationship between feeding rate per nest and inter-brood
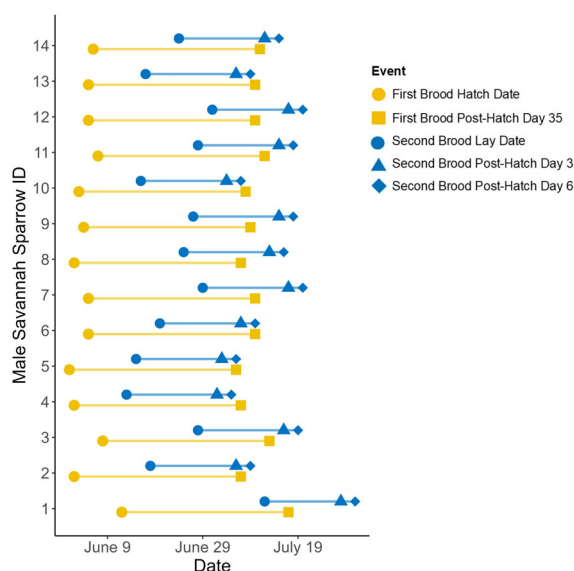
Figure 3. During second-brood parental feeding observations (3 and 6 days after hatching) in Savannah Sparrows, there were 10 cases of potential overlap between first- and second-brood parental care periods. Overall, six pairs experienced overlap between second brood post-hatch day-3 and the period between first-brood hatching and post-hatch day-35, and four of these pairs also experienced overlap between second brood post-hatch day 6 and the period between first-brood hatching and post-hatch day-35. Given that parents can continue to provide first-brood post-fledging care until post-hatch day-35, these cases represent potential overlap in brood care. There were no confirmed cases of definite overlap between second brood post-hatch day-3 or day-6 and the period between the hatching of the first brood and post-hatch day-24. During the period between hatching and post-hatch day-24, first-brood fledglings cannot yet forage independently.

interval, where males with intermediate inter-brood intervals had higher feeding rates during second broods than males with short or long inter-brood intervals (Fig. 4). There was also evidence that a male's feeding rate was positively related to the feeding rate of his mate ($\beta = 0.10$, $z = 2.94$, 95% CI = 0.03–0.17).

Influence of inter-brood interval on metrics of fitness

The global model for effects of inter-brood interval on metrics of fitness adequately fits our data (Fisher's $C = 26.19$, df = 30, $P = 0.67$; the proposed model does not significantly differ from the correlations in the data). There was no evidence that inter-brood interval affected apparent survival of females to the next season or the number of
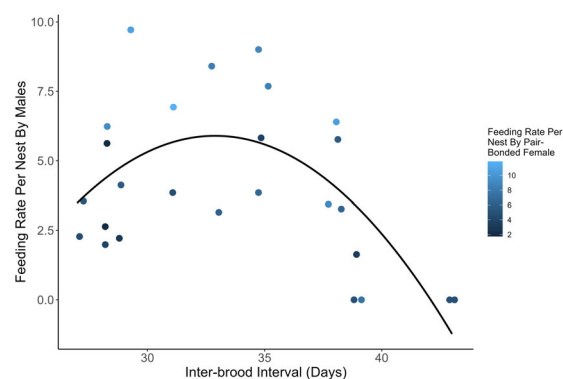

Figure 4. Feeding rate per nest by male Savannah Sparrows and their mates during the second brood plotted against their inter-brood intervals. During the second brood, males with intermediate inter-brood intervals had higher feeding rates than males with shorter and longer inter-brood intervals. Feeding rate was measured as the number of food deliveries brought to the nest per hour. The coloured points demonstrate that, within breeding pairs, male and female feeding rates were positively associated.

recruits produced from first broods (Fig. 5) and no evidence that the number of second-brood recruits was related to the number of second-brood fledglings (Fig. 5). After excluding paths for which we did not find evidence, the top model provided strong evidence that inter-brood interval affected second-brood lay dates, with long inter-brood intervals delaying second-brood lay dates (Fig. 5; $\beta = 0.69$; crit.value = 13.46, $P < 0.001$). There was also strong evidence that second broods laid later in the season had smaller clutch sizes (Fig. 5; $\beta = -0.57$, crit.value = -8.78, $P < 0.001$) and that second broods with smaller clutch sizes produced fewer fledglings (Fig. 5; $\beta = 0.49$, crit.value = 7.60, $P < 0.001$). Additionally, there was strong evidence that second broods laid later in the season produced fewer recruits (Fig. 5; $\beta = -0.27$, crit.value = -3.88, $P < 0.001$). Nests that hatched after 28 July did not produce recruits, whereas nests that produced two recruits (i.e. the maximum number of recruits produced per nest) were all hatched on or before 8 July. Calculating the total effects from the structural equation modelling, the model predicted that, for a 30-day difference in inter-brood interval, the number of second-brood fledglings would change by one and that, for a 30-day difference in inter-brood interval, the number of recruits produced would also change by one (Fig. 5).
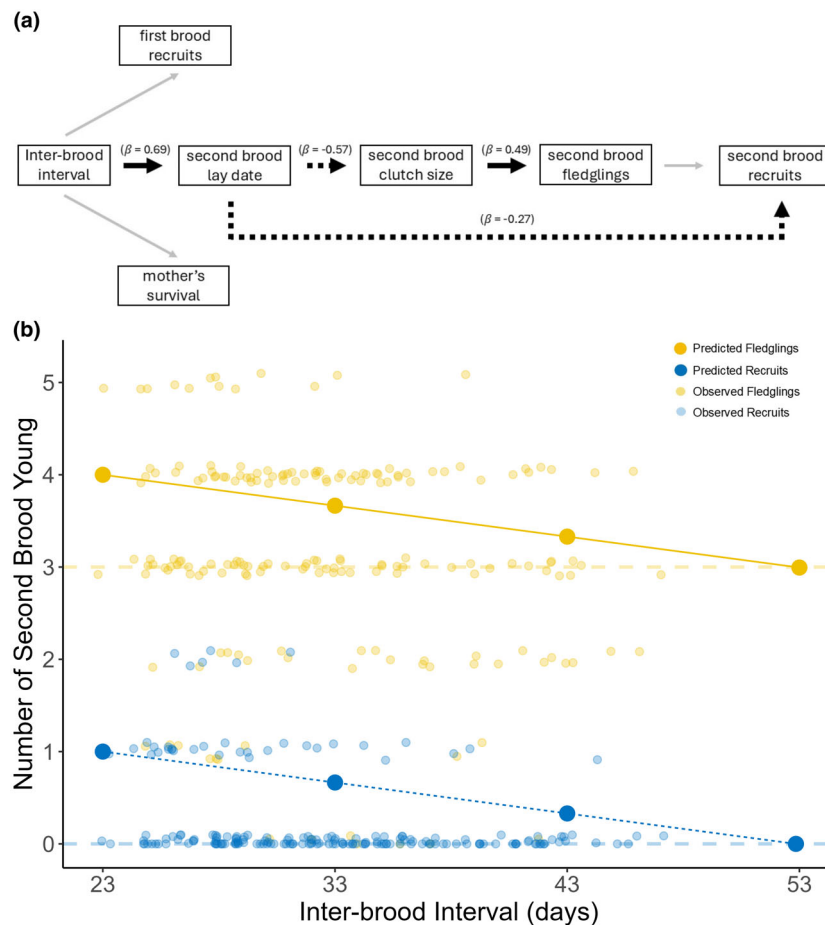
Figure 5. (a) Structural equation model (SEM) examining direct and indirect effects of inter-brood interval on metrics of female Savannah Sparrow reproductive success. Black arrows represent paths included in the top model. Grey arrows represent paths excluded from the top model. Solid lines show positive effects and dashed lines show negative effects. The values associated with each path correspond to standardized slope estimates from the sub-models. Line thickness indicates the level of statistical significance, with thicker lines representing stronger relationships. (b) Predicted (large points) and observed (small points) number of second-brood Savannah Sparrow young fledged (yellow) and recruited (blue) as a function of increases in inter-brood interval. Predicted numbers of second-brood offspring were determined by calculating total effects from the SEM. Starting values were chosen to be the average number of young produced by females with the shortest inter-brood intervals in our dataset (23 days). Subsequent changes in the variables (*y*-axis) are based on the total effect of inter-brood interval on each variable calculated from SEM (see Methods). The horizontal yellow line represents a decrease of one young fledged and the horizontal blue line represents a decrease of one young recruited.

DISCUSSION

Using 27 years of breeding data from wild Savannah Sparrows in eastern Canada, we found evidence that the inter-brood interval—the period between the hatching of first and second broods—tended to be shorter in females whose first-brood offspring fledged later in the breeding season, had a smaller number of offspring from the first-brood fledge and that produced a higher number of recruits within their lifetime. Additionally, our

study is the first to demonstrate the relationship between inter-brood interval and second-brood clutch size and recruitment: females with longer inter-brood intervals had delayed second-brood lay dates, and such females produced smaller second-brood clutches and fewer second-brood fledglings and recruits. Just as the timing of the first nest affects seasonal reproductive success (Verboven & Verhulst [1996], Siikamäki [1998], Woodworth *et al.* [2017a], Whitenack *et al.* [2024]), our results reveal that the timing of the second brood, which

was influenced by the length of the inter-brood interval, affected components of fitness. Many studies have demonstrated that females that double brood have higher seasonal reproductive output (Husby *et al.* 2009, Woodworth *et al.* 2017a) and lifetime reproductive output (Hoffmann *et al.* 2015, Zając *et al.* 2015, Zabala *et al.* 2020) including a recent demonstration of this relationship in our study population (Spina *et al.* 2025b). The results of our analysis of inter-brood interval suggest that such gains may not be equal across females and that variation between females can be influenced by how quickly females can initiate second broods.

The finding that female Savannah Sparrows with higher lifetime recruitment had shorter inter-brood intervals suggests a relationship between inter-brood interval and female quality, but the mechanism underlying this relationship remains to be determined. Females with high lifetime reproductive success (females that tend to live longer and double-brood more often in their lifetimes) probably have a superior ability to acquire resources (e.g. better foraging efficiency or nutrient retention) compared with females with lower lifetime reproductive success (van Noordwijk & de Jong 1986). In this case, high-quality females may also have sufficient resources to start a second brood soon after the first without incurring large costs later in life (van Noordwijk & de Jong 1986). Experiments providing females with supplemental food during the breeding season could test whether resource acquisition is the mechanism driving variation in inter-brood intervals.

We did not find evidence that males with shorter inter-brood intervals reduced their feeding rates of second broods because they were still feeding first-brood fledglings. Given that there were no cases of definite brood overlap in that part of our study (overlap between the second-brood nestling stage and the time when first-brood fledglings were still dependent on parental care), it is unlikely that reduced feeding rates by males with shorter inter-brood intervals were the result of males being preoccupied with feeding first-brood fledglings. Recognizing that the probability of recruitment in this population is positively related to nestling mass (Mitchell *et al.* 2012, Mueller *et al.* 2025a), and nestling growth is probably driven by resource quality rather than feeding rates (Senécal *et al.* 2021), one possibility is that high-quality resources were available for the early

second broods and that resource quality declined as the breeding season progressed. Tracking post-fledging provisioning in males while quantifying the quality of food items provisioned to young throughout the breeding season would help to determine whether males paired to double-brooded females feed second-brood offspring less frequently because they were still provisioning first-brood fledglings or because high-quality food remains available.

Although unexpected, our finding that males with longer inter-brood intervals had lower feeding rates during the second brood could also occur because of reduced food availability near the end of the breeding season. Given that inter-brood intervals affected second-brood lay dates, the males with the longest inter-brood intervals were also the males with the latest second broods ($r = 0.65$, df = 184, $t = 11.56$, $P < 0.001$). If food availability declines as the season progresses, males with longer inter-brood intervals could be expected to reduce their feeding rates simply because it takes them longer to locate provisioning items later in the season.

Our finding that males with longer inter-brood intervals had lower feeding rates during the second brood could also occur if males trade-off time devoted to parental care with initiating moult (Møller 1991). At the end of the breeding season, adult Savannah Sparrows initiate a complete definitive prebasic moult (Wheelwright & Rising 2020). Some double-brooding passerines are known to delay migration when breeding late into the season (Imlay *et al.* 2021), suggesting that trade-offs between self-maintenance and reproduction may occur in late-breeding individuals. In this population, adults have been noted to lose contour feathers by the time their second-brood offspring fledge (Wheelwright & Rising 2020). Hence, it is possible that parents could invest less in second broods produced later in the season if they have already begun moulting. Moreover, males with long inter-brood intervals could trade off parental care with preparing for migration because of decreasing brood value in late-hatched second-brood offspring (Trivers 1972). Our results provided evidence that second broods laid later in the season had a reduced probability of recruitment. If males recognize the lower potential value of late second broods (e.g. through honest signals like reduced mass; Mitchell *et al.* 2011), they may choose to reduce their feeding rates (Hainstock

et al. 2010). Males trading-off parental care to initiate moult may be unlikely, given that males depart for migration after females (Mitchell *et al.* 2012), but future studies could examine the possibility relatively easily by tracking and observing whether any males initiate moult before the fledging of their second brood, and whether this influences nestling feeding rates.

It is unlikely that sensitivity to camera placement affected the above results. We observed parents returning to normal feeding behaviour within minutes of deploying the cameras (S.L.D., H.A.S., D.R.N., pers. obs.). Additionally, given that in most cases cameras could not be seen by the birds until they approached the nest, we would probably have recorded birds approaching and leaving the nest vicinity without visiting nestlings if they had been alarmed by the camera. Males with feeding rates of zero were never recorded on camera approaching the nest during the nest watch.

Understanding factors that influence variation in inter-brood interval could be relevant for understanding how reproductive success in this population is affected by a warming climate. In this population, females that experienced higher pre-breeding temperatures had earlier lay dates (Burant *et al.* 2022) and females that initiated their first broods earlier were more likely to double-brood (Woodworth *et al.* 2017a). Among females that did have a second brood, those that initiated their second brood earlier were more likely to have second-brood offspring that recruited into the population as adults in this study. Hence, the combined results of Burant *et al.* (2022), Woodworth *et al.* (2017a) and the current study suggest that if Kent Island experiences higher spring temperatures, recruitment rates will increase. However, other studies have shown that climate warming can reduce fecundity in double-brooded populations if earlier springs result in a shorter period when food is abundant (Visser *et al.* 2003). Although sea surface temperatures in the Gulf of Maine have been increasing over the past four decades (Pershing *et al.* 2015, Townsend *et al.* 2023), there has been no long-term increase in pre-breeding temperatures, so no corresponding advancement of lay date over time in Savannah Sparrows on Kent Island. How spring temperatures impact breeding season conditions and food availability in this population are questions of interest for future studies.

Overall, our results demonstrate that variation in inter-brood intervals is influenced by the first-brood fledge date, the number of first-brood fledglings and female quality (measured as the number of recruits produced within a female's lifetime), and suggest that high-quality females can rear two broods in quick succession while maximizing their reproductive output. There was a benefit to short inter-brood intervals, with females that had less time between broods being able to initiate their second broods earlier in the season and increase the probability of second-brood recruitment. Importantly, because inter-brood intervals can have consequences for recruitment of young from second broods, further exploration of extrinsic factors like climate change, which have the potential to impact inter-brood intervals, could be important for predicting how future environmental change will influence reproductive success in double-brooded songbirds. This study demonstrates that the timing of second-brood initiation is a key factor influencing the survival of second-brood offspring. Females capable of rearing two broods in quick succession maximize the likelihood of second-brood recruitment without incurring net costs to their own survival or that of their first-brood offspring.

AUTHOR CONTRIBUTIONS

Hayley A. Spina: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; writing – review and editing; formal analysis; data curation; visualization. **Amy E. M. Newman:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; methodology; resources. **Nathaniel T. Wheelwright:** Writing – review and editing; data curation; investigation. **Daniel J. Mennill:** Investigation; funding acquisition; writing – review and editing; data curation; supervision; resources. **Stéphanie M. Doucet:** Investigation; funding acquisition; writing – review and editing; supervision; data curation; resources. **Joseph B. Burant:** Investigation; writing – review and editing; data curation. **Sarah L. Dobney:** Investigation; writing – review and editing; data curation. **Sarah D. Mueller:** Investigation; writing – review and editing; data curation. **Greg W. Mitchell:** Investigation; writing – review and editing; data curation. **D. Ryan Norris:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; methodology; project administration; data curation; supervision; resources.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

ETHICAL NOTE

None.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Adult Savannah Sparrow on Kent Island, New Brunswick. Photograph by Hayley A. Spina.

Figure S2. A Savannah Sparrow's nest on Kent Island, New Brunswick. Photograph by Hayley A. Spina.

Figure S3. Nestling Savannah Sparrows over the first 6 days post-hatching. Photographs by Hayley A. Spina.

Video S1. Savannah Sparrow parents provisioning nestlings on Kent Island, New Brunswick. Video by Sarah L. Dobney.