CLUTCH SIZES OF INTRDOUCED EUROPEAN PASSERIFORMES IN NEW ZEALAND

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INTRODUCTION

One of the most thrilling subjects for any student of evolution and systematics is species radiation as shown by birds on island archipelagos. Classical examples of this phenomenon are Darwin's Finches on the Galapagos Islands and Honey Creepers on the Hawaiian Islands. Species radiation is an historical process apparently developed over long periods, which, in the absence of fossil material, can only be reconstructed from the present day knowledge. Such evolutionary radiations can under certain circumstances proceed much faster. For example, the descendants of Rabbits *Oryctolagus cuniculus* introduced to the island of Porto Santo, in the Madeiras, developed into a small island race within 500 years, and those liberated on Diah and Theodore Islands, near Crete, developed into a subspecies *O. c. knossius* characterised by different colouration. The rapidity of the morphological changes in the above examples is greatly overshadowed by the changes which have occurred in House Sparrows *Passer domesticus,* introduced to North America. Selander and Johnston (1963), using large series of specimens, were able to show that strong selection pressures, such as extreme dryness and heat, have caused populations there to develop into well defined subspecies, characterised by colour and size, within a period not exceeding 50 years. Such evolutionary processes are of course not restricted to morphological characters alone, but also affect certain physiological characteristics. From these observations we can assume that careful analysis of introduced animals will throw more light on the manner and speed with which evolution proceeds. As New Zealand is a classical example of a country with numerous introduced mammals and birds (33 species of mammals and 34 species of birds have become established following introduction) it offers a unique opportunity for similar research.

My interest therefore was to study the morphology and ecology of introduced European mammals and birds in New Zealand and to compare them with European representatives of the same species. For this purpose I collected series of as many species as possible. In addition I was able to study introduced European passerines in the field.

I restrict myself here to a single aspect — clutch size of introduced European passerines in New Zealand. Such a study seems appropriate as the population density of these birds in New Zealand appeared in many localities to be much higher than anywhere in Europe.

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THE MATERIAL

It was known to field ornithologists with Central European and New Zealand experience, that in general, clutch sizes of introduced European passerines in New Zealand are smaller than in Central Europe (F. C. Kinsky, pers. comm.). In the House Sparrow, D. Dawson (pers. comm.) found from observations on 277 clutches observed in detail in Christchurch, that the average clutch size was 3.81 eggs. However. in England the average clutch size is 4.1, and in North America 4.73 eggs. These differences are significant. I show in Table 1 that the same tendency applies to the clutch sizes of Song Thrushes, Blackbirds, Starlings, Goldfinches and Chaffinches. Sufficient numbers of Blackbird clutches were available from New Zealand (see Fig. 1) to allow me to show that, as with British Blackbirds, the clutches during the middle of the breeding period are the largest. However, average New Zealand clutch sizes for periods throughout the breeding season proved to be significantly and consistently lower than those calculated for corresponding periods throughout the breeding season of British populations. For other species insufficient numbers of clutches were available from New Zealand to allow corresponding subdivisions of their breeding periods, and averages have been calculated for the entire breeding periods. Though statistical evidence could not be obtained, the trend towards smaller clutches with Yellowhammers, Greenfinches, Redpolls and Skylarks in New Zealand is evident. If a small series of 48 clutches can be taken as sufficient proof, Hedge Sparrows in New Zealand seem to have the same clutch

TABLE 1

Species	New Zealand n	clutch size	mean clutch	S.D.	England n		mean clutch	S.D.	Significance of difference
Turdus philomelos Song Thrush	569	(2) 3-5 (6)	3,92	0,54	1156	(2) 3-5 (6)	4,09	0,67	+
						Botanical Garden			
					222	1-6	3,84	0,83	+
Turdus merula Blackbird	218	(1) 2-5	3,44	0,73		Forest			
					125	3-5	4,10	0,66	+
Sturnus vulgaris Starling	49	2-6	4,16	0,85	194	2-7	4,81	0,80	+
Fringilla coelebs Chaffinch	44	1-5	3,64	0,70	1433	2-6	4,3	0,74	+
Passer domesticus[1] House Sparrow	277		3,81				4,1		+
Emberiza citrinella Yellowhammer	16	1-4	3,06	0,85	81	1-5	3,42	0,70	-
Carduelis chloris Greenfinch	18	4-5	4,55	0,50	1343		4,76		-
Carduelis carduelis Goldfinch	129	2-6	4,60	0,64	215	3-7	4,83	1,29	+
Prunella modularis Hedgesparrow	48	2-5	3,87	0,65	1845		3,90		-

1) according to Dawson, Ms

TABLE 1 — Comparison of full clutch sizes of nine species of European passerines introduced to New Zealand. New Zealand populations have on an average statistically smaller clutch sizes (+ = significant on the 0.5% level). The data for *Passer domesticus* were calculated from D. Dawson (Ms.), the British clutch sizes extracted as follows: for *Turdus merula* and *T. philomelos* from Snow (1955 and 1958), for *Sturnus vulgaris* from Dunnett (1955), for *Fringilla coelebs* from Newton (1964), and for *Emberiza citrinella* from Packhurst and Lack (1946). The data for *Carduelis carduelis, Carduelis chloris* and *Prunella modularis* were obtained through Mr. Mayer-Gross from the British Nest Record Scheme.

sizes as they have in England (see Table 1). For Rooks no comparative material is available as the 40 clutches mentioned by Bull (1957) as having an average of 3.4 eggs could have been either unfinished or reduced. Lockie (1955) shows that in early clutches of English Rooks the average was 4.3.

Therefore, out of 12 species of passerines in New Zealand, six species produce significantly smaller clutches and 4 species very probably produce smaller clutches, but the latter still has to be verified by further observations. The smaller New Zealand clutch size probably also applies to Rooks. Only one species, the Hedge Sparrow, apparently does not differ in clutch size from ancestral English populations. As the differences in clutch sizes between passerine birds introduced into New Zealand and the comparative British populations are evident and real, the question arises as to the reason for these differences.

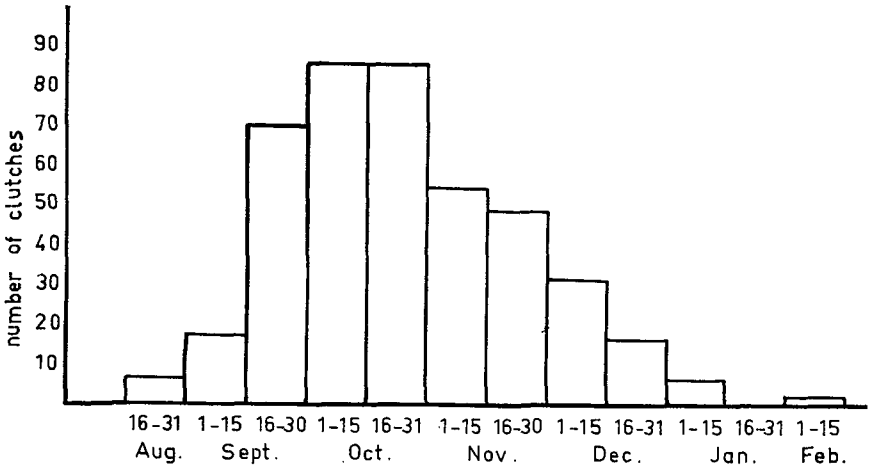

FIGURE 1 — The semi-monthly distribution within the New Zealand breeding period of 429 accumulated Blackbird *T. merula* clutch records, extracted from the O.S.N.Z. Nest Record Scheme.

DISCUSSION

The clutch size in individual species is mainly dependent on availability of food. If sufficient food is available to enable large broods to be raised, large clutches are more advantageous to nidicolous species than smaller clutches. The number of descendants, many of which could lay larger clutches again, would be greater. However the mere presence of food in the birds' habitat is not as important as its accessibility. Differences in food quality between England and New Zealand have not been studied as yet.

According to Lack (1966), the clutch size depends on the available daylight hours, which during the breeding period increase from the equator towards the pole. The longer the day the more time for feeding and the greater the possible survival rate of the chicks. New Zealand is situated between 34° and 47.5° south latitude, England between 50° and 59° north latitude. This difference in latitudinal position of the two countries leading to longer days in England during the breeding season, as compared with New Zealand, might be assumed to be significant and to be partly the reason for reduced clutch sizes in New Zealand. So as to test the validity of this assumption, I have compared in Table 2 the clutch sizes of two species (the Blackbird and the Song Thrush) originating from the north and the south of New Zealand. This table shows that there are no latitudinal differences in clutch sizes for these two species in New Zealand. If daylight hours had been significant for clutch sizes, this would have been shown in this comparison. As this was not the case, other reasons will have to be looked for.

It has been found in England that Blackbirds breeding in the countryside (forests, etc.) lay significantly larger clutches than those living in cities and gardens (see Table 1; Botanical Gardens). Havlin

TABLE 2

Species	Locality	n	clutch size	mean clutch	S.D.
Turdus merula Blackbird	North Island	122	2-5	3,41	0,70
	South Island	96	1-5	3,48	0,78
Turdus philomelos Song Thrush	North of North Island	148	2-5	3,91	0,49
	Southern South Island	141	2-5	3,84	0,58

TABLE 2 — Comparison of clutch sizes of Blackbird and Songthrush populations of northern and southern New Zealand. Sufficient data were available for the Songthrush to compare populations of the northern third of the North Island with the southern two-thirds of the South Island. The average clutch sizes show no differences attributable to latitude, or daylight hours.

(1963, b.) arrived at similar results in his investigations of Blackbirds in Czechoslovakia, where he found that city Blackbirds with a population density four times that of forest-inhabiting Blackbirds, laid somewhat smaller clutches than the latter. The population density of city Blackbirds in England is ten times higher than that of forest Blackbirds. Lack (1966) in discussing these results comes to the conclusion that city Blackbirds start breeding earlier, lay somewhat smaller clutches, have less food available for their broods, but have fewer enemies, and thus more fledglings survive. Most of the factors applying to European city Blackbirds also apply to the majority of introduced passerines in New Zealand. Blackbirds in New Zealand start breeding in August (which corresponds to February in Europe), i.e. one month earlier than in England (see Fig. 1). The breeding period is longer, which means that on the average more clutches are produced per year in New Zealand. Watson (1954) has shown that the breeding period for rabbits in New Zealand is also longer than the corresponding period in England and Spencer and Steinoff (1968) have shown for mammals, that an increase in the number of litters per season corresponds to a decrease in the number of young per litter.

Gurr (1954) reports that in the Blackbird " fledging success is lower in New Zealand than in Great Britain " and an analysis of New Zealand nest record data shows that 43% of all nestlings die before fledging. Out of a total of 220 nests with clutches, chicks fledged out of only 73. This indicates that approximately 66% of all nests with clutches are unsuccessful. However, as predation pressure on adult birds can be assumed to be very much smaller in New Zealand than in England, this is presumably one of the main reasons for the high population density of introduced birds in this country. However, no comparative figures on predation are available up to date.

TABLE 3

	Europe		New Zealand	
	years	months	years	months
Turdus merula Blackbird	9	1	8	1
	8	4	7	2
	7	11	7	1
Turdus philomelos Song Thrush	13	9	6	-
	9	2		
	8	0		
Prunella modularis Hedge Sparrow	7	10	6	3
	6	9		
	5	9		
Fringilla coelebs Chaffinch	10	0	6	3
	9	11	5	9
	8	3	5	4
Carduelis flammea Redpoll	6	1	6	2
	4	3	6	2
			6	2
			5	2
Passer domesticus House Sparrow	13	0	7	4
	13	0		
	8	8		

TABLE 3 — Comparison of longevity records of some passerines introduced to New Zealand (banded and re-trapped by S. L. Lobb, Gorge Road, Southland) with corresponding results from Europe. Six of the thirty oldest birds tabulated (i.e. one-fifth) were recorded from New Zealnd, where up to the present day only 4,500 of these six species have been banded, all within the last decade.

How quickly a bird population increases if all potential predators are eliminated can be seen from experiments made in two areas in the Province of Nordrhein-Westfalen, Germany. In these two areas throughout a period of seven years all potential enemies of pheasants and partridges (i.e. dogs, cats, foxes, polecats, stoats, weasels, crows, magpies, etc.) were systematically destroyed, and no new liberations were made. Within that period the population of pheasants increased 14 times and the population of partridges 6 times in one of these areas, and in the other area the pheasant population increased 13 times, as compared with an average increase of 30% within the whole province (H. Frank, pers. comm.).

I would now like to make a few remarks on longevity of introduced birds in New Zealand, as I believe that lack of predators brings about longer life expectancy. Although bird banding in New Zealand has been done for too short a time to enable true comparisons with European results to be made, S. L. Lobb of Gorge Road, Southland, has been able to obtain some surprisingly good longevity records from banding and re-trapping passerines in his back garden. In Table 3 the records obtained by S. L. Lobb are compared with longevity records obtained in Europe. These show that three of Lobb's oldest Redpolls are absolute records, and that three further records exceed second or third oldest European records in three other species (Redpolls, Hedge Sparrows, Blackbirds).

As to clutch sizes, it has been shown in Blackbirds, Great Tits and Starlings, and in particular, according to Berndt and Winkel (1967), in Pied Flycatchers, that older birds lay larger clutches than first-breeders. It could be expected that the ratio of older birds to first-breeders in New Zealand is higher than in Europe. Therefore average clutch sizes should be larger, but this is not the case. It can be assumed that healthier birds will arise from smaller clutches. From this it can be further assumed that smaller clutches would be favoured by selection. Mayr (1965: 325) states the same idea, as follows: "In tropical localities, where adults have a high life expectancy, there may actually be a selection pressure in favour of small clutches."

As an example of the high population density of some passerines in New Zealand, I would like to mention N. B. Mackenzie's three-acre peach orchard near Taradale. During a period of four months (17 October to 19 February) Mackenzie recorded 98 Goldfinch nests in his orchard, with a total of 397 eggs. From these, 249 young hatched, and 195 of these fledged. As New Zealand Goldfinches can produce three clutches per year (Mackenzie pers. comm.), as compared with two clutches in England, it can be assumed that about 33 pairs bred in the orchard, i.e. 11 pairs per acre. This unusually high population had an average clutch size of 4.05 eggs. As already established for birds and mammals, high population densities are correlated with small clutch or litter sizes. This has been further demonstrated by Kluijver (1951) for the Great Tit *Parus major* and Reichstein (1964) for the Mole *Microtus arvalis*. Such a correlation between population density and numbers of eggs or embryos repectively is not surprising as high population density depresses other elements of the reproductive potential. In regulation theories on population-ecological problems, density-dependent, intraspecific competition is

always presented as the only factor, or is placed at the top of all contributing factors. These work in a similar way to the feed-back in Cybernetics.

In New Zealand this dependence of clutch sizes on population density could be successfully demonstrated by comparing, for example, the Blackbird and the Chaffinch in areas of high population and in areas where the population is still relatively low, such as in bush country.

It has been said that the number of young is closely connected with the food supply available during the nesting period. As a good example of this, Walter (1968) showed that the western populations of Eleonora's Falcons *Falco eleonorae* on the Moroccan coast can catch more passerine birds in longer day hours and therefore raise more chicks per season, than eastern populations of the same species near Crete. The former lay an average of 3.05 eggs, while the latter lay only 2.1 eggs per clutch. The main pre-requisite for a high population density is a high food supply. Any rise in population density reduces the available food supply. At the same time too large a population brings about disturbances between pairs breeding too closely together and consequently the available food supply is not properly used. Thus the amount of food fed to chicks is reduced and smaller clutch sizes become advantageous, as smaller numbers of chicks would have a better chance of survival. Selection would therefore give preference to smaller broods until a point is reached when all chicks hatched have a chance to survive. These thoughts outlined here correspond to conceptions developed by Lack.

However, the question arises as to the possibility of a population reacting directly, without genetical alteration, to overpopulation by reducing clutch sizes. In this connection I would like once again to discuss findings in mammals. In some rodents, for example Voles and Lemmings, overpopulation occurs periodically, and this leads to increased excitement and aggressiveness, and to reduced food intake, reproduction and growth rate. All these factors are controlled by hormone changes and in particular by increased adrenalin production. Such a sudden physiological reaction brought on by population pressure in mammals induces an immediate adjustment between available food and reproductive rate. This could possibly occur in passerine birds, as some non-passerines react directly to available food supplies, independently of population density. It was found that some owls, such as Barn Owls *Tyto alba,* Short-eared Owls *Asio flammeus* and Snowy Owls *Nyctea scandiaca,* independent of any population factors, not only lay larger or smaller clutches according to the availability of food, but also do not breed at all if food is scarce. The German Owl *Athene noctua* normally lays only three eggs in New Zealand (Falla et al., 1966), whereas it lays normally 4 - 5 (exceptionally 6 and 7) egg clutches in Germany. This can be interpreted as meaning that food supplies for the German Owl in New Zealand are less favourable than they are in Germany.

SUMMARY

A comparison of clutch sizes of 12 species of passerine birds introduced to New Zealand from Europe showed that six species, *Turdus philomelos, Turdus merula, Carduelis carduelis, Fringilla coelebs, Sturnus vulgaris* and *Passer domesticus,* lay significantly smaller clutches

in New Zealand than they lay in the British Isles. For five of the remaining species data are insufficient to allow exact statistical comparisons, but available results indicate the same trend, i.e. smaller clutches for the New Zealand populations. Only one of the 12 species, *Prunella modularis*, does not differ from the English populations as to clutch size.

It has been shown that the daylight hours available for feeding during the breeding period did not influence clutch sizes in Song Thrushes and Blackbirds. Clutch sizes produced by populations in the north of the North Island and the south of the South Island do not differ in the least. I have suggested here that smaller clutches in New Zealand can be attributed to high population density and to the subsequent mutual disturbance of breeding pairs, causing diminished use of available food. In order to maintain population numbers in spite of smaller clutch sizes, as compared with England, more clutches are laid by individual breeding pairs during the longer breeding period in New Zealand.

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