POPULATION DYNAMICS AND AGE STRUCTURE OF STARLINGS *(STURNUS VULGARIS)* IN NEW ZEALAND

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SUMMARY: At Belmont, Lower Hutt, a population of starlings which nested in 500 nest boxes on 1500 ha of pasture land was studied from 1970 to 1979. In total, 750 breeding females and 60 males were individually banded, and of 4006 chicks that Hedged 258 females returned to nest in the study area. In different years, 3-60% of the females attempted a second clutch after a successful first brood. Clutch size of females more than 1 year old averaged 4.48 eggs (4.17 to 4.81 in different years) and declined seasonally in early (4.57), intermediate (4.40) and late clutches (4.06). On average, individual females laid 4.17 eggs per clutch in their first year, reached peak clutch size of 4.77 when 3 years old, and declined steadily to 3.9 eggs at 8-10 years old. Productivity was low: 33 % of 17 326 eggs laid produced young likely to have fledged, equivalent to 1.63 chicks per box available or 1.92 per occupied box. The annual mortality rate of starlings banded as young was only 33% in New Zealand as a whole, compared with 50-70% overseas.

INTRODUCTION

The starling *(Sturnus vulgaris)* is one of the most abundant and widespread birds on Earth. Originally a native of Europe and Asia, it has expanded its range over the past hundred years, partly because of improving climate and partly following the spread of agriculture (Berthold, 1968). Starlings were introduced into North America in 1890, South Africa in 1899, and also into Australia and New Zealand. Stragglers occur from the Maldive Islands on the equator (Strickland and Jenner, 1977) to Svalbard at 78°N (Anderson *et al.,* 1974). They have even attempted to nest at Svalbard (Voous, 1960), but the present breeding limit is about 65°-70ºN (Ojanen, Orell and Hirvela, 1979) in the Old World and 60ON in North America (Heyland, 1970; Edwards and Weir, 1972).

In many places the species' range is still expanding. Starlings reached Hong Kong in 1972 (Webster, 1975) and now nest at Fairbanks, Alaska (Kessel, 1979). On the other hand, there are signs of a recent decline in numbers in Finland (Ojanen, Orell and Merila, 1978; Haartman, 1978). In Scotland starlings declined from being a common breeding bird in 1780 to being a rare passing migrant for about 50 years until 1840, when the current increase began (Meikle, 1975; Parslow, 1973).

Starlings were first introduced into New Zealand from Britain in 1862, with many liberations made between 1865 and 1883; by 1886 they were reported to occur in "hundreds of thousands" around Napier (Thomson, 1922). The Wellington Acclimatisation Society introduced 60 in 1877, 90 in 1878, and 148 between 1881 and 1883 inclusive. Their increase was phenomenal, but A. Philpott (quoted by Thomson, 1922) considered they were far scarcer about 1916 than they had been 25 or 30 years previously, possibly because there were fewer trees to nest in. Starlings are now distributed throughout New Zealand, and have reached all outlying island groups from the Kermadecs to Macquarie Island (Williams, 1953; Darby, 1970).

The population dynamics of such a colonising species under various environmental conditions are of great interest. The present paper reports data collected during a to-year study of the effects of artificial selection for high clutch size in a wild population of starlings. The main aim was to examine the balance between known levels of gene flow and selection pressure, and this involved killing all chicks from clutches of less than the mean (about 4.5 eggs). By waiting until these chicks were 12 days old, after which nestling mortality is low, information could be collected on the survival of small broods, their body weight, and food. However, the elimination of approximately half of the production of young may have had important effects on population structure - perhaps equivalent to predation among starlings nesting in more natural sites - and this manipulation should be kept in mind in comparisons with other studies. Details of breeding biology and the evolution of clutch size will be published elsewhere.

METHODS

The study area, 16 km north-east of Wellington at Belmont (41°10'S, 174°54'E), is of 1500 ha centred on the Waitangirua Farm Settlement block,

managed by the Department of Lands and Survey. It is open, hilly pasture, 250-400 m a.s.l, grazed by sheep and a few cattle (Fig. 1). The entire farm is top-dressed with superphosphate each year, but only about 200 ha is treated with insecticides (Dipterex, Fenitrothion) to control porina moth larvae *(Wiseana* spp.). From about 1950 to 1968, DDT was used extensively to control pasture insects here as elsewhere in New Zealand, which may account for the reported decline in starling numbers in this area since 1945 (R. F. Kilmister, pers. comm., 1973); certainly four starlings found dead in nest boxes in 1970, two years after DDT had been banned on farmland, had pp'-DDE levels of 22.7 to 39.7 ppm (fresh tissue basis) in breast muscle (S. R. B. Solly, Wallaceville Animal Research Centre, pers. comm., 1970), which suggests that they had earlier been exposed to near lethal revels of DOT (Collett and Harrison, 1968).

To store army ammunition, 62 concrete magazines were built in 1942, scattered about 100 m apart over the centre of the farm (Fig. 1). Ledges in these buildings allowed 26 pairs of starlings to nest successfully, and 159 additional pairs attempted to nest, in 1969, the year before our study began. In 1970, 100 nest boxes were placed in ventilation ports 4 m above ground and 2-3 m apart in groups of 10 or 15 boxes per magazine. Each year 100 boxes were added until 500 were available to starlings from 1974 to 1979 inclusive. They were 40 cm wide, 20 cm high and 15 cm deep, formed by placing wood across the interior opening of the ventilator and an asbestos-cement sheet across the exterior opening, with an entrance hole approximately 6 cm square cut into the top edge in the centre or one side (this difference was important, because it affected the acceptability of the box). Boxes were renovated (but not cleaned out) each winter, and deteriorated little during the study. They were larger than usual (Moeed and Dawson, 1979) but clutch size in starlings does not vary with the size of nest box (Karlsson and Nilsson, 1977).

We inspected the nest boxes every second day for the first 2 weeks of the breeding season, and thereafter every 2-3 days. Female starlings were caught on the nest at night while incubating, and aged as first-year or adult by the length of the sheen on the throat hackle feathers (Kessel, 1951). Some measurements overlap among known-age birds (Fig. 2), so 7 mm was arbitrarily chosen as the lower limit for adults. The birds were then given a numbered monel-metal band on the right leg and an individual three-colour combination of plastic wrap-around bands on the left.

Chicks were marked with monel bands on the left leg, and with one or two colour bands on the right leg to indicate their year class; if re-caught in the study area in subsequent years two more colour bands were added on the left leg to provide individual identification. Male starlings deserted the nest readily when handled and no systematic attempt was made to catch them; 60 adults were individually banded, most being caught fighting in nest boxes, and all males reared on the hill were banded as chicks.

Loss of bands can seriously affect the results of

FIGURE 1. *The study area at Belmont showing open pasture and the army magazines in which nest boxes were placed.*

long-term population studies (Harris, 1980). Our starling bands showed considerable wear (to be reported elsewhere) especially monel bands adjacent to plastic ones, but badly worn bands were replaced and most birds carried so many bands that total loss was practically eliminated.

RESULTS

General biology

Starlings are social and remarkably mobile for a small passerine. In autumn and early winter those from Belmont roost on Mana Island, 12 km to the west, and in late winter they roost on Somes or Gear Island, 11 km to the south. They feed in wide-ranging flocks, and move many kilometres during the day, but most birds visit their nest sites at dawn and in the evening throughout the year except in January and February, defending an area within 1-2 m of the nest site.

By late September the birds clear out the previous year's nest and construct a new one. Early clutches are laid in mid-October, the population being so synchronised that almost all eggs are laid within 7 days (S.D. = 1.94 days) of the mean laying date (Fig. 3). An intermediate clutch follows in mid November, when birds which were unsuccessful with their first clutch re-lay, and many first-year birds lay for the first time. Late clutches follow in early to mid December, but these are relatively unsuccessful and are laid by 3% to 60% of the birds that fledge a first clutch in various years, fewer perhaps re-laying in dry seasons. Only 64 of 92 late clutches were true second clutches laid by the same female, the remainder being laid by different females.
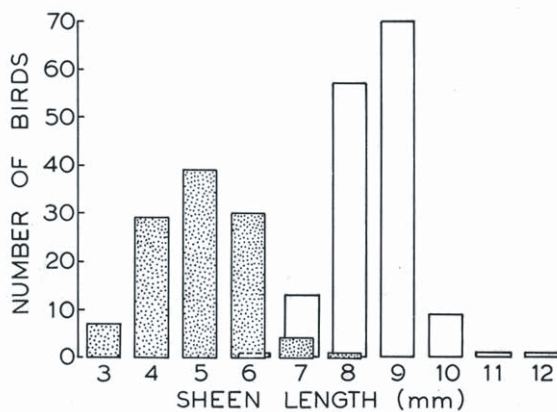
Occupation rate of nest boxes

Of the 500 boxes available from 1974 to 1979, 200 had central entrance holes and 280 had holes to one side. In every year the occupation rate was lower in boxes with central entrances (Table 1). Of 957 birds which nested in boxes with a central hole, 290 (30%) became confused and built a nest bowl on each side, and one bird even laid eggs in both. Coleman (1974) found that starlings in Canterbury preferred nest boxes with circular entrance holes to those with square holes, Lumsden (1976) that they preferred small to larger holes and Moeed and Dawson (1979) that they preferred certain sizes and shapes of boxes. Such sensitivity to apparently minor features of nest box construction (considering the birds will nest in crevices, rabbit burrows, or even on a pile of rocks) is important in interpreting whether or not the number of nest sites is limiting the population.

TABLE 1. *Percentage of 280 nest boxes* with *entrances to one side, and 220* with *central entrances, occupied each year.*

| Year | Position of entrance | |
	Side	Centre
1974	96	68
1975	92	69
1976	91	58
1977	96	72
1978	88	57
1979	90	68
Mean	92	65

FIGURE 2. *Distribution of sheen length on throat hackle feathers of 110 one year old female starlings (stippled) and 152 birds aged 2 years or older.*
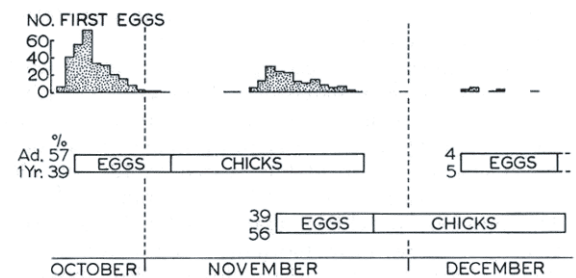

FIGURE 3. *Pattern of egg laying (stippled) at Belmont in 1978. The 1l-day incubation period and 22-day fledging period, measured at Belmont, show that the November peak of egg laying must be by starlings that were unsuccessful in their first brood, or by late nesters. The percentages of adult and first year females laying in each period are averages for the whole study.*
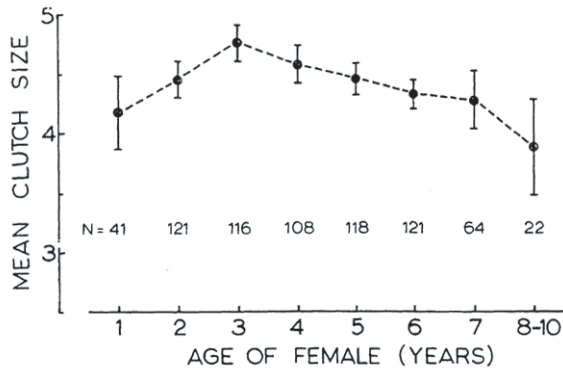
FIGURE 4. *Change* in *clutch size with age* in *female starlings. Sample size varied because full clutches were not recorded for all birds each year, and many do not start laying until 2 years old. Vertical lines are 95% confidence limits.*

Production of young

The average size ± S.E. of 2050 clutches laid by adult (2 years or older) starlings at Belmont was 4.48 ± 0.02 eggs. This figure declined seasonally in early (4.57), intermediate (4.40), and late (4.06) clutches. Between years, the average clutch size of adults varied from 4.17 in 1970 to 4.81 in 1972, and this annual variation was reflected in the clutch size of individual birds. In 130 females banded between 1970 and 1976 that lived to be at least 6 years old, clutch size increased in the first 3 years of life and then declined steadily (Fig. 4). The proportions of eggs hatched, and of chicks fledged, by different birds in different years also varied; the extent of this variation should be kept in mind in considering the overall patterns summarised here.

The numbers of breeding females present each year, eggs laid, eggs hatched, and chicks that reached 12 days old (Fig. 5) illustrate surprisingly high mortality. Only in 1973 was an average of more than 2.5 chicks per occupied box reared to 12 days old. The overall average was 1.92 chicks (range 1.2-2.7). The numbers of chicks that actually fledged each year show how little mortality took place at this stage, except in 1979 when stoats killed about 50 chicks.

Age structure

The age composition of the population of banded females breeding at Belmont could be assessed each year when they were caught incubating. Annual cohorts of adults of unknown age (2 years or more), first-year birds, and chicks returning to nest (Fig. 6)

have been compensated for individuals not recorded in some years but subsequently found alive; those missed formed about 10% of the population. They may have attempted to nest as roughly the same percentage was known to be present (by counting occupied boxes) but not caught, usually because they deserted too soon after laying. The numbers of adult females entering the area each year to nest there for the first time were relatively constant (30-68), while the numbers of first-year females were more variable (4-43). Also interesting is the decline in annual return (Fig. 6) from 84% over the first 2 years to 70% during the last 5 years, with an overall mean of 72 %. This return rate is a minimum survival (some birds may have moved, or may return in future) and implies a maximum mortality of 28 % per annum.

Mortality rates can also be calculated from the age at death of birds banded as chicks (Table 2), using Lack and Schifferli's formula (1948):

$$M= \frac{D_1 + D_2 + D_3 .... D_n}{D_1 + 2D_2 + 3D_3 .. . . nD_n} \times 100$$

where M is the percentage mortality and D_n the number of birds found dead aged n years. For starlings it is not necessary to treat mortality in the first year separately, as it is the same as for older birds (Coulson, 1960). Haldane (1955) devised a correction to allow for birds banded in the last years of study which have not yet had time to die and be reported, but we had insufficient data to apply the correction uniformly to all the studies which we wished to compare. The differences are so marked
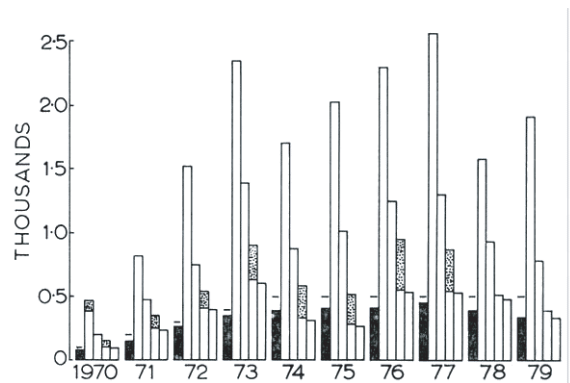

FIGURE 5. *Productivity of starlings nesting at Belmont, 1970-79. Key (columns from left): breeding{ females present (black, with horizontal bar showing number of nest boxes available); eggs laid; eggs hatched; 12-day-old chicks; chicks fledged. Artificial selection (stippled) stopped after 1977.*
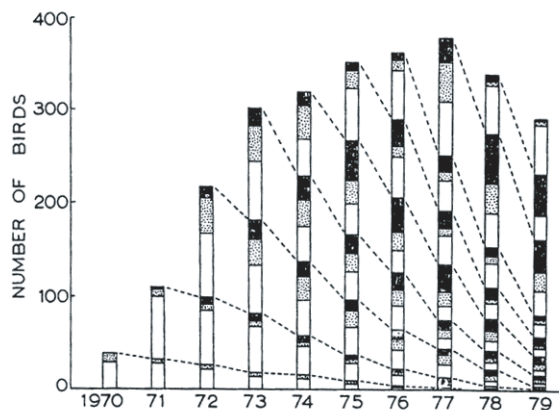
FIGURE 6. *Age structure of female starlings breeding at Belmont. 1970-79. Key: open columns - adult females 2 years or older; stippled - first-year females; black - females reared at Belmont returning to nest. Dashed lines separate annual cohorts. The final column is approximately 10% low because birds missed have not been recorded in subsequent years.*

(Table 2) that fine analysis in unnecessary: annual mortality at Belmont (34 %) is similar to that elsewhere in New Zealand (33%), and very distinct from the high mortalities recorded in all the other countries listed (51-70%).

To investigate the low mortality rate in New Zealand, we tabulated the causes of death (Table 3). Compared with Britain, far fewer starlings are shot and more are killed by cats. This suggests that the low mortality in New Zealand might be a result of the lack of shooting here. However, although mortality rates based on recoveries of shot starlings in Britain (59.8%) exceed the average (52.8%), rates from starlings dying of all other causes (including cats) lay between 49.4 and 54%; and in London, where most starlings are killed by cats and relatively few are shot, the mortality rate is 49.2 % (Coulson, 1960). Hence the lack of shooting in New Zealand does not seem sufficient to explain the greater longevity here.

Deaths among adult starlings at Belmont during the nesting season followed a different pattern. Many were unexplained and veterinary examinations of 8 such birds by Wallaceville Animal Research Centre revealed no obvious cause of death. Some of these may have resulted from fighting. Of 36 pairs of birds picked up fighting in boxes (19 male, 17 female, but no mixed pairs) many were locked together with their feet grasping the other's bill. Claws penetrated

the eye socket in at least a dozen birds, two blinded starlings were found, and deaths caused in this way would be very difficult to diagnose.

DISCUSSION

Sokal and Rohlf (1969) make a useful distinction between a biological population, which comprises the individuals found in a given area at a given time and a statistical population, which is all the individual observations about which inferences are to be made. At Belmont the biological and statistical populations of starlings are the same, which is unusual and important to remember. Thus, the average clutch size of adult females in our boxes was 4.48 eggs. As all clutches are included, this is the exact population mean, not a sample with confidence limits; and because Belmont is a bleak, atypical area for starlings to nest in, this -average clutch size is not likely to apply to any more widespread statistical population. If one wished to study population dynamics of the starlings of the Wellington region, existing nest sites should be examined, or perhaps a few widely scattered boxes.

This limitation of the study area seems most marked in estimates of productivity. Of 17 326 eggs laid, only 33.3% produced young to 12 days old, by which age most were likely to fledge, with extremes of 20.4% and 42.0% in different years. In comparison, 89.3 % of eggs gave rise to fledged young in Germany (Schoenfeld and Brauer, 1972), 81.0% in Holland (Lack, 1948), 78.6% in Canada (Collins and de Vos, 1966), 76.1 % in America (Kessel, 1957), and 60.7% in Scotland (Anderson, 1961). Gibo *et al.* (1976) found that productivity varied from 63.9% in good habitats to 15.7% in marginal habitats with heavy predation in Ontario, Canada. In Finland, at the northern limit of the starling's range, productivity was 32.1% (Tenovuo and Lemmetyinen, 1970) - almost the same as at Belmont. Within New Zealand, other estimates range from 27.6% in the Manawatu (powlesland, 1976) to 63.5% in Canterbury (Coleman, 1972), and 25% for natural sites in Hawke's Bay (D. G. Dawson, DSIR, pers. comm.). The high levels of production in most studies may simply reflect a tendency for workers to provide good-quality nest boxes in favourable areas.

The average of 1.92 chicks per occupied box per year at Belmont seems far lower than normal; indeed productivity as high as 5.2 chicks per occupied box was recorded for 3 I boxes at Ohau, only 60 km north of Belmont, in 1977 (P. C. Bull, DSIR, pers. comm.). Nevertheless, even 1 chick per pair is sufficient to maintain the Belmont population, because so few adult birds die. The 72 % annual

TABLE 2. *Age at death and average annual mortality rates (%) of starlings banded as chicks in New Zealand and other countries*.*

Year of Death	New Zealand		USA	USA	USA	Belgium	UK	Czech.	Germany	Switz.
1	24	31	104	95	152	42	737	679	64	433
2	21	15	43	44	74	20	337	203	30	97
3	17	21	31	22	38	6	157	52	12	45
4	17	10	16	11	17	4	85	21	3	8
5	3	3	9	5	9	0	33	11	0	7
6	5	10	1		8	1	19	8	0	1
7	5	1	0		4	1	11	10	1	0
8	1	3	1			0	3	4		0
9		2				1	1	2		0
10							1	1		0
11								0		0
12								1		1
13								2		
14								1		
15								2		
Total	93	96	205	177	302	75	1384	997	110	592
Average annual mortality ± S.E.**	34±3	33±3	51±3	56±3	52±2	54±4	53±1	62±1	62±5	70±2

Notes: * Data, in order, from this study, NZ Banding Office, Kessel (1957), Frankhauser (1971), Stewart (1978), Delvingt (1962), Coulson (1960), Beklova (1972), Schneider (1955), and Lack and Schifferli (1948).
** Lack and Schifferli's (1948) method, with S.E. from Haldane (1955).

return at Belmont is far higher than the 50% reported by Kluijver (1935) and Kessel (1957) for the return of marked breeding starlings in Holland and America respectively. The difference could be partly explained by our large study area and number of boxes, but probably mainly reflects different mortality because most female starlings return to the same boxes in subsequent years. The mortality rate based on starlings banded as young at Belmont is similar to that over the rest of the country, and both are about half the rates found in Europe and America (Table 2). Niethammer (1970), who first pointed out the exceptional longevity of introduced passerines in New Zealand, suggested that it might be a result of reduced predation. Comparative predation levels are very difficult to assess however, and the predators present in New Zealand may have fewer alternative foods. Increased longevity seems a feature of tropical avifaunas (Snow and Lill, 1974)

despite high numbers of predators, so the absence of severe winters is a more likely explanation.

High mortality might be expected to follow high clutch size in a stable population where births and

TABLE 3. *Cause of death (%) of 151 starlings at Belmont during the breeding season, and as reported by the public for 53 birds from Belmont, 278 from the rest of New Zealand, and 1384 from the UK (Coulson, 1960).*

	Found at	Reported by public		
Cause of death	Belmont	Belmont	NZ	UK
Found dead	76	51	58	67
Killed by cat	2	32	27	8
Shot	0	2	3	18
Killed by stoat	12			
Fighting	7			
Other	3	15	12	7

deaths must balance. Swiss starlings, with the highest mortality rate (70%) lay on average 5.2 eggs per clutch (Lack, 1948) compared with 4.5 eggs at Belmont where the mortality rate is almost exactly half (34 %). Hence the difference in clutch size seems too small to explain the low mortality of adult birds in New Zealand, and it is hard to see how the very variable annual production of young could affect the mortality of old ones.

The increase in numbers breeding over the first 4 years was linear, in proportion to (and probably a result of) the numbers of boxes provided (Fig. 6). With unlimited nest sites, the population increase could be expected to be logarithmic, as the Christmas bird censuses have shown it to be in America (Davis, 1950). Although many empty boxes seemed available, the difference in occupation rate of boxes with central and side holes showed that the birds were very critical when they had a choice of sites, and the proportion of boxes used did not vary uniformly with time (Table 1). In addition, as boxes were only 2-3 m apart, aggressive birds may have prevented others from using adjacent boxes. Even with 500 boxes on the 1500 ha area, nest sites still seemed to be limiting. Rough counts of starling flocks on the study area in winter suggested that the total population increased from an initial 300 birds in 1969 to at least 3000 in 1978, and most of these must be unable to find nest sites.

The population dynamics of starlings, and probably other hole-nesters, are complicated by these large numbers of potential breeders which cannot find nest sites; mortality affects the whole population, but the fraction that nest provide all the recruitment. Such species will normally have excess food available when nesting, to which Cody (197 I) attributes their relatively large clutch sizes compared with open-nesting birds. Lack (1968) suggested that freedom from predation allowed hole-nesters to raise more young more slowly on a given supply of food, while open-nesters were better to raise a few young as quickly as possible. Woodpeckers, which construct their own nest holes, have clutch sizes of 5.9 eggs on average, intermediate between hole- (6.9) and open-nesters (5.1), based on data from central Europe in Tables 11 and I3 in Lack (1968). This may be a measure of the relative contributions of predation and abundance of nest sites to the clutch size of hole-nesting species; but studies using nest boxes seem unlikely to provide the type of data needed to explain what happens under natural conditions.

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