Abstract  
Island biogeography theory has contributed greatly to both theoretical and applied studies of conservation biology (e.g., design of nature reserves, minimum viable population sizes, extinction risk) and community composition. However, little theoretical and empirical work has addressed how island isolation and size affect reproductive ecology. We investigated the reproductive ecology of great tits (*Parus major*) on one offshore and one nearshore island, as well as on the Danish mainland. Tits breeding on the offshore island bred later, laid smaller clutches, and laid larger eggs than those on the nearshore island and mainland. In addition, the level of ectoparasite infestation in nests was highest on the offshore island, intermediate on the nearshore island, and lowest on the mainland. These insular effects may occur due to lower food abundance on islands, to density-dependent effects, or to effects related to low genetic diversity within island populations. Whatever the cause, the results emphasize that future studies of forest fragmentation/population isolation should consider not only gross measures of reproductive success, but also fine-scale measures such as clutch size, timing of breeding, and parasite prevalence.

Key words  
Island biogeography · *Parus* · Reproduction · Clutch size · Ectoparasites

Introduction  
Insular bird populations have been the focus of intensive study in recent decades, and much of this research has focussed on species assemblages (e.g., MacArthur and Wilson 1967; Diamond 1975a; Wiggins and Møller 1997), relative population densities (MacArthur et al. 1972; Wright 1980), and morphological adaptations (Grant 1972; Alatalo and Gustafsson 1988). Island bird faunas tend to be depauperate and island populations are often morphologically (Grant 1979; Carrascal et al. 1994) and behaviorally (Alatalo 1981; Sørensen 1997) divergent from mainland populations. These insular characteristics appear to be determined by some combination of island size, island isolation, and habitat diversity (e.g., Haila and Järvinen 1983; Martin et al. 1995; Wiggins and Møller 1997).

Island biogeography theory has also had important impacts on conservation biology – for example, the development of both theoretical and applied studies of extinction risk, minimum viable population sizes, and the design of nature reserves (e.g., Diamond 1975b; Soulé and Wilcox 1980; Soule 1987) has largely grown from initial studies of small populations on islands. However, one important effect of the size and isolation of islands has largely been ignored in such studies – insular bird populations may also show divergence in reproductive traits including timing of breeding (Blondel et al. 1990), clutch size (Ricklefs 1980; Crowell and Rothstein 1981; Isenmann 1982; Blondel 1985), nestling development rates (Higuchi 1976; Higuchi and Momose 1981; Bosque and Bosque 1995), and adult survival (Cody 1966; Atwood et al. 1990; Blondel et al. 1992; Faaborg and Arendt 1995). Relative to mainland populations, insular bird populations are typified by smaller clutch sizes, later laying dates, prolonged nestling development, and (in some cases) increased adult survival. However, these studies have all focused on single island/mainland comparisons and we know of no previous studies relating avian reproductive traits to the size and isolation of multiple islands.
Although previous studies have suggested that climatic variables may be responsible for insular effects on avian breeding ecology (e.g., Blondel 1985), little theoretical work has addressed this point. One possibility is that gene flow is restricted on smaller, isolated islands, and, in combination with the effects of the marine environment, leads to a more optimal adjustment of breeding traits to the local environment (cf. Dhondt et al. 1990). Clutch size, for example, is often smaller among island populations, and this effect may increase with decreasing island size and increasing isolation (e.g., Higuchi 1985). The extent to which other reproductive traits (e.g., egg size) may be affected is unclear. However, whether such insular effects are brought about by reduced gene flow (and associated effects such as inbreeding depression), climatic differences, or a combination of these factors, the strength of the effects are likely to increase with decreasing island size, and increasing island isolation.

We focus here on the reproductive traits of insular and mainland great tit (Parus major) populations. We summarize data on laying dates, clutch sizes, egg sizes and ectoparasite levels among great tits breeding on the Danish mainland and on populations breeding on a nearshore and an offshore island.

Materials and methods

We studied tits breeding in wooden nestboxes on the islands of Anholt and Læsø, off the east coast of Denmark, and on the Danish mainland at Mols Bjerge (Fig. 1). Anholt is a small (22 km²) offshore island, located in the Kattegat sea, 44 km east of the Danish mainland. Læsø is a large (116 km²), nearshore island, 50 km north of Anholt and only 18 km off the Danish mainland. Nest boxes (60 at Anholt, 140 at Læsø and 100 at Mols Bjerge) were erected at the three study sites in February 1995. During the autumn of 1996, a further 40 boxes were erected at the Anholt site. In an attempt to control for habitat variation among sites, we placed nest boxes in a mixture of deciduous (Betula spp., Fagus sylvatica, Quercus robur) and coniferous (Pinus spp., Picea spp.) woodlots at each study site. Boxes were normally checked at 3- to 4-day intervals during the 1995 breeding season (mid April to early July). In 1996, four visits were made to Anholt, and two to Mols Bjerge between 1 May and 15 July. In 1997, we made two visits to both Anholt and Læsø in early and late May, and several visits to Mols Bjerge from late April to late June.

Data on clutch size were only included here if we were certain that laying had finished and incubation had started. Furthermore, we included data only from clutches initiated after that date are typically replacement or second clutches. Laying dates were determined by nest checks in late April (1995 only) and early May, and, on some occasions, by backdating from the date of hatching (hatch date minus 13 days minus clutch size). Maximum egg length and breadth were measured with digital calipers to the nearest 0.01 mm. Egg volumes were calculated according to the standard formula for great tits (length × breadth² × 0.51; van Noordwijk et al. 1981). There were many cases in 1996 and 1997 when estimating clutch size and/or laying date was problematical, and we excluded such nests from the analyses.

In 1995, we attempted to catch adults on the nest while they fed young, usually 7–10 days following hatching. Adults were given aluminum rings and measured (tarsus length and bill length with digital calipers to nearest 0.01 mm, and wing length with ruler to nearest 0.5 mm). A few adults were also captured in 1996 and 1997. As our overall sample sizes for adult measurements were small, and because males were often not captured (especially in 1996 and 1997), we include data on adult size for females only. In cases where ringed females were captured in multiple years, we used morphological data from their first capture.

We quantified ectoparasite (hen flea Ceratophyllus gallinae) infestation by collecting nests just after the young had fledged. Nests were placed in thick plastic bags and subsequently in a Berlese funnel for extraction of fleas. A cotton cloth was placed over the funnel to prevent fleas from escaping. After 24 h, fleas were removed and counted to assess their relative abundance in different nests (cf. Allander 1995; Dufva 1996).

Results

The mean size of first clutches was similar on Læsø and at Mols Bjerge, while clutch sizes on Anholt were significantly smaller (Table 1). In 1995, the only year for which we have complete seasonal data, a similar percentage of Great Tits laid second clutches (after successful first clutches) on Anholt (4 of 6 pairs) and at Mols Bjerge (6 of 7 pairs). Laying dates were slightly, but significantly later on Anholt than on either Læsø or Mols Bjerge (Table 1). Although part of the reduction in clutch size on Anholt may simply have resulted from later laying dates, we can dismiss this possibility as great tits at Mols Bjerge and on Anholt showed no seasonal decline in the size of first clutches in any of the 3 years (Spearman rank correlations, all P > 0.2).

Female Great Tits on Anholt laid significantly larger eggs than did females on Læsø and at Mols Bjerge (Table 1). Although we have not yet gathered a robust data set on the size of adult tits at the three study sites, preliminary data suggest that there are no differences in

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Fig. 1 Map of the Danish archipelago, with location of the three study sites