Abstract The extent to which male parental care increases offspring survival is an important factor shaping avian breeding systems. However, the consequences of male assistance with incubation and the circumstances under which males incubate are poorly understood. We studied a starling population in which male participation in incubation was variable. Incubation periods were shorter, while hatching success and hatching mass were greater in nests where males assisted females with incubation. These effects did not appear to arise because males incubated only on high-quality nests or when mated to high-quality females. Instead, we suggest that male assistance improved incubation performance by directly improving the conditions experienced by developing embryos. Although females incubated less when males assisted, the male’s contribution increased total nest attendance. Males maintained clutches at marginally lower equilibrium temperatures than females but rewarmed cool clutches more rapidly. Clutches consequently spent more time at temperatures likely to facilitate embryonic development. The improved incubation performance resulted in improved breeding success in nests where males assisted with incubation. Male incubation was associated with social monogamy, but many males mated polygynously and did not incubate. Males that incubated had nests that insulated poorly and were initiated relatively late within colonies. Male participation in incubation may therefore decline with a male’s ability to provide a high-quality nest and attract multiple females. However, by destroying secondary females’ nests, primary females may have been able to increase their chance of receiving male assistance with incubation.

Keywords Nest attentiveness · Nest quality · Intersexual conflict · Egg temperature · Parental care

Introduction

The extent to which parents care for offspring has evolutionary consequences for animal morphology and physiology, and for the social structures of populations (Ketterson and Nolan 1994; Kokko 1998; Webb et al. 1999). A major goal of behavioural ecology is consequently to elucidate the factors that shape patterns of parental care (Clutton-Brock 1991) and to do so, the fitness costs and benefits of caring or deserting offspring must be understood (Székely and Cuthill 1999; Huber and Teferi 2000).

In birds, parental care is generally required during both incubation and chick-rearing if breeding is to be successful. Females frequently provide care during both periods, whilst the male’s contribution is more variable (Clutton-Brock 1991; but see Eens and Pinxten 2000). A female’s ability to breed successfully without male help has been suggested to influence breeding system evolution, affecting frequencies of extra-pair copulations and mate desertion and the stability of social monogamy (Kokko 1999; Székely and Cuthill 1999, 2000; Möller 2000). Assessing the value of male care is therefore of considerable interest.

The consequences of male assistance with chick-rearing have been studied in several passerine species. Paternal provisioning can increase fledging success and improve chick growth rate and fledgling condition, thus increasing female fitness (Johnson et al. 1992; Smith et al. 1994; Bjornstad and Lifjeld 1996; Markman et al. 1996; Moreno et al. 1999). However, time spent provisioning one brood of offspring can be costly for males, reducing their ability to attract further mates or provision other broods (Sandell et al. 1996; Hunt et al. 1999; Moreno et
al. 1999). The consequent sexual conflict over the extent of paternal chick-provisioning has been linked to mating system evolution and multiple related aspects of breeding behaviour (Davies 1985; Davies and Hatchwell 1992; Houston et al. 1997; Smith and Sandell 1998; Alonzo and Warner 2000).

Considerably less is known about the occurrence and effectiveness of male assistance with incubation. Males can improve incubation performance indirectly by provisioning incubating females on the nest (Lyon and Montgomery 1985; Nilsson and Smith 1988). However, as males of many species lack well-developed brood patches (Bailey 1952), their ability to contribute directly to incubation remains relatively unclear. Trade-offs between paternal care and mate attraction may be particularly marked during the early season incubation period, and male participation in incubation can vary with a male’s mating status (Pinxten et al. 1993; Smith et al. 1995; Smith and Sandell 1998). However, despite this knowledge, the possibility that sexual conflict over male incubation might arise and influence mating systems has scarcely been discussed.

We studied a facultatively polygynous population of European starlings (Sturnus vulgaris) in which some males assisted females with incubation whilst others did not. We investigated the ability of males to incubate effectively, the circumstances under which they incubated, and the consequences of their help for female time budgets and breeding success. Based on these findings, we discuss the possible role of male incubation in influencing the starling mating system.

Methods

A population of cavity-nesting starlings was studied in the Ebro Delta, Spain (41°N, 2°E) between March and June 1999. Nests were situated in holes in roofs of widely scattered agricultural buildings. Each roof contained between two and ten nests.

To determine whether females incubated alone or with male assistance, each nest was observed for a minimum of three (mode of five) 2-h spells spread across the incubation period. A 2-h period was sufficient to observe multiple change-overs, and the times of male and female arrivals and departures were recorded. Males either contributed substantially to incubation or did not incubate at all. Non-incubating males were easily recognised as they frequently stood outside nest cavities. Multiple nests were observed simultaneously, and thus observations of nests where males did and did not assist with incubation were paired in time. Males assisted with provisioning all their broods of chicks.

To determine how many nests were attended by each male, colonies were observed on at least eight further occasions during the breeding attempt (as Smith et al. 1994). A maximum of six males bred within a single colony (mode of three). Possibly as a result of occasional hybridisation with spotless starlings (S. unicolor), the study population exhibited considerable plumage variation. Thus, within each colony, males could be distinguished using individual plumage characteristics. Four different observers independently attributed the same mating status to males during both simultaneous and consecutive observation periods, and hence designations were repeatable. As colonies were separated by up to 2 km of open paddyfields and males remained within sight of their known colony almost continuously during observation periods, the same male is very unlikely to have bred simultaneously in different colonies. Data from two colonies containing nests where male identity remained uncertain were excluded from the analyses.

To investigate the incubation ability of males and females, model eggs containing thermistors were placed in 38 nests the day after full incubation commenced, and were removed the day before the clutch was due to hatch (see Reid et al. 2000a for details). In 19 nests, the addition of the model egg enlarged the natural clutch size. In the remaining 19 nests, the model replaced a real egg that was removed as part of another experiment (see Reid et al. 2000a). As the occurrence of male incubation had been determined before model eggs were deployed, we ensured that the enlarged clutches were evenly distributed between nests where males did and did not incubate. In no case did the addition of a model egg alter whether or not a male incubated, and the presence or absence of an extra egg was not retained as a significant factor in any of the analyses. Model eggs had similar thermal properties to real eggs (Reid et al. 2000a). Thermistors were positioned in the centres of model eggs, and TinyTalk data loggers (Gemini Data-loggers Ltd, Chichester, UK) were used to record model egg temperature every 72 s throughout the incubation period.

The nest observations were used to link model egg temperatures to the presence of either the male or the female on the nest. Nest mates to the pre-folding chick that the males should assist with incubation on that nest, the model replaced a real egg that was removed as part of another experiment (see Reid et al. 2000a). Egg-laying dates were recorded in each nest, and eggs were weighed on the day of laying and again the day before hatching was due. The number of chicks hatching and fledging and the dates on which they did so were recorded in each nest. Chicks were weighed within 24 h of hatching and again at 16 days, when maximum tarsus length was also measured. The ratio of mass to tarsus1 was calculated as a measure of pre-fledging chick condition (Freeman and Jackson 1990). Proportional data were arcsine transformed and parametric statistical tests were used unless data distributions violated the assumptions, in which case, equivalent non-parametric tests were employed. All tests were two-tailed, and means are presented ± SE.

Results

Twelve of the 35 males whose mating status was confidently ascertained were monogamous, attending only one nest. All 12 assisted with incubation on that nest, and were responsible for 42.3±1.8% of nest attendance on average. The other 23 males were polygynous, each initially attending two active nests. However, 11 (47.8%)