Nest site digging by starlings is not common overseas. Dr L. Szlivka (pers. comm.1987) made nest sites for starlings in Yugoslavia by boring holes in a loess bank. He was surprised to learn that starlings can dig their own nest sites in New Zealand, and in correspondence reaffirmed that they did not do so in his study area: "We haven't noticed anything like that in our region. The European population doesn't drill holes". They do, of course, take over holes in banks made by other species such as sand martins (*Riparia riparia*) in both Britain (Mead & Pepler 1975) and America (Robbins 1985). Also in America, Michael & Taylor (1978) examined 105 road cuttings and found 81 starling nests. Limestone cuttings were preferred to shale or earth, and they wrote: "The cavities were the result of erosion, weathering, and pressures from blasting and excavation during highway construction". There was no suggestion of starlings burrowing, and no other species were found nesting in the cuttings. Finally, neither Bent (1950) nor Kessel (1957) mention digging in long reviews of nest sites in America, nor Feare (1984) in his monograph on starlings.

There are, however, a few records of starlings constructing nest sites in Britain. Morris (1870) says they "even have been known to occupy the holes deserted by rats, more or less fashioned for themselves". Kirkman (1911) states: "Starlings, no doubt, prefer to occupy a ready-made nesting-hole to enlarging or making one...(but) are able to make holes for themselves when occasion demands", and he instances E. Selous' records of starlings forming colonies in sand-pits by making short, roomy caverns that were distinct from sand martin burrows; and making holes in a rotten tree like a woodpecker. Thomas (1957) quotes R. Fisher that a starling removed enough flints to make a hole sufficiently large to nest in.

During a 10-year study of a population of starlings at Belmont, Lower Hutt (Flux & Flux 1981) a careful search was made for birds using natural sites. These sites were very varied for such a small area: tree holes, hollow tree-fern trunks, an open 200 litre drum, holes in buildings, behind a boarded window, between rafters, in chimneys, in vents behind hanging sheets of steel which the birds pushed aside on each visit; and nests open to the sky on ledges, in cypress trees and in the crown of tree-ferns. Unexpectedly, the number of natural sites used increased as nest boxes were provided nearby. Starlings often copied each other: one pair nested in a hole in a bank of shattered greywacke in 1970, and two more pairs nested alongside from 1971 to 1973 using existing crevices which they enlarged. This site was abandoned in 1974 after a slip. Four pairs nested in a deserted house on the study area in 1970, all behind the softboard

Fig. 1 Part of a starling colony 5km north of Hunterville, February 1987. Note the selection of soft horizantal strata for burrowing. The small holes are 5cm diameter and widen with use to about 20cm.

wall-lining. The following year 15 pairs nested in this building, 12 pairs having made neat circular holes, 5cm in diameter, through the softboard, probably starting at cracks or nail-holes. Unfortunately, the house was demolished in 1972 before nesting started. In 1977 one pair raised chicks in an open nest in the crown of a tree-fern, and the following year seven pairs nested successfully in similar sites in adjacent tree-ferns. Rats (*Rattus rattus*) then eliminated this colony.

It is curious that starlings do not take advantage more often of this ability to make their own nest sites. Many populations are clearly limited by the physical or social availability of nest sites. At Belmont, for example, about 3000 birds were waiting to use 500 nest boxes (Flux & Flux 1981). Although, on average, 30.5% (range 20% to 37%) of these boxes remained unused each year, they were not always the same boxes; evidently some boxes were socially unavailable for other starlings to nest in, probably because a dominant male controlled adjacent boxes. At least 50 boxes of the 500 available in the years 1974-79 remained unused each year, despite being well away from the influence of dominant birds (20-200m). The presence of local birds ready to breed but unable to do so was verified by an experiment (approved by the Animal Ethics Committee of Ecology Division, DSIR) on 31 October 1980 when 18 incubating females were killed in adjacent boxes; by 22 November all except one of these boxes contained eggs or newly hatched young, and the age of the chicks showed that at least five of the new females had laid on the seventh day after the box became available. Although there were suitable road cuttings close to the boxes, none of these starlings

had attempted to burrow or to use the empty boxes nearby; yet intraspecific fighting for boxes was the main mortality factor for starlings nesting at Belmont (Flux & Flux 1992). The costs of burrowing, in time and energy, seem small compared with the risk of fighting.

According to Kirkman (1911) "Darwin cites a case in which no less than thirty-five (starlings) were shot one after another at the same nest, both males and females, the last pair bringing off the brood". Darwin suggested that for some species territorial behaviour might produce this effect; but persecuted crows, jays and magpies must have many empty territories, yet immediate replacements are available if one of a pair is shot. He concludes "it is difficult to suggest any explanation".

Although predation or bad weather would eliminate starlings that used poorly constructed sites, such selection should rapidly lead to the evolution of birds which made good burrows in safe places. The early increase at Napier from four to "hundreds of thousands" in 11 years (C. Hutchins, quoted by Thomson 1922) is theoretically possible, and seems largely due to the birds' ability to dig their own nest sites. Why is this behaviour not more widespread in New Zealand, and apparently almost unrecorded overseas? Wynne-Edwards (1962) gives many similar examples of birds that refrain from breeding despite the apparent availability of suitable sites. His explanation, that this is a population regulating mechanism, is not widely accepted; most scientists agree with Lack's (1954) contention that populations must be near the food limit or selfish individuals would take the excess for themselves. Recent evidence, that many wild vertebrate populations are self-limited well below the food limit (Flux 2001), tends to favour Wynne-Edwards' view. Hence the early expansion of starlings into empty habitat in New Zealand may have allowed them to throw off conventional population regulating mechanisms, at least until carrying capacity was reached. In established populations there appears to be some form of social constraint which prevents the expansion of the colony, or the construction of burrows, despite the large pool of birds available and ready to breed. It is hard to imagine any ecological factor that would make starlings risk a fight to the death to take over an occupied box, rather than nest in an empty box 20m away that had been used to rear chicks successfully the previous year.

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LITERATURE CITED

Bent, A. C. 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. Order Passeriformes. *Bulletin of the United States national museum 197*: 1-411.

Feare, C. 1984. *The starling*. Oxford University Press. Oxford.

Flux, J. E. C. 2001. Evidence of self-limitation in wild vertebrate populations. *Oikos 92*: 555-557.

Flux, J. E. C.; Flux, M. M. 1981. Population dynamics and age structure of starlings (*Sturnus vulgaris*) in New Zealand. *New Zealand journal of ecology 4*: 65-72.

Flux, J. E. C.; Flux, M. M. 1992. Nature red in claw: how and why starlings kill each other. *Notornis 39*: 293-300.

Hodgkins, M. 1948. Birds in Tauranga district. *New Zealand bird notes 3*: 116-125.

Kessel, B. 1957. A study of the breeding biology of the European starling (*Sturnus vulgaris* L.) in North America. *The American midland naturalist 58*: 257-331.

Kirkman, F. B. 1911. *The British bird book*. T. C. & E. C. Jack, London.

Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, Oxford.

Mead, C. J.; Pepler, G. R. M. 1975. Birds and other animals at sand martin colonies. *British birds 68*: 89-99.

Michael, E. D.; Taylor, C. 1978. Use of interstate highway cuts as starling nesting sites. *Condor 80*: 113-115.

Morris, F. O. 1870. *A history of British birds*. Bell & sons, London.

Robbins, C. S. 1985. Bank-nesting starlings. *Maryland birdlife 41*: 23.

Thomas, H. F. 1957. The starling in the Sunraysia district, Victoria. Part V. Nesting. *Emu 57*: 325-337.

Thomson, G. M. 1922. *The naturalisation of animals and plants in New Zealand*. Cambridge University Press, Cambridge.

Wynne-Edwards, V. C. 1962. *Animal dispersion in relation to social behaviour*. Oliver & Boyd, Edinburgh.

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