Reproductive Strategies in Great Tits

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Most female Great Tits lay one egg each day until the clutch is complete. However, some exceptions are found. "Pause day/s" most frequently occur after the 1st egg is laid. In general, egg-size increases with laying sequence, but there is year-to-year variation. The relationship between egg size and laying sequence is found more significantly in relatively larger clutches than in smaller ones. Great Tits tend to advance the hatching of their chicks by starting to incubate earlier in relation to clutch completion as the breeding season progresses. Hatching asynchrony affects chick's growth rate, but when the effect of laying date on hatching asynchrony is controlled, the effect of hatching asynchrony on growth rate is not found. These findings support the 'hurry-up' hypothesis.

Introduction

The Great Tit is perhaps the most-studied bird in the world (McCleery and Perrins, 1988). Between 1979 and 1993, over seven hundred scientific papers were published presenting information on this species (Gosler, 1993). The first serious population study on the Great Tit was carried out in the Netherlands by K. Wolda in 1912 (Gosler, 1993). He used nest-boxes to monitor the Great Tit population. In 1936 H.N. Kluijver began to ring the nestlings in the nest-boxes each year in the Netherlands. Kluijver's studies of the early 1950s have had considerable influence on ornithology and ecology (Kluijver, 1950, 1953). Between 1947 and 1950, David Lack, the father of modern ornithology, set up a long-term project on the Great Tit in the Oxford University estate at Wytham near Oxford, England. Today there are over 1000 nest-boxes in 375 ha of the Wytham Woods and the nest-boxes are visited regularly. All nestlings and adults were ringed every year. The ringing studies provide most important information on the ecology of the Great Tit, for example, birth and survival rate, immigration, emigration, pair-bond, etc. In the last 50 years, the long-term study on the Great Tit at Wytham Woods has made an enormous contribution to the fields of animal ecology, behaviour and evolutionary biology. In many respects, the Great Tit is a suitable candidate for behavioural study as well as population study. First, Great Tits are found easily because they are very common. Secondly, both the nestlings and adults can be ringed easily, because it readily accepts artificial nest-boxes in which to breed and the parents do not usually abandon their young even when we caught them while they were rearing their young.

For the last few decades, many theories and hypotheses have been developed and proposed to explain the life history of the Great Tit. In this paper I introduce a number of hypotheses and theories in relation to its reproductive strategy, and ask how these hypotheses may be tested in the field.

Materials

For this work, many existing scientific papers concerning the reproductive strategies in Great Tits were examined. My unpublished data on Great Tits and the database of the Edward Grey Institute of Field Ornithology, Oxford were also used.

Theories and hypotheses

Determination of the timing of the breeding season

Natural selection has caused each species to lay its eggs at such a time that the young will hatch when conditions are most favorable for rearing them. The reproductive cycle in relation to egg laying is under the close control of the endocrine glands. The activity of the glands, of course, is responsive to a variety of environmental stimuli. Since, at temperate latitudes spring and early summer are the typical breeding seasons for most birds, the environmental changes that occur as winter gives way to spring have been widely investigated as possible stimuli triggering reproduction: temperature, precipitation, length of day, light intensity, psychic stimuli, food availability, and others (Baker, 1938; Kendeigh, 1941; Immerlmann, 1971; Arheimer, 1978; von Harrtman, 1990).

Many studies showed that the main proximate factor bringing wild birds into breeding condition in spring is the increasing daylength (Scott and Payne, 1937; Suomalainen, 1937; Rowan, 1938; Kendeigh, 1941). Daylength increases at a constant rate each year. But since the average laying date of the Great Tit varies by up to five weeks, there must be at least one modifying factor. Some authors examined why the date of laying of the Great Tit varies between years although daylength increases at a constant rate each year (Kluijver, 1951; Lack, 1955, 1958; Perrins, 1965; van Balen, 1973; Perrins and McCleery, 1989). There is evidence that the laying date of the Great Tit each year is strongly correlated with the temperature in March and April, and to some extent with the temperature in February (Kluijver, 1951, 1952; Lack, 1955, 1958; Perrins, 1965; Perrins and McCleery, 1989). As the gonads mature, behaviour patterns are initiated in both sexes that are concerned with breeding, such as establishing territory, nest-building, and mating. This breeding behaviour must be energetically demanding if temperature and other environmental conditions are not favourable.

It has been shown that single-brooded species such as tits time egg laying so they hatch when food is most abundant (Rowan, 1926; Baker, 1938; Lack, 1954; Källander, 1974). However, Perrins (1970) pointed out that to have their young in the nest when food for them was most abundant, the parent must lay its eggs at a time when food is not so abundant. If we consider a nest with 9 eggs, the laying period is 9 days because female tits generally lay one egg each day. The incubation period is 13 days for Great Tits (Yoo, 1993). In a nest with 9 eggs, therefore, the first egg in the clutch will be laid some three weeks before the young hatch. If we add the period of egg formation of about 4 days (von Haartman, 1990), and consider that the highest feeding rates usually occur when the nestlings are about 9-10 days of age (van Balen, 1973), the tits may have to prepare themselves for the metabolic strains of egg-laying some 5 weeks before the caterpillars, on which the chicks will be fed, are present in abundance. Therefore, Great Tits have to select the laying date, balancing between the advantage of early breeding in relation to raising their nestlings and physiological body condition for laying. Most female Great Tits select a proper laying date in relation to their body condition, but some fail to do so (Yoo, 1993). Most female Great Tits lay one egg each day until the clutch is complete, but some have "pause day/s" during laying. The " pause day/s" occur more often in the first stage of laying than in the middle stage of laying. The mean fresh weight of eggs laid before the first " pause day" tended to be lighter than that of eggs laid after the first "pause day". "pause day/s" may reflect the temproal and energetic constraints on the laying females' physiological condition for egg formation. These findings suggest that some laying females fail to time their laying optimally in relation to their own body condition for egg formation. This gives a clue to why the laying date is widely spread form early April to early June even though early breeding Great Tits are at a considerable advantage in terms of raising their chicks as shown by Perrins (1970).

Optimal clutch size

Since natural selection favours those individuals who most abundantly leave offsprings to the next generation, birds may want to lay as many as they can produce. However, since reproduction is energetically expensive, a higher investment in reproduction does not always guarantee a higher reproductive success or an increased recruitment to the next generation. Instead, a high investment in reproduction may increase the risk of mortality or reduce future fecundity as shown in domestic fowls by Romanoff and Romanoff (1949). Therefore, in order to maximize their own lifetime reproductive success, laying females need to allocate their reproductive effort in response to both proximate factors and ultimate factors (Yoo, 1993). To find out a trade-off between clutch size and the probability of surviving to breed again or fitness of offspring, it is necessary to know overwinter survival rate of young and adult birds, clutch size and laying date in subsequent breeding seasons, the probability of producing a second brood in the same season, and the size of second brood in experimentally enlarged broods (see Yoo, 1994 for more details).

Lack (1948, 1954) proposed that birds lay the number of eggs in a clutch which results in the largest number of surviving young. This is the most commonly accepted theory for the evolution of clutch-size. However, Pettifor *et al.* (1988) experimentally enlarged clutches and found that the most productive clutch size is greater than the most common clutch size in Great Tits. This study confirms Boyce and Perrins' hypothesis (1987), suggesting that it is more advantageous, in the long term, to lay clutches smaller than the most productive clutch size because "poor years" for survival of young affect individuals laying larger clutch sizes much more than they effect those laying smaller clutches.

The individual optimization hypothesis (lack, 1966; Perrins and Moss, 1975; Pettifor *et al.*, 1988) proposes that individual parents lay that size of clutch from which they can maximize recruitment: experimental increases or decreases of any size clutch will result in lowered recruitment. This is based on the idea that individual differences in the ability to rear offspring mean that the optimum clutch differs between individuals. In Great Tits, indeed, clutch size varies between females, ranging 5-12. Yoo (1993) showed that growth rate is not related to brood size (=clutch size). Boyce and Perrins (1987) argued that the cost of reproduction as it affects adult survival is neither necessary nor sufficient for clutch size optimization in the Great Tit.

Ecological significance of egg size

Although some exceptions are found, a general trend towards increasing egg size up to about the sixth egg is found in the Great Tit when data are pooled, but thereafter size of eggs tend to be constant or slightly decreased. The relationship between egg size and laying sequence is found more significantly in relatively larger clutches than in smaller ones. The above findings may reflect the female's physiological constraints for laying in terms of reproductive cost. However, as various patterns in intra-clutch egg size variation are found even in clutches of the same size which have the same laying date or are just one-day apart in laying date within a year, individual females are likely to respond in different ways under the same environmental conditions when the patterns of intra-clutch egg size variations are examined. These findings suggest that variations of egg size and composition reflect the laying female's body condition rather than an adaptive breeding strategy.

There is year-to-year difference in intra-clutch egg size variation in the Great Tit. The year-to-year difference in intra-clutch egg-weight variation may be correlated with the the year-to-year difference in caterpillar food availability and the weather of winter and early spring, from January to the end of March. As cold weather causes birds to increase their metabolic rate to compensate for a greater heat loss, this may constrain individuals preparing for the additional metabolic costs of egg laying.

Hatching pattern and growth rate

In Great Tits, there is a trend in the timing of the onset of incubation in relation to the end of laying; females that lay clutches late in the seasom tend to start incubating some days before the clutch is complete. This leads to greater hatching asynchrony in these clutches. These findings suggest that, in order to maximize their breeding success, Great Tits tend to advance the hatching of their chicks by starting to incubate earlier in relation to clutch completion as the breeding season progresses. This strategy seems to be particularly important because early breeding Great Tits can have their young in the nest at about the time when their caterpillar food is most abundant.

Most females can hatch all their eggs in the clutch, but some fail to hatch one or two. The mean fresh weight of hatched eggs was heavier than that of unhatched eggs in the clutch. As larger eggs can be reached more easily by the brood patch of the incubating female than smaller ones within the clutches, larger eggs in a nest may hatch first and the first hatchings may interrupt the females incubating the unhatched eggs in the nest. This may reduce hatchability in smaller eggs of a clutch in some nests.

Growth rate decreased as hatching asynchrony increased ($r=-0.634$, $p<0.001$, $n=24$ nests). However, when the effect of laying date on hatching asynchrony was controlled, residual hatching asynchrony was not related to the factor ($r=-0.305$, non-significant), indicating that the effect of hatching asynchrony on growth of Great Tit chicks is confounded by the laying date. This finding supports the 'hurry-up' hypothesis (Clark and Wilson, 1981), suggesting the asynchronous hatching may be an adaptation to take advantage of peaked or declining food resources.

Discussion

Slagsvold *et al.* (1984) suggested that birds adopting the "brood-reduction strategy" have a small final egg so that if food becomes scarce, the youngest offspring within the brood can be rapidly eliminated without too much loss of already-invested parental effort, particularly those birds with large clutches. In Great Tits, there is no differences in size between the last egg and the mean of the rest. If Slagsvold *et al.* (1984) are correct, Great Tits are unlikely to adopt the "brood-reduction strategy".

In Great Tits, a most striking difference is found between the first egg and the rest of the clutch; its size tending to be much smaller than that of subsequent eggs. As I mentioned earlier, 'pause day/s' occur most frequently after the laying of the first egg. If laying female's can predict these conditions, they may be able to produce less variable eggs throughout the laying sequence in a clutch. However, females may find it difficult to determine how large, and how many, eggs they have to produce to maximize their breeding succes in relation to their body condition. Therefore, many females may lay smaller first (and sometimes second as well) eggs in a clutch as an insurance for unpredictable environmental conditions during the period of laying, although some exceptions were found. This tendency may be found more commonly in a bad year in terms of caterpillar food availability than a good year. The smaller first (and sometimes second as well) eggs in a clutch may also result from a selective pressure to start breeding as early as possible.

There are some evidence that Great Tits tend to hatch their young as early as the breeding season progresses. First, the timing of the onset of incubation was closely related to the laying date: females that lay clutches late in the season tend to start incubation some days before the clutch is completed. As I mentioned earlier, this leads to greater hatching asynchrony in these clutches. Secondly, if the effect of the timing of onset of incubation was not considered (see Yoo, 1993 for more details), the length of the incubation period decreased as the breeding season progressed.

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