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Proficient incubation by inexperienced Savannah Sparrows *Passerculus sandwichensis*

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We compared the incubation behaviour of 1-year-old female Savannah Sparrows *Passerculus sandwichensis* nesting for the first time with that of older females that had nested in previous years on Kent Island, New Brunswick, Canada. Using temperature probes inserted into 32 nests, we determined the length and variability of incubation shifts and recesses over 99 nest-days. At 14 of the nests, known-age females were matched, each pair consisting of an inexperienced yearling and an experienced older female, and nest temperatures were measured simultaneously. In addition, we quantified the duration of night-time incubation and the mean length and variation of more than 1350 incubation shifts and recesses as a function of female age, weather, time of day and date. In all respects, yearling and older females had equivalent incubation behaviour. The similarity between yearlings and older females suggests that fundamental aspects of incubation behaviour may be largely innate and unaffected by prior reproductive experience or other age-related variables.

Certain types of behaviour in birds are presumed to be too complex to be innate or 'hard-wired'. Instead, their mastery is thought to require time and experience. For example, the ability to forage efficiently or migrate accurately improves with age in numerous bird species (Perdeck 1967, Orians 1969, MacLean 1986, Able & Able 1996). A more dramatic example is reproduction, which involves so many complex behaviours, including foraging and migration, that older, experienced birds generally outperform younger, inexperienced birds (Stutchbury & Robertson 1987, Smith *et al.* 1989, Wheelwright & Schultz 1994, Daunt *et al.* 1999).

An important component of reproductive behaviour in birds is incubation. Unlike behaviours such as foraging or predator-avoidance, incubation cannot be taught by parents or other birds. Proficient incubation requires regulating egg temperatures within a relatively narrow range. The amount of time birds spend on the nest during the incubation period reflects a trade-off between the needs of the developing embryos and the needs of adult birds (Skutch 1962, White & Kinney 1974, Webb & King 1983, Drent *et al.* 1985, Smith & Montgomerie 1992). If an incubating bird leaves its eggs unattended for too long, the embryos may die from exposure to low temperatures or the clutch may be taken by predators, the incubation period may be prolonged, and the risk of brood parasitism or predation may increase (Kendeigh 1940, Webb 1987, Martin 1999). On the other hand, an incubating bird requires time off the nest in order to satisfy its own energetic and social demands. Birds breeding for the first time have not had an opportunity to learn how to co-ordinate their incubation recesses effectively. Moreover, their inexperience foraging or their lower social status may require them to spend longer off the nest. Consequently, one might predict that birds would become more proficient at incubation with age and experience. For species in which only one sex incubates and incubating birds are not fed on the nest by their mates, differences between yearlings and older females should be even greater because the lack of experience of first-time breeders would not be compensated for by assistance from an experienced mate. Inefficient incubation by birds breeding for the first time could partly explain why reproductive success tends to increase with age in birds (Daunt *et al.* 1999).

We addressed this question in a study of a population of Savannah Sparrows *Passerculus sandwichensis* of known age and reproductive history. By placing temperature probes in 32 nests, including the nests of seven matched pairs of females (each pair consisting of a yearling that had never nested before and an older female with previous breeding experience)

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where temperatures were measured simultaneously, we compared the length and variation of incubation shifts and recesses, and the duration of night-time incubation, between females of different age. In addition, we investigated the effect on incubation behaviour of environmental variables such as weather, time of day and season. We hypothesized that 1-year-old Savannah Sparrows would be less effective at incubation than older birds because of their inexperience at breeding. Moreover, young birds may withhold reproductive effort (Reid 1988), have inferior foraging skills or have less access to food (MacLean 1986, Moreno 1989), additional factors that would make them less effective at incubation. In particular, we predicted that yearling females would have shorter night-time incubation periods, shorter incubation shifts, longer incubation recesses and lower nest temperatures during their absences than older females. We also expected that younger birds would have more variable incubation shift and recess lengths than older birds. Finally, if yearlings proved to be less effective at incubation, we predicted that their incubation periods would be prolonged and their hatching success reduced compared with that of older females.

STUDY AREA AND METHODS

Our study site was the Bowdoin Scientific Station on Kent Island, New Brunswick, Canada (44°35′N, 66°45′W). Cooled by the Labrador Current, Kent Island has a mean temperature of only 11.1 °C during June, the first and main month of the Savannah Sparrow breeding season. On average, there are 13.5 foggy days and 3.8 cm of precipitation in June (based on 52 years of weather data). The two years of this study (1997 and 1998) were warmer than the 52-year average for Kent Island (1997: 12.3 °C; 1998: 11.4 °C), although not very different from the average for the last 10 years (11.9 °C). There were 11 foggy days in 1997 and 17 in 1998; precipitation was 2.1 cm in 1997 and 7.9 cm in 1998. The cold, foggy environment of the Bay of Fundy may exacerbate age-related differences in incubation behaviour and their impacts on reproductive success by elevating foraging costs for incubating females (Williams 1987) and increasing the vulnerability of unattended eggs (Webb 1987).

Savannah Sparrows breed at high densities on the isolated, 80-ha island. The birds start to arrive from southerly wintering grounds in late April or early May. By late May, females begin to build cryptic grass-covered cup nests on the ground in open habitats. Yearlings and older females build nests of similar size, although there is a tendency for yearling nests to be slightly smaller (Wheelwright & Schultz 1994). If the first brood successfully fledges, most females lay a second clutch several weeks later. Males do not incubate or provide food to the incubating female. Brown-headed Cowbirds *Molothrus ater*, which sometimes parasitize the broods of Savannah Sparrows on the mainland, do not occur on Kent Island during the breeding season (Wheelwright & Rising 1993).

All adults in the study area were uniquely ringed with a random combination of three plastic colour bands and a Canadian Wildlife Service aluminium band. Because of high rates of natal (12%) and breeding (45%) philopatry, most adults in the breeding population had been banded as nestlings or juveniles and their exact ages and reproductive histories were known (Wheelwright & Mauck 1998), which enabled us to avoid the problem of confounding age and reproductive experience. Most birds retain approximately the same territory throughout their lives and first breed at 1 year of age. As a result, the territories of yearlings and older birds are interspersed, with no age-related differences in size and no apparent differences in quality (N.T. Wheelwright *et al.* unpubl. data). In this regard they differ from species such as the Northern Wheatear *Oenanthe oenanthe* (Part 2001).

Quantifying incubation behaviour

We quantified incubation behaviour by measuring nest temperatures, which indicated the presence or absence of incubating females. Remote temperature sensors (Hobo Temp XT, Onset Computer Co., Pocasset, MA, USA) recorded temperatures inside the nest every 30 s for 2–4 days per nest. Temperature probes were inserted through the side of the nest lining so that their tips protruded *c.* 1 cm into the nest cup. Probes were anchored to the ground outside the nest so that they could not be pulled out or moved by activity in the nest; the 5 × 5-cm dataloggers were hidden in the grass 1–2 m from the nest. Because the position of temperature probes differed slightly between nests and did not necessarily touch the eggs or the incubating female's brood patch, we did not attempt to determine incubation temperatures *per se*. However, when females were absent, the temperature probes provided an accurate measure of nest temperatures.

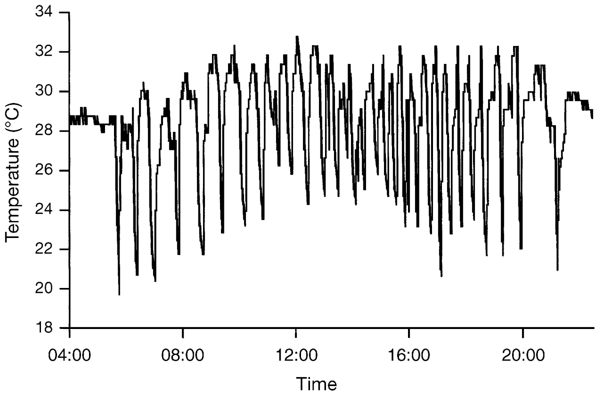

Figure 1. Temperature of a representative Savannah Sparrow nest during the incubation period, measured from before sunrise until after sunset on 16 July 1997. Steep and sustained drops in temperature indicated departures of the incubating female (and the initiation of incubation recesses); steep and sustained rises in temperature indicated returns of the incubating female (and the initiation of incubation shifts).

Whenever an incubating female left the nest, the nest temperature dropped abruptly; upon her return, it immediately rose sharply (Fig. 1). To verify that temperature fluctuations indicated the presence or absence of the incubating female (vs. merely shifts in her position on the nest), we observed four nests for 1–2 h each at various times of day. Departures and arrivals by the female coincided with distinctly steep, unidirectional and continuous changes in nest temperature. On the basis of these observations, we interpreted any drop in temperature of more than 2 °C that occurred within a 1-min period and that continued for at least 2 min as indicating a departure from the nest (and the end of an incubation shift and beginning of an incubation recess; see Zerba & Morton 1983). Any similar rise in temperature signified an arrival at the nest (and the beginning of an incubation shift and end of an incubation recess). The terms 'incubation shifts' and 'recesses' correspond to 'attentive' and 'inattentive' periods of Davis *et al.* (1984). Questionable events were eliminated from our analyses, which is why sample sizes of incubation shifts and recesses are not always equal. The duration of night-time incubation was the time between returning to the nest for the last time in the evening and leaving the nest for the first time in the morning. Females never left the nest in the middle of the night.

Temperature measurements were taken between 4 June and 24 July at 26 nests in 1997 and at six nests in 1998 on a total of 99 nest-days. For eight females we measured more than one nest during the same year (some females are double-brooded) or in different years. The total sample included 13 yearlings and 11 older females; older females ranged in age from 2 to 5 years (mean ± sd = 3.0 ± 1.1 years). For a subset of 14 nests, temperatures were recorded simultaneously at two nests in the same area, one the nest of a yearling known to be nesting for the first time, the other the nest of a female that had bred in one or more previous years on Kent Island. On average, older females in the matched pair sample were 2.8 ± 1.1 years old and had already produced 3.3 ± 2.3 nests each (range: 1–7). The subset of matched pairs allowed us to compare incubation behaviour of yearlings and older females while controlling for date, weather conditions, habitat and other factors.

Most nests were found within the first few days of the 10.7-day incubation period, and there was no difference in the stage of incubation at the time of observation between focal nests of yearlings and older females (as estimated by the number of days from the first day of observation until eggs hatched: mean ± sd 8.6 ± 3.5 vs. 7.2 ± 3.1 days, respectively; paired $t = 0.40$, $df = 5$, $P = 0.70$ (note that eggs failed to hatch in some nests due to predation after incubation was measured)). The mean clutch sizes of focal yearlings and older females were also similar (mean ± sd 4.1 ± 0.7 vs. 4.4 ± 0.5 eggs, respectively; paired $t = -1.55$, $df = 6$, $P = 0.17$). Yearlings and older females in the entire sample and in the matched pair subset were similar in all measures of body size (mass, wing length, tarsus length, bill length, bill depth; unpaired and paired *t*-tests: $P > 0.20$).

The timing of nest departures and arrivals (and therefore the lengths of incubation shifts and absences) were determined to within 30 s. Mean lengths of incubation shifts and absences were calculated for each of six daily time periods (05:00–07:00 h, 07:00–10:00 h, 10:00–13:00 h, 13:00–16:00 h, 16:00–19:00 h and 19:00–21:00 h). As an index of variability in incubation behaviour, we calculated coefficients of variation (sd/mean) of the lengths of incubation shifts and recesses and of minimum nest temperatures. If yearlings nesting for the first time had difficulty maintaining a regular incubation schedule, we predicted that they would show greater coefficients of variation for each of these variables, even if the mean lengths of incubation shifts and recesses did not differ. The proportion of time spent on the nest ('nest attentiveness' or 'incubation constancy': Skutch 1962, Yerkes 1998) was calculated for each time period and day. Weather variables (ambient temperature,

Table 1. Incubation behaviour of yearling vs. older female Savannah Sparrows. Data are presented as means (± 1 sd) of the within-nest means for each of the variables below for seven nests of yearlings and seven nests of older females based on observations over 30 nest-days and measurements of 938 incubation shifts (454 for yearlings and 484 for older females) and 941 incubation recesses (452 for yearlings and 489 for older females). Nests were matched (one yearling with one older female) and observed simultaneously. Only one nest was observed per female. For this analysis, we excluded incubation shifts and recesses occurring earlier than 07:00 h or later than 19:00 h. CV = coefficient of variation. *P*-values are based on paired *t*-tests.

	Yearlings	Older females	Difference (se)	*t*	*P*
Incubation shift length (min)	12.6 (2.0)	13.6 (3.5)	–1.0 (1.7)	–0.56	0.60
Incubation recess length (min)	9.2 (2.6)	8.3 (2.2)	0.9 (0.6)	1.43	0.20
Minimum temperature (°C)	23.7 (2.4)	24.7 (3.5)	–1.0 (1.5)	–0.69	0.52
Incubation shift CV	47.1 (17.2)	47.6 (12.4)	–0.5 (3.6)	–0.14	0.89
Incubation recess CV	31.9 (14.9)	32.0 (9.1)	–0.1 (3.3)	–0.03	0.98
Minimum temperature CV	12.3 (3.8)	10.4 (3.9)	1.9 (1.5)	1.24	0.26

Table 2. Incubation period lengths and hatching success of the nests of yearling vs. older female Savannah Sparrows. Exact incubation periods (assuming incubation began after the penultimate egg was laid) were determined for 39 nests that had been discovered while the clutch was still incomplete between 1987 and 2003 (i.e. not focal nests in which incubation temperatures were measured). The time between discovery and hatching was determined for 1179 other nests whose precise date of initiation was unknown, and used as a relative index of incubation period length for yearlings and older females (assuming the nests of both age classes were discovered at similar stages). Hatching success = (number of eggs that hatched)/(number of eggs laid). Data are presented as means (± 1 sd, *n*). *P*-values are based on unpaired *t*-tests.

	Yearlings	Older females	Difference (se)	*t*	*P*
Incubation period (days)	10.9 (0.9, 21)	10.6 (1.0, 18)	0.3 (0.3)	0.95	0.35
Time between nest discovery and hatching (days)	6.1 (5.4, 589)	6.1 (5.4, 590)	0.05 (0.4)	0.12	0.91
Hatching success (proportion of eggs hatched)	0.96 (0.12, 589)	0.96 (0.11, 590)	0.06 (0.2)	0.38	0.66

solar radiation, precipitation) were recorded instantaneously at 08:00 and 20:00 h daily, and at 10-s intervals around the clock using a Campbell Scientific CR10 datalogger.

Statview (Abacus Concepts 1999) and JMP software (SAS 1997) were used for statistical analyses. Because sample sizes (incubation shifts and recesses, nest temperatures) varied between nests, we calculated means for each variable for each nest and compared yearlings and older females by using *t*-tests. For the subset of matched pairs, we used paired *t*-tests. Because the small sample sizes of some of our analyses raises the issue of power in detecting differences, we calculated standard errors (se) of the differences between the means of yearlings and older females (Tables 1 & 2). Standard errors can be used to determine 95% confidence intervals (= difference between means ± 2.45 se), which in turn allows the calculation of statistical power (see Barker Bausell & Li 2002). We also performed two-way ANOVAs on the original data, using nest and age class as factors, and performed mixed-model ANCOVAs for multivariate analysis on the entire dataset. Except where noted elsewhere, we restricted our analyses to the 07:00–19:00 h data to avoid the extreme and variable incubation shifts and recesses that occur around sunrise and sunset. The total number of unambiguous incubation shifts and recesses measured during these periods were 1386 and 1354, respectively. The mean number of incubation shifts measured per nest was 69.3 (± 41.5); the mean number of incubation recesses measured per nest was 67.9 (± 42.4).

RESULTS

Yearlings vs. older females

The yearling Savannah Sparrows in our sample had had no more than a few days experience incubating eggs prior to our observations. Nevertheless, their incubation behaviour was indistinguishable from that of older, experienced females in almost all respects, both in the entire sample and in the subset of matched pairs (Table 1). Most females began night-time incubation 1–1.5 h before sunset, after which they remained on the nest all night (Fig. 2a). However, there was substantial variation among individuals, many of whom did not enter the nest

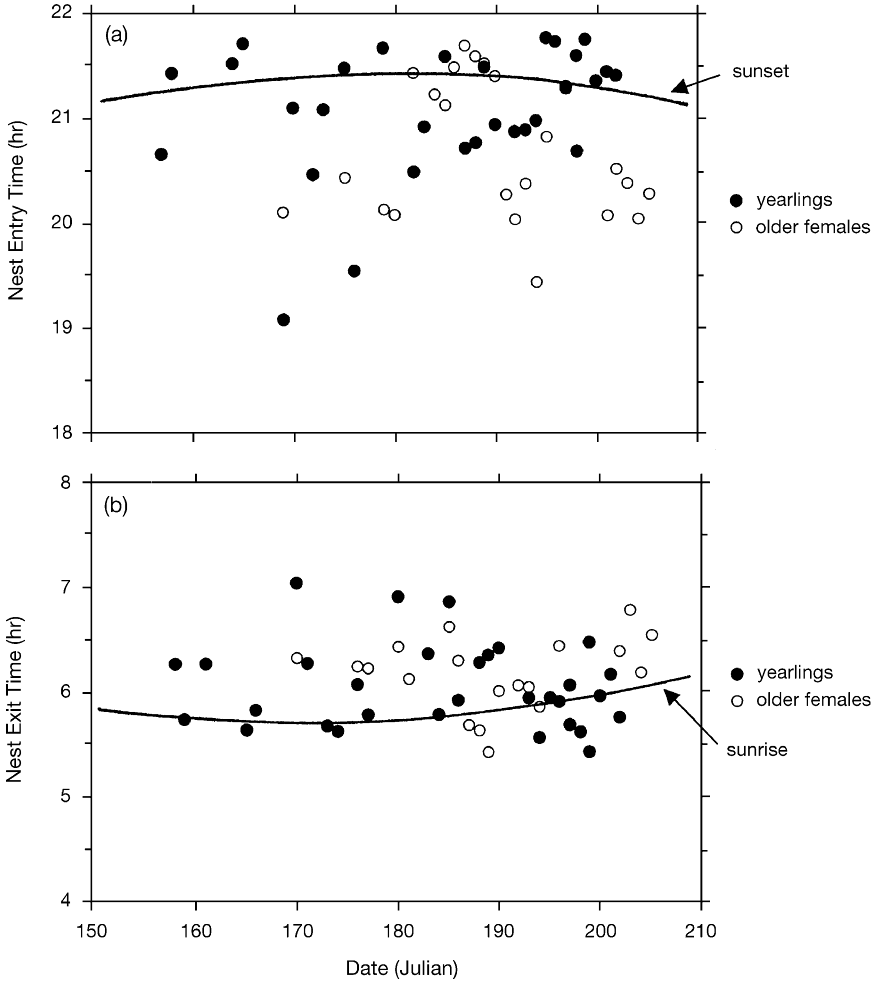

Figure 2. Timing of (a) initiation of night-time incubation (nest entry time) and (b) earliest nest departure in the morning (nest exit time) for yearling (solid circles) and older female Savannah Sparrows (open circles) as a function of Julian date. Julian date 160 corresponds to 9 June. Solid lines depict the time of (a) sunset and (b) sunrise.

until after sunset. In the morning females generally did not leave the nest for the first time until about 0.5 h after sunrise (Fig. 2b). For 13 yearlings and nine older females measured on 53 nest-nights, we determined the mean time at which females entered the nest at night, the time they left the nest in the morning and the total time they spent on the nest during the night. Controlling for date, female age had no significant effect on nest entry time at night, nest departure time in the morning or total time spent on the nest during the night (ANOVAs: $F_1 = 0.86$, $P = 0.37$; $F_1 = 1.41$, $P = 0.25$; $F_1 = 0.06$, $P = 0.81$, respectively). Within the subset of matched pairs there were also no significant differences between yearlings and older females in nocturnal incubation behaviour (paired *t*-tests: $df = 6$, $P > 0.86$).

The mean length of incubation shifts during the day did not differ significantly between yearlings and older females (Table 1; Fig. 3a). We ran mixed-model ANCOVAs on the entire sample of 32 nests, while controlling for date and time of day, to test whether yearlings and older females differed in aspects of incubation behaviour (SAS 1997). Julian date was included as a covariate and the categorical variables 'time of day' and 'female age class' were modelled as fixed effects. To control for variation among individuals the models were made conditional on female identity, with female identification modelled as a random effect. As no interaction terms proved to be significant, they were dropped from the final models. Although there were significant effects on incubation of date, time of day and individual

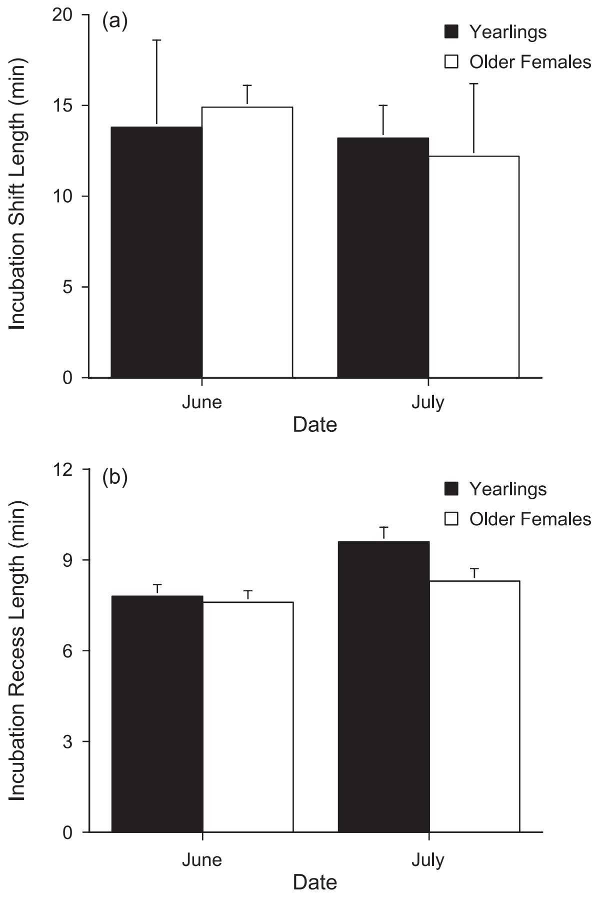

Figure 3. Mean ± sd length of (a) incubation shifts and (b) incubation recesses (min) for yearling (solid bars) and older female Savannah Sparrows (grey bars) in June and July, based on measurements of 1386 incubation shifts and 1354 incubation recesses. The mean length of incubation shifts and recesses did not differ significantly between yearlings and older females (mixed-model ANCOVAs: $P > 0.13$).

(see below), the length of incubation shifts was independent of age class (ANCOVA: $F_1 = 2.36$, $P = 0.13$; difference between means (se) = 0.07 (0.05)). Similarly, the coefficient of variation of incubation shift length was independent of age class ($F_1 = 0.46$, $P = 0.50$; difference between means (se) = 0.13 (0.11)).

As with incubation shift length, there was no difference between yearlings and older females in the length of incubation recesses during the day (ANCOVA: $F_1 = 2.23$, $P = 0.14$; difference between means (se) = 0.20 (0.13)). Nor were yearlings more variable than older females in the lengths of their incubation recesses (as measured by coefficients of variation) ($F_1 = 0.16$, $P = 0.69$; difference between means (se) = –0.02 (0.03)). Results from the subset of matched pairs were similar: there were no differences in incubation shift or recess length or variability (paired *t*-tests: $P > 0.20$; Table 1).

Yearlings did not differ significantly from older females in terms of the average minimum temperature of their nest during their absences or the variability in minimum nest temperature (ANCOVA: $F_1 = 1.33$, $P = 0.25$; difference between means (se) = 0.13 (0.11); Table 1). Rarely did minimum nest temperatures drop below 20 °C. Because our probes were inserted into the nest but not within eggs (Davis *et al.* 1984), the minimum nest temperatures that we recorded were probably several degrees lower than the temperatures actually experienced by embryos because eggs cool more slowly than the surrounding air during incubation recesses. Nonetheless, because minimum nest temperatures rose during the course of the day (Fig. 1; see also Zerba & Morton 1983), our data do not suggest that females timed their incubation recesses so that the temperatures of their eggs fell only to a certain critical temperature.

Effect of date, weather, time of day and previous incubation shift

As the breeding season progressed, night-time incubation began slightly later on average, morning departures from the nest occurred earlier and the duration of night-time incubation decreased (Fig. 2). Results from the mixed-model ANCOVAs indicated that date had a significant effect on several aspects of incubation behaviour, independent of female age. As the breeding season progressed and daily temperatures rose, the mean length of incubation shifts during the day decreased, the mean length of incubation recesses increased and minimum nest temperatures during recesses increased (all $P < 0.05$; Fig. 3). Between 07:00 and 19:00 h, attentiveness (proportion of time spent on the nest) averaged 64.3% early in the season and 59.7% late in the season. For six double-brooded females, we measured incubation behaviour at their first and second nests. The mean length of incubation shifts (averaged within nests) was significantly shorter in second-clutch nests (paired $t = 3.83$, $df = 5$, $P = 0.01$). Among our limited sample of double-brooded females, seasonal differences in mean incubation recess length were not significant (paired $t = 0.06$, $df = 5$, $P = 0.95$).

Although the mean lengths of both incubation shifts and incubation recesses were longer under more favourable weather conditions, differences were not significant after controlling for female age class and

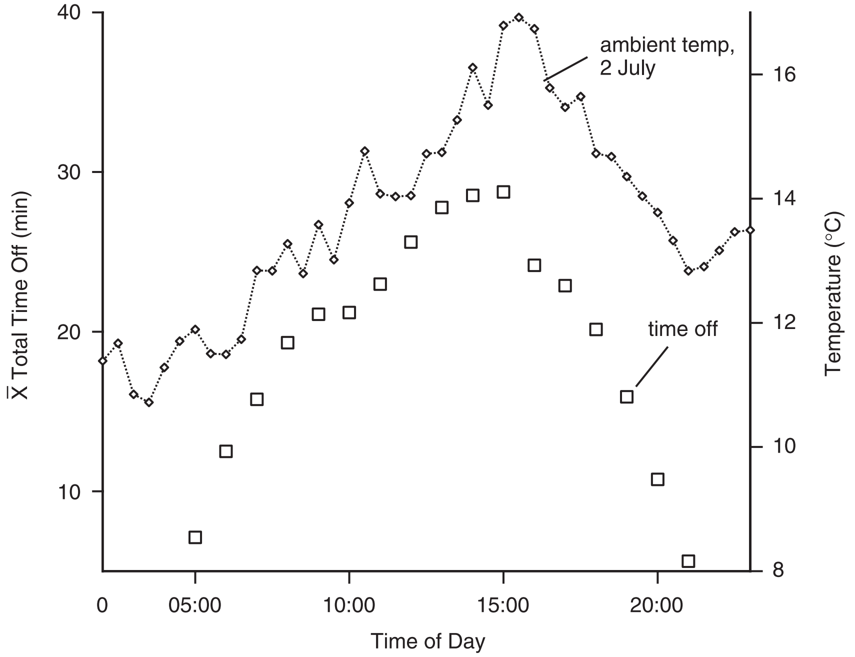

Figure 4. Mean ambient temperature (°C) on Kent Island on a typical sunny day during the breeding season (dotted line), and mean total time (min) off the nest per hour for all females (open squares) as a function of time of day.

identification (ANCOVA: $F_1 = 0.19$, $P = 0.66$; $F_1 = 3.66$, $P = 0.057$, respectively). Yearlings and older females did not differ in their reaction to inclement weather; none of the interactions between age and ambient temperature, solar radiation or rain was significant ($P > 0.05$). During the middle of the day, incubation shifts were on average shorter and incubation recesses longer ($F_5 = 44.00$, $P < 0.001$; $F_5 = 7.70$, $P < 0.001$, respectively). As a result, the total time off the nest per hour tended to be highest in the early afternoon, when ambient temperatures peaked (Fig. 4). However, there was no significant difference between the mean incubation shift lengths of yearlings and older females with respect to time of day (all interactions between female age class and time of day: $P > 0.30$).

One might expect that incubating females should have to spend more time on the nest to rewarm their eggs immediately after prolonged absences from the nest. Moreover, females should be able to spend more time on the nest after having had longer to forage (Davis *et al.* 1984, Biebach 1986, Conway & Martin 2000). However, we found no correlation between the length of a female's incubation shift and the length of either the recess that followed or the recess that preceded the incubation shift (linear regressions: $P > 0.05$).

Incubation and reproductive success

Given the fact that yearling and older Savannah Sparrows did not differ significantly in any aspect of their incubation behaviour that we measured, one would not necessarily expect differences in the length of their incubation periods or hatching success. We were able to determine the incubation period for 39 nests that were discovered before the clutch was complete. The clutches, laid by 21 yearlings and 18 older females, did not differ in size or hatching date (*t*-tests: $P > 0.20$). Assuming that incubation by both age classes effectively begins after the penultimate egg is laid, there was no difference in the length of the incubation period between yearlings and older females (Table 2). Taking advantage of a much larger sample of nests that were not discovered until incubation was already underway (and assuming that the nests of yearlings and older females are on average found at the same stage of incubation), we found no difference between yearlings and older females in the time between discovery of the nest and hatching (Table 2), which provided additional evidence that incubation periods do not differ between age classes. Hatching success (number of eggs that hatched per egg laid for nests in which at least one egg hatched) was virtually identical for yearlings and older females (Table 2).

DISCUSSION

Both theory and the limited empirical evidence that exists on age-related incubation behaviour suggest that birds should become more proficient at various aspects of reproduction as they age. Not only have older females gained experience timing incubation shifts and recesses, they are likely to be more efficient at foraging or have better access to food because of increasing social dominance, and possibly to invest more in reproduction with age (Stutchbury & Robertson 1987, Reid 1988, Daunt *et al.* 1999). Yet we found that yearling and older Savannah Sparrows had very similar incubation behaviour, despite the fact that none of the yearlings had had experience breeding and all of the older females had nested in previous years. We found no significant differences between age classes in the mean length of incubation shifts or recesses, in variation in the length of incubation shifts or recesses, in minimum nest temperature or variation in minimum nest temperature during incubation recesses, or in the duration of night-time incubation. It should be noted, however, that the relatively small sample size of the subset of matched pairs, and the relatively large standard errors of the estimated differences in incubation behaviour (Table 1), reduced the power of that analysis; to have found significant differences between age groups using *t*-tests, there would have had to have been marked differences between yearlings and older females in each aspect of incubation behaviour. Moreover, the direction of differences between age groups tended to be in the direction predicted, although the differences themselves were not significant. Using the entire dataset and applying mixed-model ANCOVAs, standard errors were much smaller, which increased our confidence that any differences in incubation behaviour between age groups were small or non-existent (see also Table 2).

If experience (as opposed to age *per se*) were critical in incubation behaviour, one might expect that, as the season progressed, individual birds would become more proficient at incubation. In particular, their incubation shifts should become longer and less variable, and their incubation recesses shorter and less variable. We found instead that variability in the lengths of incubation shifts and recesses did not change seasonally within individuals, and that incubation shifts were shorter and incubation recesses were longer later in the breeding season for both yearlings and older females, in parallel with rising ambient temperatures. Our results suggest that environmental conditions are more important than age or experience in explaining variation in incubation behaviour.

The demonstration that environmental conditions influence incubation behaviour in Savannah Sparrows is consistent with previous studies. Nest attentiveness tends to decrease during favourable weather (Kendeigh 1963, Haftorn 1978, 1981, 1988, see Davis *et al.* 1984) and at mid-day (Weeden 1966, Haftorn 1978, Morton & Pereyra 1985, Weathers & Sullivan 1989). When food is abundant, Common Quail *Coturnix coturnix* are more attentive and less variable in incubating, and their incubation period is shortened (Rodríguez-Teijeiro *et al.* 1997). Davis *et al.* (1984) demonstrated that Belding's Savannah Sparrows *P. sandwichensis beldingi* increased nest attentiveness (proportion of time on the nest) when eggs were experimentally cooled, and decreased attentiveness when eggs were warmed. Changes in incubation behaviour with experimental manipulations included both incubation shift and recess length. In other studies, however, the length of incubation recesses appears to be more flexible than the length of incubation shifts. For example, Rauter and Reyer (1997) found that female Water Pipits *Anthus spinoletta* were more likely to respond to inclement weather by shortening their incubation recesses than by changing the length of incubation shifts. Similarly, Northern Wheatears that were provisioned with additional food decreased the length of incubation recesses but did not increase the length of incubation shifts (Moreno 1989; see also Drent *et al.* 1985, Nilsson & Smith 1988).

Conceivably, age-related differences in incubation behaviour may only be revealed during environmentally stressful years. For example, when food is scarce young Great Skuas *Catharacta skua*, which are not as experienced as older birds in finding food, suffer a greater decline in breeding success (Hamer & Furness 1991). Arguing against this, however, is our unexpected finding that yearling and older female Savannah Sparrows responded equivalently to inclement weather.

There are few detailed studies of the incubation behaviour of birds of known age with which to compare our results. Two of them deal with waterfowl. Yerkes (1998) showed that older Redheads *Aythya americana* spent a greater proportion of the day on the nest than yearling females, and Aldrich and Raveling (1983) found that, in captivity, older, more experienced female Canada Geese *Branta canadensis* were more attentive than females nesting for the first time. Redheads and Canada Geese might not be representative of other bird species because body condition plays such a critical role in incubation behaviour and is known to improve with age in waterfowl (Aldrich & Raveling 1983, Yerkes 1998). Even in songbirds, however, at least some components of incubation are influenced by food availability (Moreno 1989; see also Smith *et al*. 1989, Rauter & Reyer 1997). One would expect to see age-related differences in incubation behaviour in species in which older females are clearly more efficient at foraging than yearlings. No evidence of age-related changes in foraging skills has been found in Savannah Sparrows once they become independent (Wheelwright & Templeton 2003).

The similarity between yearlings and older females suggests that, in Savannah Sparrows at least, many aspects of incubation behaviour may be largely innate and affected only marginally by experience or other age-related variables. Specifically, if the rhythm of attentiveness at the nest is controlled by 'internally regulated oscillations', as argued by Davis *et al*. (1984; see also Haftorn 1978, 1981), the ability to establish such a regular incubation pattern is already well developed in yearlings after only a few days experience incubating. Environmental variables and possibly food availability are likely to play more important roles in modifying incubation behaviour (Davis *et al*. 1984, Moreno 1989, Rodríguez-Teijeiro *et al*. 1997). Determining whether these results apply to other bird species will require studies of known-aged birds while controlling for factors such as reproductive history, date, weather, clutch size, stage of incubation and body size of incubating females.

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