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INCUBATION IN THE STARLING, *STURNUS VULGARIS*: RESOLUTION OF THE CONFLICT BETWEEN EGG CARE AND FORAGING

by

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SUMMARY

Complementary studies on Starlings nesting on the Frisian island Schiermonnikoog included estimation of total energy expenditure of the parent birds, evaluation of the cost of incubation, experiments on the effect of manipulated nest temperature on incubation rhythm, and observation of prey intake rates during foraging trips. Typically the eggs were covered 95% of the time, and experimentally it could be shown that a fall in nestbox temperature elicited an increase in sitting activity. It is argued that this relation is brought about by responsiveness to egg temperature at the outset of the sitting spell, as this will determine the shape of the warming curve and hence the time until equilibrium incubation temperature has been restored.

In years of poor food supply the parents compensated by making longer foraging trips and extending their active day. An inter-season comparison suggests that the length of the foraging trip is set to collect a given amount of food. In years of high densities of the principal prey (larvae of *Tipula paludosa*) and hence high intake rates, the parents spent more time in alternate feeding sites thereby constituting a more varied diet. In the year of poorest food supply the sitting bout was extended to allow the off-duty partner sufficient time to collect food. In rich years some females managed to incubate unassisted.

The energy cost of incubation involves a modest increment in the daily energy budget. Flight at this time is greatly reduced and this savings more than offsets the cost of heating the eggs, such that during incubation the parent birds probably enjoy the lowest demand of any phase of the breeding cycle. The main problem posed by incubation is thus how to collect enough food in the time available, rather than coping with excessive energetic costs.

INTRODUCTION

Some twenty-five years ago BAERENDS (1959) provided an ethological view on incubation, drawing together the threads of the broad fabric he was weaving on the Herring Gull and its egg (later published in full, see BAERENDS & DRENT, 1970, 1982). At the time Baerends em-

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phasized the relations between various functional mechanisms subserving the regulation of egg temperature, but he made two reservations about the approach. First, he pointed out that what the parent bird actually does will represent some sort of compromise between conflicting tendencies, and that therefore a functional analysis should be broadly-based. Secondly, realizing the limitations of field experiments involving the manipulation of egg temperature, Baerends advocated 'more detailed physiological and ethological research on birds incubating under controlled conditions to follow up these questions derived from work in the field'. Although one of us (RD) has made persistent attempts to observe birds incubating in captivity, the lure of the field has always been too strong and we here present data from a halfway station; the Starling incubating in a nestbox. Although the events outside the nestbox were not interfered with in any way, this nesting mode allows the experimental manipulation not only of egg and air temperature, but also the monitoring of energy expenditure. More specifically, we seek answers to three questions: (1) is the rhythm of egg care under the influence of the temperature (of eggs and nestbox), (2) is the rhythm of egg care (nestbox time) under the influence of food supply, (3) is the act of incubation likely to involve such costs that the pattern of alternation of duties between the sexes can be given a functional interpretation.

METHODS

The work was done on Schiermonnikoog, a Dutch Waddensea island, where a small Starling colony of about 15 pair nesting in boxes was studied intensively in the period 1973-1982. In two seasons some of the boxes were fitted with heating elements (copper radiators) through which water was pumped from a controlled temperature water bath, and other boxes were fitted with an artificial clutch of copper eggs, again through which water could be circulated from a water bath. During the night when as a rule incubation is by the hen and is continuous, the nestbox served as an openflow respirometer and by monitoring oxygen and carbon dioxide concentrations in the air the metabolism of the sitting bird could be estimated. To obtain records of the rhythm of egg care, several nest entrances were fitted with a copper lip which had to be thrust aside by the parent bird when entering or leaving the nest, making an electrical contact distinguishing between 'in' and 'out', and connected to a pen recorder (paper speed 15 cm per hour). Internal egg temperature was also recorded, and the role of the sexes was determined by keeping a continuous watch of the nestbox (three observers taking turns through the day). Most of the parent Starlings were colour-ringed, and several pairs were observed intensively during their foraging activities by a second team of observers maintaining a dawn-to-dusk watch from a nearby tower overlooking the colony and adjacent feeding grounds (for further description see TINBERGEN, 1981). In the years considered here, crane fly larvae, *Tipula paludosa* ('leatherjackets') were the predominant prey, and it was possible to obtain prey collecting rates of the foraging parents by direct observation with the aid of a telescope (15-45X).

RHYTHM OF EGG CARE AND THE INFLUENCE OF TEMPERATURE

In common with other observers (KLUIJVER, 1933; WALLRAFF, 1953; BOGUCKI, 1972) we found without exception the female to spend the night in the nestbox, whereas during the day the male takes a variable share in the incubation duties, with an increasing trend in the course of incubation (see figure 8). With few exceptions the parents showed a strict alternation in sitting spells, the higher share of the female in daytime incubation resulting mainly from longer periods in the nest than her mate. Rarely, the sitting bird made a brief excursion and resumed sitting thereafter. In four nests watched intensively (three different seasons) once steady incubation had set in constancy during daylight averaged 95%, and the major part of the interruptions accounting for the remaining 5% of the time were caused by disturbances at the colony. The lower attentiveness reported by other workers for daylight incubation (65-78%, DELVINGT, 1963; 77%, JOHNSON & COWAN, 1974; 53%, PRINZINGER *et al.*, 1979) probably reflects the milder weather conditions experienced elsewhere (we suspect the chill factor of the strong winds prevailing in our study area to play an important part).

DELVINGT (1963) working in Belgium, noted a negative correlation between ambient air temperature and incubation rhythm in the Starling, the eggs being covered a higher percentage of the time at lower air temperatures on account of a lengthening of the sitting spells (an effect especially marked during the incubation of a second clutch when mean ambient temperatures ranged from 10° to 17°C). That these changes might be mediated by responsiveness to temperature of the eggs or of the nestbox was suggested by the experiments of von HAARTMAN (1956) who demonstrated that the Pied Flycatcher, *Ficedula hypoleuca*, shortened the sitting spells when the entire nest was heated thermostatically.

For the Starling we confirmed this relationship by manipulating nestbox temperature through the range 10-28°C on days of similar ambient temperature (10-14°C). An example of one of the heater experiments is presented in fig. 1, and a summary of the relation between constancy of incubation and nest air temperature is shown in fig. 2. In the Starling, sitting spell lengthened and nest absences shortened as the nest air temperature declined.

These relatively crude experiments do not answer the question as to which cues the parents responded to, as it was not possible to manipulate nest air temperature independently of egg temperature. From registrations of internal temperature obtained at another nest, a strong dependence of sitting spell length on the egg temperature at the

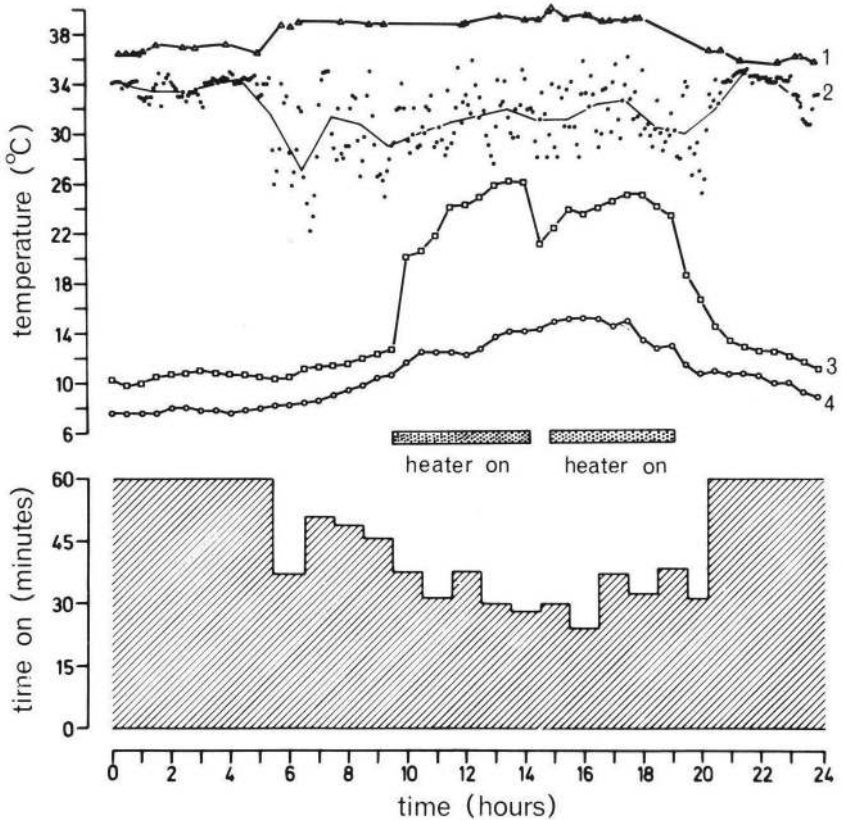


Fig. 1. Sample record of heating trial (horizontal bars denote period during which hot water was circulated through the radiators located in the nestbox) in the Starling. Temperatures are shown for 1 = egg/brood-patch interface, 2 = internal egg temperature, 3 = nest-air temperature, 4 = ambient air temperature. Lower panel shows minutes per hour that one of the parent birds was on the eggs.

moment of return of the parent Starling is apparent (fig. 3), suggesting that egg temperature might be a primary cue.

HAFTORN & REIMERTSEN (1982) have recently managed to obtain precise recordings of the deep body temperature, internal egg temperature, respiratory rate and attentive behaviour of a free-living Great Tit, *Parus major*. By inserting heated or cooled eggs during nest absences it was possible to discriminate between the influence of egg temperature as such and the nest air temperature. As in the Starling data, a significant negative relation between the egg temperature at the moment the parent returned and the subsequent sitting spell

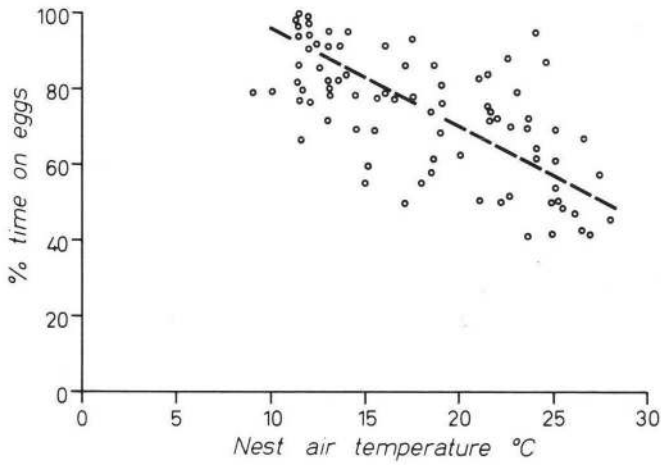


Fig. 2. Attentiveness in the Starling (% time one of the parents was on the eggs) in relation to nest air temperature (range extended by heater experiments). Each point refers to a 2-hr session during daylight.

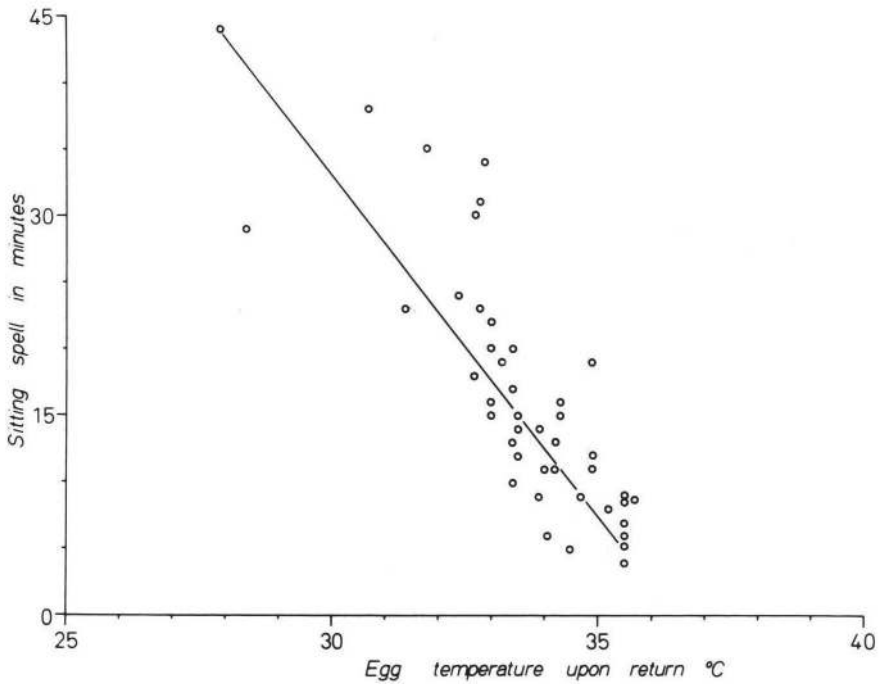


Fig. 3. Sitting spell of the female Starling (in minutes) in relation to internal egg temperature upon return of the parent.

emerged from these experiments, whereas an influence of air temperature as such could not be established. Particularly revealing is a trace these authors give of events following a nest absence (here reproduced as fig. 4). Repercussions for the deep body temperature (determined by aid of a miniature transmitter implanted in the body cavity) reveal adjustment of the close contact between brood-patch and the eggs. Only a few eggs can be directly heated at a time (MERTENS, 1977, 1980) and contact with a new batch of cold eggs is accompanied by a sudden drop in body temperature of the sitting bird as heat is transferred to the eggs and the clutch gradually warmed to the equilibrium temperature. The respiratory rate can be viewed as indicative of the underlying adjustments in heat production of the sitting

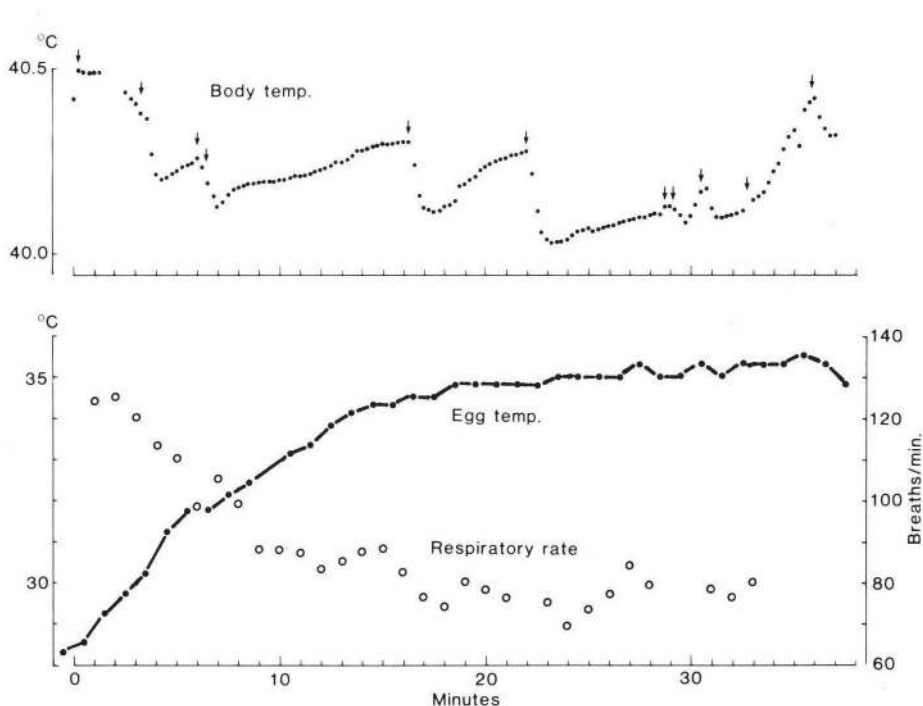


Fig. 4. Egg warming bout in the Great Tit (*Parus major*) as recorded by HAFORN & REIMERTSEN (1982). Body temperature of the sitting hen was recorded from an implanted telemetry device (top panel, arrows indicate re-settling activities accompanied by shifting the eggs). Internal egg temperature gradually reaches an equilibrium value (bottom panel), and breathing rate of the sitting hen was determined from analysis of video monitor shots. Note the initial fall in internal body temperature and high respiratory rate when the hen returns to the nest and settles on cold eggs (clutch of eight). After minute 32 a warm-up phase prior to nest departure can be distinguished.

bird. WHITE & KINNEY (1974) introduced the concept of 'release temperature', arguing that only when the internal egg temperature reaches a given value would the sitting parent tend to end the sitting spell. For the Great Tit at least if such a mechanism would tend to inhibit premature departure of the sitting bird, the analysis of PRINZINGER (1978) points to an equilibrium value depending on ambient conditions rather than an invariable peak egg temperature acting as a release switch.

The role of egg temperature in modifying incubation rhythm has also been investigated experimentally in an open-nesting bird, *Passerculus sandwichensis* (DAVIS *et al.*, 1984). Day-long manipulation of egg temperature was achieved by directing a stream of heated or cooled air through the bottom of the nest. Compared to the control days (egg temperature 35.5°C) when the female incubated 66% of the time, cool eggs (30.6°C) elicited heightened attentiveness (88%) and warm eggs (40.4°C) a decrease in egg care (37% of the time).

It would be an over-simplification to conclude that the rhythm of egg care can be explained solely by the responsiveness of the parent to egg temperature. In several single-sex incubators there is good evidence that extreme conditions can inhibit nest departure (particularly in open-nesters) even though internal egg temperature has presumably reached equilibrium incubation levels. For the alpine-nesting White-crowned Sparrow, *Zonotrichia leucophrys*, ZERBA & MORTON (1983) showed that the female alone was able to maintain internal egg temperature at a mean of 37.3°C during daytime incubation (the eggs rarely being allowed to cool beyond 34°C). When exposed to direct sun the hen usually stayed on the nest, thus avoiding the problem of overheating of the clutch, and WEBB & KING (1983) have pointed out that foraging trips are more likely at moderate than at low air temperatures, and that below 12°C long excursions are avoided altogether. Figures on average attentiveness are not yet available from these recent studies, but judging by earlier work compiled by KENDEIGH (1952) the hen covers the eggs some 70% of the daylight hours.

EGG CARE AND FEEDING OPPORTUNITY

Having established the fact that parent birds are responsive to conditions in the nest, and most likely react specifically to the temperature of the egg in adjusting their incubation rhythm, we also wanted to know if conditions during the period away from the nest (the foraging forays) would impinge on the sitting rhythm. KENDEIGH (1952: 86-92) in reviewing his extensive work on the House Wren, *Troglodytes aedon*,

postulated that the length of the foraging trip would be determined by the time required to fill the stomach with food, and the length of the sitting spell would reflect the time required to digest this. This basic time skeleton would be modulated by temperature (the sitting period being shortened under warm temperature conditions).

Our approach to this problem has been to compare the mean values for the periods on and off the eggs for each observation nest, with the mean food intake rate achieved by the Starlings in that season. Our data are assembled in fig. 5. Indeed the foraging periods (periods 'off') are shorter in years with a richer food supply (the years with a higher density of *Tipula* larvae, see TINBERGEN, 1981). What sets the length of the foraging period? If we take the amount of food collected during the mean 'off' period in the poorest year, 1976, as a basis of comparison, then the time required to obtain the same ration in other years can be

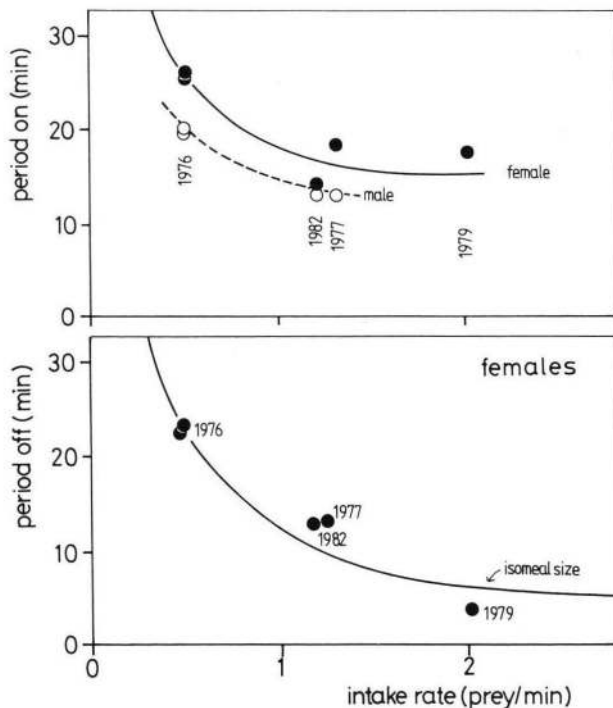


Fig. 5. Incubating rhythm (periods on the eggs above, periods off = foraging trips below) in the Starling in relation to observed food intake rates in the years concerned (expressed as leatherjackets captured per minute of active foraging). Each point refers to the mean value for one nest (in 1979 the female incubated unassisted). The size of the dot corresponds to the 95% confidence interval of the mean.

computed (the 'isomeal line' of 10 *Tipula* larvae in the figure). Clearly the observed periods in the other years do not deviate far from this expected value and support the supposition that nest absence is adjusted to yield a given food ration. How much food is actually collected in this time? Our most detailed records concern the 1979 birds. When unassisted by the male, the foraging absence of the female averaged 4.8 minutes ($n = 41$) and on average she captured 5.3 *Tipula* larvae and 2.1 'small prey' for a total estimated intake of 1.11 g (fresh weight). On three dates when the male participated in incubation, the mean absence of the female was extended to 8.6 minutes ($n = 83$) and the ration collected increased to 1.8 g. We believe this meal size reflects the filling of the stomach, since the food collected in one bout by a tame Starling fed with mealworms ranged from 1.1 to 1.65 g (fresh weight). To this extent Kendeigh's working hypothesis that the periods of nest absence are determined by the time required to fill the stomach is indeed borne out for the Starling. Two complications are at once apparent in our data. Digestion must be relatively rapid, since one individual observed during an extended foraging bout captured 14 *Tipula* (mean fresh weight 0.186 g) in succession for an estimated total intake of 2.6 g and for the 1976 season computations (see next section) on the mean ration collected during the 22 minute 'off' period average 2.6 g. We must conclude that the foraging bout of an incubating bird is at least long enough to allow the stomach to be filled, but that due to high throughput times an extended foray may allow multiples of this amount to be collected. A second complication concerns the composition of the diet. Taking up a suggestion from KLUIJVER's (1933) work on diet in Starlings, TINBERGEN (1981) was able to show that in a choice situation parent Starlings prefer *Cerapteryx* to *Tipula* larvae when feeding the young, and that the parents are willing to invest considerable time in collecting the former, even though they must fly much further and search longer to find one. Only when under the pressure of extreme hunger stimuli from the young (manipulated by the experimenter) does the parent resort to a monotonous diet of the easy to collect *Tipula*. There are indications that the parent follows similar rules in assembling its own diet. For example, the 1979 female devoted 60% of her feeding absences to *Tipula* sites when unassisted by the male, and reduced this to 30% when the male participated in incubation thus allowing her more extended absences (sample of 35 and 20 complete foraging records respectively). That absence times tend to exceed expectation based on *Tipula* intake alone in the richer years can probably be explained by assuming that the parents devoted more time to alternate prey, i.e. they were less committed to *Tipula* in years of high intake rate.

A less easily explained result from our analysis was that the sitting bouts also tended to be the longest in the poor year (see upper panel of fig. 5). We have considered but rejected two possible causes relying on temperature effects. The responsiveness of the sitting birds to temperature is expressed in a negative relation. DELVINGT (1963) was able to show that as air temperature declines, the sitting spell increases (in our interpretation implemented by the responsiveness of the birds to egg temperature). The first question is then, if by chance the air temperatures prevailing during the poor season were lower than in the other years. In fact the mean ambient air temperature for the daylight period of observation in 1976 was 15° compared to a mean of 12° for the 'normal' years 1977 and 1982. We cannot explain the longer sitting spells in 1976 on the basis of temperature, and in fact a plot of the daily means (as in Delvingt's figure 4) demonstrates that while in the 'normal' and 'rich' years our values match the trend of Delvingt's data for an increasing sitting spell at lower temperatures, the 1976 'poor season' spells are consistently long and show no dependence on temperature. A second possible temperature-mediated explanation was suggested by our observation that the 1976 male was a less effective incubator than his mate. Registrations of internal egg temperature showed that early in incubation the male was less capable of warming the eggs than his mate, and was often not able to achieve more than hold the eggs at the temperature to which they had cooled when he commenced sitting. Even during the last three days of incubation the eggs were cooler at the start of sitting bouts by the female (33.7°C) than when the male took over from her (34.6°C , in both cases $n = 34$). Since within ten minutes the female had always managed to return the eggs to the requisite temperature (in these data 35.9°) there is no reason to accept this difference as explaining the 28 minute sitting spells of the female in this year.

Since egg coverage in the 1976 season averaged 95% of the daylight period (fig. 6) and actual breaks in egg contact were generally brief (72% of all interruptions being less than 1 minute, see fig. 11) the sitting spell of the male should thus correspond with the foraging bout of the female, and *vice-versa*. The simplest explanation for the extended sitting period of the female in this season is thus that the feeding requirements of the male have led to an extended foraging trip, and that the female has in effect been waiting for his return. Although we lack sufficient observations on intake rates over the entire feeding trip of the male to test this idea, the male 'off' period in 1976 did increase by the same factor as that of the female when compared with the 'normal' years 1977 and 1982 (the mean values being 21.5 minutes, $n = 116$, contrasted to 39.0 minutes, $n = 138$, an increase by a factor, 1.8, iden-

tical to the rise in the female feeding period as shown in fig. 5). We thus favour the hypothesis that foraging needs drive the sitting rhythm. Only detailed observations can give insight into why the male requires more time than the female; added tasks such as nest defence, inspection of other nestholes and temporary defence of feeding areas come to mind. An indirect shred of evidence on the importance of feeding conditions for the incubation rhythm comes from the meticulous studies of WALLRAFF (1953) who observed incubating Starlings in a garden on the outskirts of Nürnberg (Bavaria). In both constancy and the alternating pattern his observations match ours, but

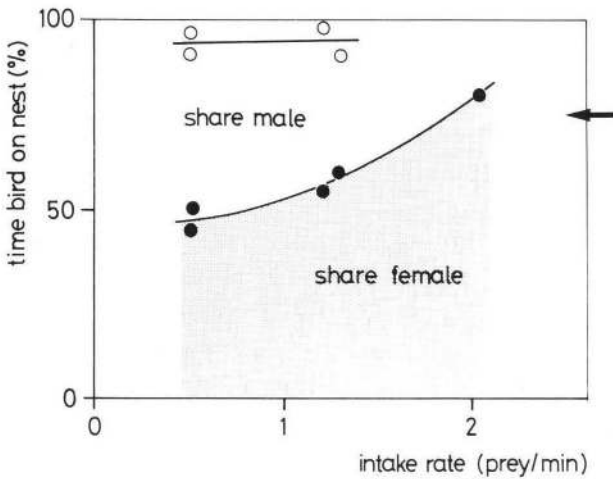


Fig. 6. Share of the sexes in daylight incubation duties in the Starling in relation to observed food intake rates in the years concerned (expressed as leatherjackets captured per minute of active foraging). Each point refers to one nest (to identify years see fig. 5). The arrow indicates the 75% contribution of the female typical for species where the male assists by bringing food to the nest (see Table I).

he found the mean sitting spell for females to be 51 minutes, for males 40 (mean for thirteen nest-days). An interesting difference from our colony, and in our mind a crucial one, is the distance to the main feeding area: 600 meters for the Nürnberg colony, compared to 150 meters for ours.

Turning now to the overall time budget for incubating during the daylight period (fig. 6) we see that the richness of the food supply affects directly the contribution the female makes towards egg care, the male providing a compensatory role. In the richest year of this data set polygamy was widespread, and the female of one observation nest incubated unassisted by the male. In this season, her performance

TABLE I
Incubation parameters in selected passerine birds

<i>species</i>	<i>daytime constancy (%)</i>	<i>daytime egg temp. (°C)</i>	<i>authority</i>
a) hen only incubates			
<i>Empidonax difficilis</i>	63%	34.3°	VLECK, <i>in press</i>
<i>Icterus galbula</i>	63%	32.6°	VLECK, <i>in press</i>
<i>Pipilo erythrophthalmus</i>	67%	37.0°	VLECK, <i>in press</i>
<i>Passerculus sandvicensis</i>	66%	35.5°	DAVIS <i>et al.</i> , 1984
<i>Zonotrichia leucophrys</i>	c.70%	37.3°	ZERBA & MORTON, 1983; KENDEIGH, 1952
<i>Hirundo rustica</i>	72%	35.7°	WESTERTERP & BRYANT, 1984; TURNER, 1980
b) hen only incubates, cock assists by feeding			
<i>Carpodacus mexicanus</i>	73%	32.1°	VLECK, <i>in press</i>
<i>Psaltiriparus minimus</i>	55%	34.7°	VLECK, <i>in press</i>
<i>Parus major</i>	74%	36.4°	HAFTORN, 1981
<i>P. montanus</i>	75%	36.2°	HAFTORN, 1979
<i>Regulus regulus</i>	75%	36.5°	HAFTORN, 1978
c) both sexes incubate			
<i>Delichon urbica</i>	95-99%	36.8°	WESTERTERP & BRYANT, 1984; PRINZINGER <i>et al.</i> , 1979
<i>Toxostoma redivivum</i>	99%	38.0°	VLECK, <i>in press</i>
<i>Sturnus vulgaris</i>	95%	35.8°	this study*)

*) Egg temperature averaged from four daytime spans of unbroken thermocouple recording; an identical value is given by PRINZINGER *et al.*, 1979.

reached the level typical for species where the male provides food at the nest (but does not himself incubate) as summarized in Table I.

The parents minimized the effect of lessened feeding rate in the poor years by extending the feeding day (fig. 7), the female leaving the nest earlier in the morning and making her last feeding flight later in the evening. The net effect of this extended activity span is to add approximately 50 minutes to the feeding day. Our observations in the 'normal' food year 1982 match the findings of BOGUCKI (1972) who noted incubating Starlings in Poland to become active about 10 minutes after sunrise, and to settle in for the night about 25 minutes before sunset. HAARHAUS (1968) recorded values intermediate between our 'normal' and 'poor' years for incubating Starlings studied in Schleswig Holstein. The 'normal year' routine corresponds exactly

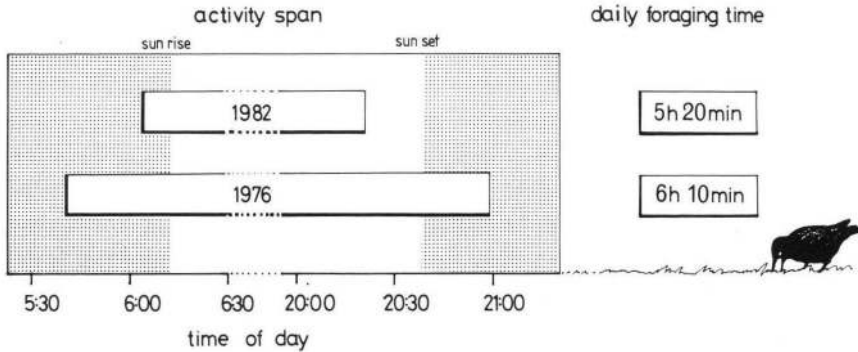


Fig. 7. Activity span of incubating female Starlings (left, showing mean morning departure times and last evening excursion) in a year of plentiful food (1982) contrasted to a year of scanty food (1976). The total time available for foraging is shown at right (= time outside the nestbox) as determined from direct observation.

digestibility .8 (field trials of J. Prop). Assuming the feeding birds with the onset and cessation of spontaneous feeding activity in caged Starlings (0615 and 2015 respectively) maintained under normal daylight conditions in the nearby laboratory (Haren) whereas the 'poor season' extension matches the total activity period in the laboratory, as measured by perch hopping activity (approximately 0500-2100 at that season) according to the extensive registrations of GANSHIRT *et al.* (1984).

IMPLICATIONS FOR THE ENERGY BUDGET

Will the 'isomeal' of ten *Tipula* larvae alluded to in fig. 5 serve to balance the budget of the incubating Starling? The most direct test is to consider the 1976 ('poor season') data as the feeding flights that season were predominantly oriented on the *Tipula* meadow adjacent to the colony (roundtrip flight time 15 seconds). Total feeding time of the female can be computed by correcting the time available outside the nestbox (6.2 hours per day, see fig. 8) for time spent in flight (11 minutes) and in comfort activities (preening, bathing) yielding 5.6 hours foraging time per day, divided into 17 forays (each of 22 minutes' duration, with 20 effective foraging minutes and the observed intake rate of 2 minutes per *Tipula* resulting in the 'isomeal' of ten larvae). The mean dry weight of an individual *Tipula* has been determined at this season (batches varying from .035 to .073 g) and the energy content is 18.97 kJ/g (WESTERTERP *et al.*, 1982) and the

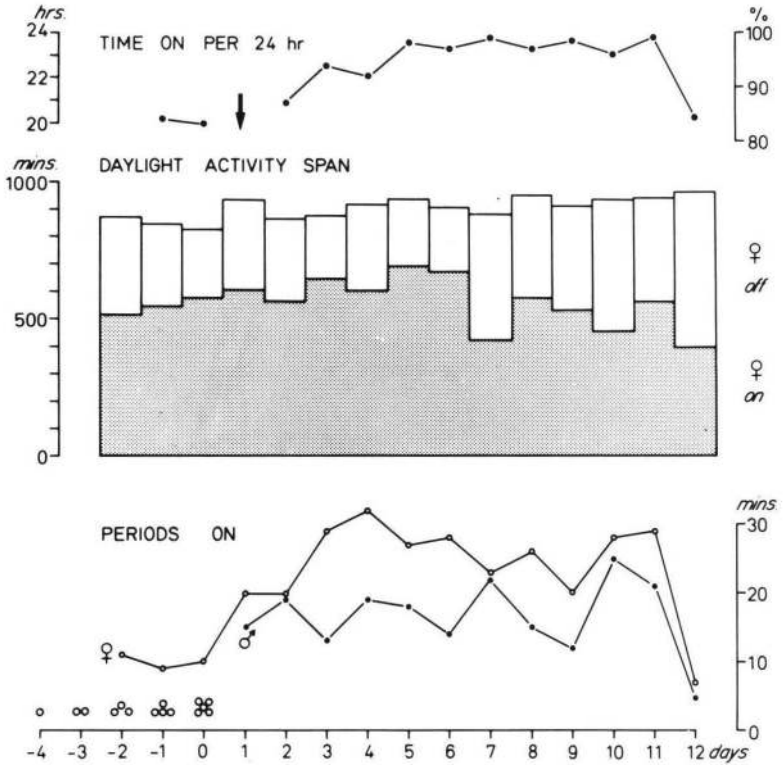


Fig. 8. Incubation rhythm in the Starling (one of the nests observed in 1976) in relation to day of incubation (0 = day of completion of the clutch of five, see symbols along axis) including total time incubated per day (top), time budget of the female during daylight (centre) and median sitting spells (in minutes, below). Three eggs hatched on day 12, the remainder one day later.

selected the larger larvae, a single foraging trip would yield $10 \times .073 \times 18.97 \times .8 = 11.08$ kJ digestible energy, and on this basis the daily ration of digestible energy works out at 188 kJ (for 17 foraging trips). Employing the doubly-labeled water technique (see BRYANT & WESTERTERP, 1980, for a description) Westerterp was able to measure the total daily energy expenditure of six incubating female Starlings, arriving at a mean value of 177 kJ (WESTERTERP & DRENT, *in press*). We conclude that the field estimates of daily intake are compatible with the measured daily energy expenditure.

It is instructive to compare the prey collecting rate during incubation recesses with the collecting rates prevailing when the parents later

tend the nestlings. When computed in terms of the digestible energy that one parent must collect per hour of active foraging (fig. 9) we see that for the Starling in the 1976 season the foraging return demanded during incubation is as high as that in the nestling stage. The same applies to the House Martin, *Delichon urbica*, studied by BRYANT & WESTERTERP (1980). These comparisons emphasize the interpretation that energy balance in the incubation phase is in a state of precarious balance. It should be remembered that *Tipula* larvae, the main food for the Starling throughout both periods, are growing rapidly at this time of year and will be a more profitable prey when feeding nestlings.

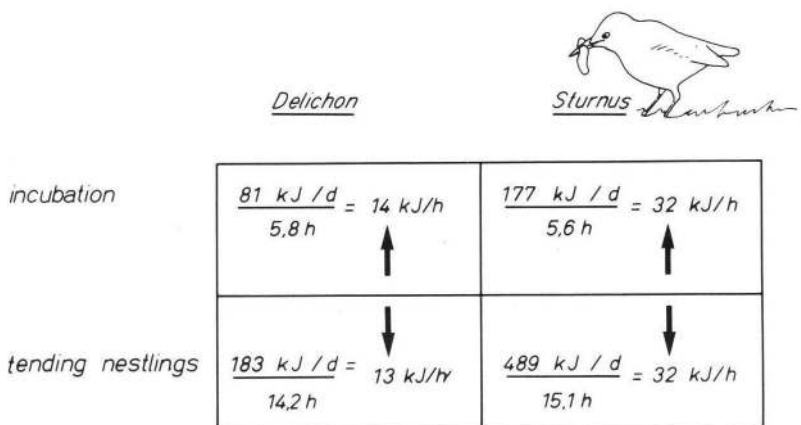


Fig. 9. Mean prey collecting rates during incubation (above) and while tending nestlings (below) for the House Martin (*Delichon urbica*) and the Starling in terms of metabolizable energy collected per hour of active foraging (units: kilojoules). Note that prey collection rate is maintained at the same rate during egg and chick phases in these species (from WESTERTERP & DRENT, in press).

The curtailment of feeding time during incubation in other species, who are likewise forced to collect food at rates equal to or even exceeding those obtaining during the nestling period, seems to be a general phenomenon (WALSBERG & KING, 1978).

Having established that the parent is as hard pressed to find food in the incubation phase as when tending nestlings, we can now consider the magnitude of the energetic drain imposed by the act of incubation itself. Working in our study colony, BIEBACH (1979) was able to measure the nocturnal energy expenditure of incubating birds by monitoring gaseous exchange, and later extended this approach to a captive colony where similar measurements were made of birds incubating various clutch sizes (BIEBACH, 1981) and by utilizing

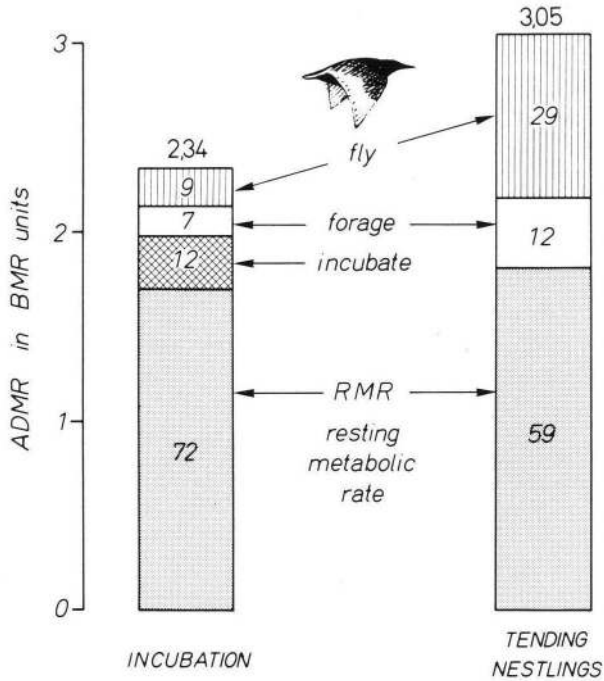


Fig. 10. Components of daily energy budget in free-living female Starlings (ADMR = average daily metabolic rate, in units of BMR = basal metabolic rate) during incubation (left) and while tending nestlings (right). On the top of each bar ADMR is shown as determined from doubly-labeled water injections (means of 6 and 26 individuals respectively). Figures in the bars show the percentage of the daily energy budget devoted to the activity shown, as a cost supplementary to the resting metabolic rate (from WESTERTERP & DRENT, in press).

nestboxes fitted with self-closing gates gaseous exchange during daytime incubation was also investigated (BIEBACH, 1984). The main conclusion from this work was that at the ambient conditions experienced by Starlings in the field, the act of incubation incurs an increment over resting metabolic level almost all of the time. A reconstruction of the daily energy budget by using cost factors determined empirically in our studies for flight, foraging, and incubation and our time budget data provides an estimate of daily energy requirement compatible with the actual value according to the doubly-labeled water technique alluded to above and is shown in fig. 10. Incubation itself claims a modest 12% added cost above resting metabolism over the 24-hr period, but due primarily to the sharply reduced time

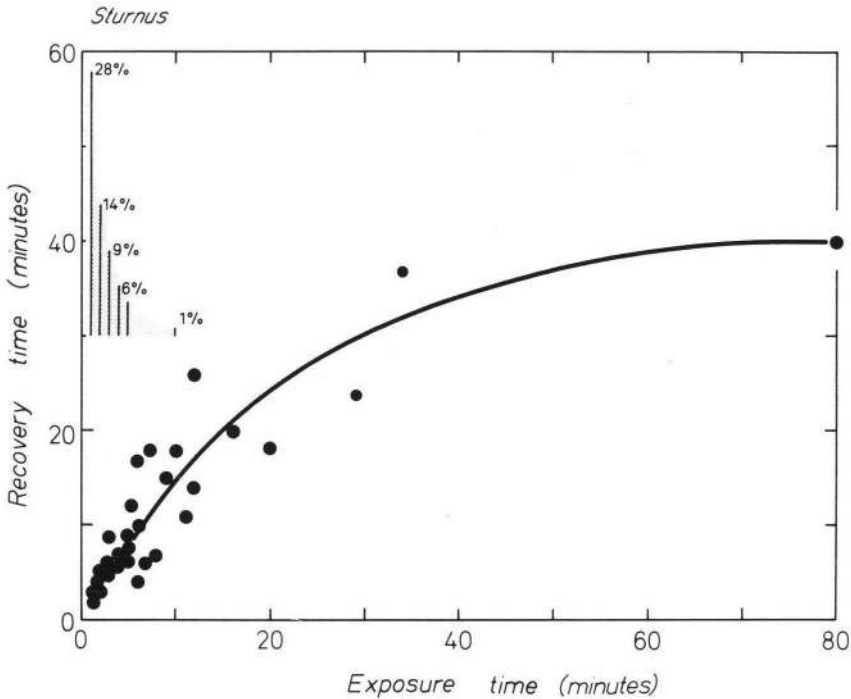


Fig. 11. Time required for internal egg temperature to return to previous plateau value (recovery time, in minutes) in relation to the preceding exposure time (= time no bird on eggs, also in minutes) in the Starling. The inset shows the distribution of exposure times during undisturbed incubation in one control clutch ($n = 225$) in the form of a cumulative percentage distribution (28% of all exposures are 1 minute or longer, 14% are 2 minutes or longer etc.). Not depicted are the exposures shorter than 1 minute (72%).

devoted to flight, total costs are much lower than in the nestling period.

We can now explore the consequences of a modified incubation rhythm in the Starling. Imagine that the female would be forced to incubate alone, in a year such as 1976 requiring a 20-minute foraging break. The first question is, how long would it take for the female to warm the eggs to the equilibrium incubation temperature. By plotting 'recovery time' against 'exposure time' for internal egg temperature at a nest where occasional disturbance provided natural opportunities (fig. 11) we find that the minimal sitting spell would be in the neighbourhood of 25 minutes for the regime of a single-sex incubator departing for 20 minutes at a time. The energetic implications derive

from the cost of warming the eggs, and can be estimated empirically from the captive colony as being equivalent to a 30% extension of the sitting spell. The daily energy requirement for the female incubating on her own would thus increase only slightly (by only about 10 kJ) and as her feeding time would comprise 6 hours the foraging intake required would not transcend the observed performance. The egg temperature regime achieved by the female alone with this rhythm (44% constancy by day) would, however, entail a three day extension in incubation and indeed would probably entail a lowered probability of hatch (compare the failure of the female Zebra Finch, *Poephila guttata*, to hatch the clutch when her mate, normally sharing the duties, died, VLECK, 1981). It can be inferred from table I that successful incubation entails covering the eggs at least 60% of the daylight hours, and quantification of this constraint is an urgent next step in the analysis.

Our preliminary calculations suggest that the thermal regime required for successful incubation, rather than the energetic cost associated with repeated and extensive rewarming of the clutch, is the factor operating to restrict the feasibility of single-sex incubation in the Starling. Judging from empirical performance, nest absences cannot be tolerated in excess of 8-10 minutes on a regular basis, for incubation to be successful. Until the penalties of excursions in egg temperature have been quantified by incubator experiments our analysis remain incomplete.

This discussion on the Starling should not be generalized to mean that incubation is never a time of energetic stress. For the Swallow, *Hirundo rustica*, for example TURNER (1980) has indicated how precarious the balance between cost and intake can be under normal conditions when the female incubates alone. WESTERTERP & BRYANT (1984) found the daily energy expenditure of an individual incubating female in this species to be as high as during nestling rearing. The dilemma of the Swallow is that foraging entails a high cost, the bird being continually on the wing when feeding relying on the energetically expensive mode of flapping flight, and limits to performance will more quickly be reached than in the Starling with its more modest foraging cost.

PROSPECT

In this report we have tried to put the short-term responsiveness of Starlings to experimental manipulation of nest temperature in perspective by considering the time demands made on the parents for self-feeding. Our tentative conclusion, that feeding conditions (intake

rates and distance to feeding sites) dictate the crude framework of the timing of incubation duties, to which is added the fine adjustment modulated by egg temperature, opens a perspective on experimental research aimed at defining the optimal allocation of time between egg care and self-feeding. There are many analogies to the models of central place foraging dealing with the optimal decision of the parent as to where to go and how long to stay when collecting food for the nestlings. For the Starling, the inclusion of energetic considerations has brought the empirical data and the model output in congruence (KACELNIK, 1984). The novelty of this approach was to train the parent to collect food from a movable feeding table, where rate of reward and distance to nest could be varied in competition with natural food sources. A similar approach to the incubating parent suggests itself, where coordinated experiments would include both manipulating the demands of egg care (by cooling or warming the eggs) and of self-feeding (adjustment of supplementary food). The influence of the egg temperature regime on the viability of the clutch can be considered a constraint acting on the time patterning of incubation, and deserves a separate series of experiments. We close in perfect agreement with BAERENDS (1959) who warned that 'the collection of a great amount of quantitative data, a time-consuming and sometimes monotonous task, is badly needed here'.

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