dominated by Allolobophora caliginosa or A. terrestris, were found.

These examples can be taken as typical of what has happened wherever native vegetation has been cleared and replaced by pasture. There has been no competition between native and introduced species, either for food or for living space. All but subsoil species among the native earthworms have died out before the introduced lumbricids became established, and the few subsoil earthworms that have remained do not compete with the lumbricids, as the latter are confined to the topsoil.

Where native vegetation has not been interfered with introduced earthworms are usually absent, and if present they are usually rare. An exception to this generalisation is found at Raoul Island, where the dominant earthworm of forest litter and topsoil is Eisenia foetida, an introduced lumbricid. E. foetida is usually found in New Zealand, and in Europe, in compost and manure heaps, and is rare in agricultural soils. Its presence in forest soils at Raoul Island probably results from the high rate of decomposition of forest litter in a warm climate, producing conditions that would not be found in forests in the cooler climate of New Zealand. In addition to the higher rate of litter breakdown, the spread of E. foetida has apparently been facilitated by the absence of native topsoil earthworms on Raoul Island. The native earthworm fauna

of Raoul consists of only two species of very small leaf mould earthworms. So in this case too, there has apparently been no competition either for food or for living space between introduced and native species.

The introduction of European earthworms has been accompanied by far reaching changes in the soil environment, brought about by man. The result has been that the native earthworm fauna has been destroyed, but its destruction stems directly from the man-induced environmental changes, and is not a result of interaction between introduced and native species. The same can be said of many groups of soil invertebrates, and may well be true of other animal groups.

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# THE INTERACTION OF NATIVE AND INTRODUCED BIRDS IN NEW ZEALAND

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The purpose of this paper is to outline the factors which are believed to influence the status of native and introduced birds—including their interaction—and as a background it will be necessary to re-examine the history of settlement. Some effects of settle-

ment are obvious: the clearing of forest and the acclimatisation of birds from overseas were major events transforming certain aspects of the environment. Other events, especially the arrival of mammalian predators and probably of avian diseases, did not at first seem unduly important and are still little understood. All these events moved so rapidly that any form of scientific record, if attempted, would have been difficult; and, today, the opportunities for research are restricted to investigations of bird populations that are already modified. The extent of modification, is however, largely unknown.

It is necessary, in attempting to assess the effect of settlement upon native and introduced birds, to consider the history of modification in some detail, both from contemporary accounts of the course taken by settlement and through what is known of changes in the bird fauna. Intensive settlement began in about 1850 (there had been local settlement for several decades earlier), and from this date until approximately 1920 there was rapid and extensive change: forest was cleared and other environments (especially swamp) were changed or eliminated. Introduced birds became established while these changes were in progress.

In the writer's opinion too much importance has been attached to the total effect of environmental modification. Too little consideration has been given to the fact that the country was, indeed, settled in an irregular, or "patchwork", pattern. Comparatively soon after the establishment of the first settlers, a certain amount of tree and shrub cover which could be used by forest species would probably be available. The settlers' gardens and orchards and their hedgerows, shelter belts and plantations were becoming established as the forest was destroyed. Much would have depended upon the extent of nearby forest clearing, but certainly in most districts there were remnants, at least, of forest even though much was cleared.

The modification of the environment was not simultaneously in progress throughout the country. In 1880 settlement in the South Island was advanced, while the forests of the centre and south of the North Island were still little touched. The plains of the South Island — clothed in tussock and scrub — were especially tractable, and the comparatively small areas of bush were readily cleared. In the North Island, the main period of forest clearing in the lowlands of Taranaki and the Manawatu did not occur until 1880-1910; the forests of the hill lands of the North Island were still being destroyed

actively up to 1925 (Masters, Holloway & McKelvey 1957, Cumberland 1949).

It is only possible to surmise the effect of this pattern of environmental change upon the native species: early accounts at least make it clear that some evidently adaptable forest birds appeared in settled environments from the first — fantail (Rhipidura fuliginosa), grey warbler (Gerygone igata), silvereye (Zosterops lateralis) and morepork (Ninox novaeseelandiae); the silvereye, an Australian self-introduced arrival of the early settlement period, is a special case. The kingfisher (Halcyon sancta), an inhabitant of both forest and open areas, also expanded into modified habitats. These are still common species in modified as well as unmodified habitats. For a further species, the falcon (Falco novaeseelandiae), the introduced birds represented a new source of prey, but shooting prevented it from expanding into settled areas.

J. Kikkawa, who is at present studying forest bird populations, suggests that fantail, grey warbler and silvereye may prefer the forest edge habitat, and may thus have readily entered the newly established exotic vegetation, and even regenerating native vegetation, soon after settlement (pers. comm.).

It seems reasonable to believe that those forest species which were slower to adopt modified environments found at least some food in the newly settled districts. These are species which now appear to be increasing (discussed below, under present trends).

Open country produced by settlement was probably acceptable from the first to harrier (Circus approximans) and pipit (Anthus novaeseelandiae): the harrier now includes in its range strictly pastoral country, but the pipit is found in rough pasture and waste land, avoiding pure pasture. (An extension of habitat was also provided for certain waders, not discussed here.)

Introduced species were liberated in the new settlements. It is notable that of 125 species brought to New Zealand, some 90 species were liberated during the period 1860-1880 (Wodzicki 1950). They thus arrived at a comparatively early stage, doubtless spreading in the wake of settlement. Inform-

ation on the introduction and spread of every species is given by Thomson (1922) and Guthrie-Smith (1921). Of the total, only 25 are now established species.

As mentioned above, certain native forest birds from the first appear to have entered modified environments where there were trees. Tree cover is also one of the requirements of most of the introduced species, and this may have meant some interspecific competition between native and introduced species. Whatever its extent, this did not preclude the establishment of certain species, both native and introduced. The present blend of native and introduced species in modified environments seems stable, but the increase in the number of native species in such environments possibly may upset the balance.

It is noteworthy that only a few introduced species now occur in forest: blackbird (Turdus merula), song thrush (Turdus ericetorum) and chaffinch (Fringilla coelebs) are the only species within the forest; the hedge sparrow (Prunella modularis) occurs in forest edges; and the redpoll (Carduelis flammea) at the subalpine level in both open country and forest. Whether there was interspecific competition when these introduced species became established cannot now be determined, for the forest bird populations may already have changed. Certainly there now appear to be stable, or increasing, populations of these introduced species in forest. So far there has been no indication that introduced species "drive out" native species, as is often popularly supposed.

Certain partly seed-eating introduced species probably spread rapidly into native grasslands; and several species, notably the redpoll, are at present well established in the remaining relatively unmodified grasslands now limited to the alpine zone. As mentioned earlier, most of these are species which may feed in the grassland but require shrubs or trees for shelter and nest sites; the skylark (*Alauda arvensis*) is the main exception. The appearance of introduced seed-eating birds in grassland might have affected only one native species, the New Zealand quail (*Coturnix novaezeelandiae*); but it was extinct by 1870.

In summary, this account has dwelt particularly upon the native forest birds which were able to become established in the environment produced by settlement. It should be stressed that the destruction of forest meant violent transformation of the environment over large areas. Relatively few forest birds adopted the modified environment, but these — together with introduced birds — produced the mixture of native and introduced species now found throughout settled districts. Native forest and grassland habitats were entered by a few introduced species.

It is not intended to suggest that the ecological results of settlement are over. It is possible to be more specific, for there is a record of increasing occupation, since about 1920, of the modified environment by native birds. One reason for this may be that there has been little change in the extent of native vegetation in most areas for some time. In addition, exotic trees and shrubs have reached maturity: shelter belts, hedges, plantations and orchards are now well grown, and are in established positions. The tendency of native species to enter such vegetation is especially marked in plantations of pines and other exotics, which now have vigorous populations, native and introduced (Gibb 1961); the adoption of plantations of mature age by forest species in Britain has been recorded by Lack (1933, 1939).

Of other factors which may have caused this increase, legal protection probably has had considerable effect. Up to 1895, legislation was entirely devoted to the introduced birds — more especially game species — and a comprehensive and effective bird protection Act did not appear until 1921. It is perhaps significant that this so closely coincided with the last stages of intensive deforestation. Writings of the succeeding period form a direct contrast with those of the beginning of the century: thus Myers (1923) was already speaking hopefully of the position of a range of native species, in contrast with Buller (1905) who expressed the widely held opinion that the extinction of a large proportion of native forest birds must inevitably result from settlement. The latter opinion was so widely prevalent during the period of settlement that it must, in a number of ways,

have aggravated the adverse effect of man upon the native birds.

For certain species, e.g. the bellbird (Anthornis melanura), apparently the only factor which could have caused the acute reduction in population was disease. Reinvasion of areas from which species were eliminated by disease would probably later occur, and for the bellbird this is, in fact, taking place in one area (Turbott 1953).

The principal species that appear to be increasing in settled habitats are the kiwi (Apteryx australis), weka (Gallirallus australis), pigeon (Hemiphaga novaeseelandiae), bellbird and tui (Prosthemadera novaeseelandiae). Others, especially tit (Petroica macrocephala), rifleman (Acanthisitta chloris), brown creeper (Finschia novaeseelandiae) and kaka (Nestor meridionalis), may appear in modified habitats, but probably require an adjacent forest area. The extent to which the latter requirement applies to the other species listed is not knewn. An investigation of the present status, and history as far as known, of each of these species would be of the greatest interest. As pointed out by the writer (Turbott 1957) such species contrast markedly with those forest birds which cling to the native forests that remain, and show no tendency to appear in environments to any extent modified.

The writer believes that population changes of native birds such as those mentioned provide an opportunity to obtain information on the ecology of these birds, and especially their interaction with introduced birds. There is also the possibility of further changes in the populations of introduced birds, such as the recent northward expansion of the myna (Acridotheres tristis) in the Auckland district.

Specifically, interaction between native and introduced birds may occur in four ways:

(1) Competition for food.

(2) Competition for nest sites.

(3) Aggressive behaviour.

(4) Predation.

Of these, interaction through competition for food is indirect, but information on food can be compared and might prove to be cor-

related with population changes. However, there has been little detailed investigation of foods of native and introduced birds so far. A notable exception is that of Marples (1942) on the little owl (Athene noctua). Every opportunity should be taken to develop such studies, if possible in relation to population change, e.g. investigation of competition in settled districts by bellbird for insects, and by pigeon for fruits and buds. The introduced chaffinch is numerous, and possibly increasing, in most native forest areas and may compete for insects with native birds.

Competition for nest sites, most readily observed in hole-nesting species, has been recorded frequently between introduced starling (Sturnus vulgaris) and native king-fisher. An additional report, which is likely to be of similar competition, refers to the disappearance of the morepork in the Christ-church suburban area simultaneously with the increase of the little owl (L. W. McCaskill, pers. comm.). However, these species now occur together in other parts of the South Island. Recently chasing of one species by the other was reported to the writer in the foothills of Canterbury.

Aggressive behaviour (which may include territorial behaviour) is exemplified by the Australian magpie (Gymnorhina hypoleuca), which frequently chases both native and introduced species, although this is sometimes actually predation. While it is doubtful whether aggressive behaviour alone would result in the exclusion of a species (cf. the interaction of the red and introduced grey squirrels in Britain), strongly aggressive and/or territorial introduced species may have this effect. Specially interesting were early observations on the Australian magpie by Moon (1956), who recorded the destruction of two successive clutches in a nest of the Australian white-faced heron (*Notophoyx* novaehollandiae) soon after the arrival of the latter species in North Auckland. Yet, subsequently, the heron has had a history of successful establishment throughout New Zealand, in areas with large populations of magpies, and it seems possible that the incidents recorded by Moon were competition for a nest site.

Predation of introduced species by the native falcon was mentioned earlier; the Australian magpie has been recorded killing

native species on various occasions; and the food of both native morepork and introduced little owl includes small birds, either native or introduced.

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# RELATIONS BETWEEN SALMONIDAE AND THE NATIVE FRESHWATER FAUNA IN NEW ZEALAND

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The freshwaters of New Zealand provide an environment into which relatively few exotic species have penetrated, partly because the problems of survival during transportation are so difficult for a freshwater animal as to make accidental immigration very unlikely, and partly because the motives which may stimulate deliberate importation by man are so few in this case. So much remains to be done in the study of our freshwater fauna that a number of exotic species of the smaller invertebrates may exist unrecorded in this country, but the known freshwater fauna of non-native origin is limited to one snail and some dozen species of fish all deliberately introduced.

Most of the fish were introduced to provide sport, and it is not surprising that a large proportion of them belong to the Salmonidae since in its native Northern Hemisphere this family contains the majority of the most highly regarded game species. Of the species that were introduced, two have established themselves successfully over a large part of the country, and a third in a more restricted area. These are the brown and rainbow trouts (Salmo trutta and S. gairdnerii) and the quinnat salmon (Oncorhynchus tschawytcha) respectively. A few other species exist in small numbers in limited areas. For simplicity, I propose to limit consideration of the introduced freshwater fauna largely to these few highly successful species of Salmonidae; both because of their widespread abundance and because, on account of their popular esteem, they have been relatively intensively studied.

It should be realised that fresh waters