bacon); black epidermis and white muscle, and white muscle from the body wall of the holothurian *Holothuria atra*. Each of the foods was placed in a separate glass jar and carried to a species-rich fringing reef near Leong Creek where they were separately hand-fed to approximately 20 fish each time (30 May 1979), principally damselfish [*Abudefduf coelestinus* (Cuvier, 1830)], *Paraglyphidodon* [*Abudefduf*] *melas* (Cuvier, 1830), and a few wrasses (*Halichoeres* sp.). A second series of similar foods was prepared, consisting of bait (uncooked, unsmoked bacon), black epidermis, and plastic-coated (Varathane exterior liquid plastic) items. Small pieces of black epidermis and of epidermis with white muscle of *H. atra* were dipped in liquid plastic and air-dried, carried to the same reef, and fed to fish (2 June 1979).

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# Extinctions and Introductions in the New Zealand Avifauna: Cause and Effect?

Abstract. *New Zealand, like many other islands, has suffered extinctions of native species and successful introductions of exotic species. It has been uncertain whether the introductions caused the extinctions or whether the extinctions permitted the introductions. On New Zealand's Hauraki Gulf islands, which are unusual in their near lack of introduced mammalian predators and complete lack of mammalian browsers, exotic bird species abundant in mainland New Zealand forest and reaching these islands are virtually absent from unmodified forest. Exotic bird species disappeared from Cuvier Island's forest after elimination of mammalian predators and browsers. Hence extinctions of native species were not due to competition from introduced species but to other factors (such as mammalian predators and habitat alteration). Only after decimation of native species and forest alteration by browsing mammals could exotic birds invade forest.*

On many oceanic islands, native plant and animal species have become extinct since discovery by Europeans, while species introduced from elsewhere ("exotic species") have become established. In fact, island populations account for most modern extinctions and many currently endangered species (*1*). A familiar example is the Hawaiian avifauna, which lost native species and gained exotic species introduced from Asia and North America, such that in most of Hawaii one sees mainly introduced birds (*2*). The causes of these extinctions, and their relation to the introductions, are much debated. Did competition from exotics contribute to extinctions of natives? Were the extinctions instead due to factors such as predation, disease, and habitat changes? Are island communities ecologically saturated, such that exotics can become established only at the expense of natives (*3*)? These questions are of practical importance for conservation, as well as theoretically interesting.

We explored these problems in nonmarine bird communities of Pacific islands. Especially instructive are distributions of native and exotic species on islands of New Zealand's Hauraki Gulf, islands that are unusual in their almost complete lack of introduced European mammals (*4-7*).

Avifaunas of tropical Pacific islands illustrate the difficulties in understanding how introductions of exotics relate to extinctions of natives. On seven archipelagoes (New Guinea, Bismarcks, Solomons, New Hebrides, Figi, Samoa, and Cooks) no exotic bird species occurs in closed forest, and the native avifauna is nearly intact (no extinctions among forest passerines). Interpretation of these facts is equivocal, because all the introduced species are ones confined to open habitats in their land of origin and do not penetrate closed forest even when native forest passerines are few and rare (for example, Rarotonga of the Cook Islands). Thus, these archipelagoes yield no clue whether competition from exotics affects natives, or whether natives can exclude exotic invaders. In Hawaii numerous introduced bird species are ones that do occur in forest in their land of origin and have become common inside native Hawaiian forest (*2*). However, the native Hawaiian forest avifauna has been decimated (13 species are extinct, and 12 are nearly so), and introduced mammalian predators and browsers are widespread. Hence, without further information it cannot be decided whether extinctions of native Hawaiian birds were the cause or result of exotic species penetrating the forest. Similarly, in Tahiti the introduced *Zosterops lateralis* is common in forest, but native forest passerines are extinct or rare, so that the causative relations remain unclear.

Comparison of mainland and island bird communities in the New Zealand archipelago permits us to distinguish cause and effect. New Zealand's biota evolved in the absence of nonmarine mammals except bats. Since man and his associated mammals arrived, New Zealand's avifauna has suffered heavy losses. Subfossil remains show that at least 34 native nonmarine bird species became extinct during the Maori occupation before Europeans arrived (*8*, *9*). Of the approximately 77 native nonmarine species present when European settlement began in the early 19th century, about 8 have become extinct and 13 have become rare or local. At least 143 exotic species, many of them forest birds in their land of origin, were introduced in the 19th century, and about 34 remain established (*8-10*). The causes of the native extinctions are debated (*8*, *11*). Suggestions include (i) predation by introduced mustelids, cats, and rats, as is illustrated dramatically by rapid extinctions of populations of five species on Big South Cape Island after ship rats (*Rattus rattus*) arrived in 1962 (*12*), (ii) reduction in forest area by clearing, (iii) changes in forest structure, and depletion of native food plants important for birds, by introduced browsers (deer and other cervids, goats, pigs, and Australian possums), (iv) competition from introduced bird species, and (v) diseases.

The situation on the New Zealand mainland (North and South Islands) is as follows. Introduced mammalian predators and browsers are widespread. Six of the 16 native forest passerine species present on European discovery are now either absent (extinct, or confined to offshore islands), or else rare and local. Introduced species are common even within large tracts of closed native forest. For example, censuses during breeding season in 28 mainland native forests by J.M.D. (Table 1) showed that five introduced European passerines (*Fringilla coelebs, Turdus merula, Turdus philomelos, Prunella modularis, Acanthis flammea*) account for 18 ± 12 percent (mean ± standard deviation) of all bird individuals; the self-introduced Australian passerine *Zosterops lateralis* accounts for 13 ± 10 percent; and native forest passerines account for only 64 ± 12 percent (the remaining 5 percent are native nonpasserines). Censuses by others (*6*) yield similar results: European passerines, 17 ± 12 percent; *Z. lateralis*, 10 ± 6 percent. Indeed, *Z. lateralis* is often the most abundant bird species in native forest, and *F. coelebs* and (less often) *T. merula* are sometimes among the five most abundant species. In open habitats and in forests of exotic tree species, exotic bird species are far more abundant than native ones.

Most large, forested, offshore islands in the New Zealand region support introduced mammalian predators, browsers, or both. Unusual in this respect are some islands in Hauraki Gulf including Little Barrier Island (area, 3053 ha) (*13*), Hen Island (476 ha), and several smaller islands known as the Chickens. These islands have no nonvolant mammals except the Polynesian rat (*Rattus exulans*), plus cats on Little Barrier. Little Barrier is the largest island of the New Zealand group free of browsers, mustelids, and European rats. Little Barrier and Hen are largely covered by climax forest little affected by humans (*14*). Because browsers are absent, the forest on these islands differs structurally from browsed mainland forest in the greater leaf litter, denser and more varied understory, and greater abundance of native food plants (for example, *Coprosma* species) used by birds. Lady Alice (138 ha) and Mauitaha (20 ha) islands of the Chickens group differ in that they were burned by Maoris in the recent past and now support a more open successional forest, in an earlier successional stage on Mauitaha than on Lady Alice. The sole native land bird population that was found on these islands in the 19th century and that subsequently disappeared is *Philesturnus carunculatus*, which was exterminated on Little Barrier by cats. Little Barrier supports every native forest bird species that is widespread on the North Island mainland, plus the sole surviving population of the honeyeater *Notiomystis cincta* (now extinct elsewhere). Hen is similar except for having retained *P. carunculatus* and for lacking *N. cincta, Acanthisitta chloris, Mohoua albicilla*, and *Petroica australis*. The number of resident native bird species is about 20, 13, 12, and 8 for Little Barrier, Hen, Lady Alice, and Mauitaha, respectively; of resident native forest passerines, about 9, 6, 6, and 4.

Relative abundances of bird species in Little Barrier forest differ greatly from those in mainland forest (Table 1). To observers accustomed to mainland bird communities, the most astonishing difference is the virtual absence of the five common European exotics and the Australian *Z. lateralis* in Little Barrier forest. We observed occasional *Z. lateralis*, plus occasional *T. merula* and *F. coelebs* (mainly at the forest edge), accounting in breeding season for only 0.2 percent of all bird individuals (compared to 19 to 38 percent in mainland forest). Kikkawa's counts of birds per acre in breeding season yield the same conclusion (*5*). This near absence of introduced species from the forest is not due to lack of access, as nine introduced species (including *Z. lateralis* and four of the five European species common in mainland forest) breed in the 20-ha clearing around the ranger's house, and nine other introduced species have been recorded as visitors. Evidently, introduced species that penetrate mainland forest are excluded from Little Barrier forest. Similarly, introduced species are absent from Hen forest except for an occasional *T. merula* and *Z. lateralis*.

The relative abundances of native species also differ between Little Barrier forest and mainland forest, notably in Little Barrier's much higher abundance of *M. albicilla*, *Anthornis melanura*, and *Prosthemadera novaeseelandiae* and lower abundance of *Gerygone igata*. These differences are those expected from the absence of browsing mammals and predators on Little Barrier (*15*).

In most of these respects the avifaunas of Lady Alice and Mauitaha are intermediate between those of Little Barrier and Hen, on the one hand, and the mainland, on the other, with Mauitaha being more mainland-like. Thus, exotic species (mainly *Z. lateralis*, *T. merula*, and *F. coelebs*) occur regularly in forest on Lady Alice and Mauitaha, in greater numbers on Mauitaha; *Z. lateralis* is about the second most common forest bird spe-

Table 1. Relative abundances of bird species in climax native forest. Relative abundances are average values calculated from numerous censuses in breeding season. Kikkawa data are from (*5*). Absent indicates absent from the entire island.

| Avifauna | Little Barrier Island | | New Zealand: North Island | New Zealand: South Island |
|---|---|---|---|---|
| | Veitch | Kikkawa | Diamond | Diamond |
| *Native species* | | | | |
| *Hemiphaga novaeseelandiae* (N.Z. pigeon) | 0.7 | 1.7 | 0.3 | 1.0 |
| *Cyanorhamphus* spp. (parakeets) | 15.2 | 2.0 | 0.9 | 3.3 |
| *Nestor meridionalis* (kaka) | 0.3 | 1.4 | 1.4 | 1.4 |
| *Nestor notabilis* (kea) | Absent | Absent | Absent | 0.7 |
| *Chalcites lucidus* (shining cuckoo) | 0.0 | 0.0 | 0.7 | 0.3 |
| *Eudynamis taitensis* (long-tailed cuckoo) | 0.0 | 0.0 | 1.3 | 0.9 |
| *Acanthisitta chloris* (rifleman) | 5.0 | 1.4 | 14.6 | 11.6 |
| *Rhipidura fuliginosa* (fantail) | 2.9 | 5.0 | 2.6 | 4.1 |
| *Petroica macrocephala* (tomtit) | 4.3 | 5.3 | 7.8 | 12.1 |
| *Petroica australis* (robin) | 0.4 | 2.2 | 0.1 | 0.9 |
| *Finschia novaeseelandiae* (brown creeper) | Absent | Absent | Absent | 4.2 |
| *Mohoua* spp. (whitehead, yellowhead) | 34.5 | 45.8 | 4.6 | 4.9 |
| *Gerygone igata* (grey warbler) | 4.0 | 3.8 | 28.3 | 14.6 |
| *Notiomystis cincta* (stitchbird) | 6.8 | 5.0 | Absent | Absent |
| *Anthornis melanura* (bellbird) | 10.1 | 13.7 | 2.6 | 10.2 |
| *Prosthemadera novaeseelandiae* (tui) | 15.8 | 12.4 | 4.8 | 1.1 |
| *Self-introduced species* | | | | |
| *Zosterops lateralis* (silvereye) | 0.1 | 0.0 | 12.0 | 14.6 |
| *Exotic species* | | | | |
| *Turdus philomelos* (song thrush) | 0.0 | 0.0 | 0.5 | 0.9 |
| *Turdus merula* (blackbird) | 0.1 | 0.2 | 5.2 | 3.7 |
| *Prunella modularis* (dunnock) | 0.0 | 0.0 | 0.7 | 1.1 |
| *Acanthis flammea* (redpoll) | 0.0 | 0.0 | 0.4 | 2.3 |
| *Fringilla coelebs* (chaffinch) | 0.0 | 0.0 | 11.0 | 6.0 |

cies on both islands; and *G. igata* is more common than on Hen and Little Barrier.

Changes with time on another offshore island, Cuvier, are also instructive. Until 1959 Cuvier supported cats, wild goats, and domestic stock animals, and at least five exotic bird species bred in the forest. After eradication of cats and goats and fencing of stock by 1964, a dense understory regenerated, and the four European exotics disappeared from forest, the Australian *Z. lateralis* nearly disappeared, and *G. igata* declined. These changes are the same as the ones observed when one goes from mainland forest to Little Barrier.

From these facts we draw the following conclusions.

1) Exotic species that successfully penetrate browsed mainland climax forests with decimated native bird communities are excluded from unbrowsed island climax forests with intact native bird communities. We can speak with confidence of exclusion as opposed to nonarrival, because exotic species breed on Little Barrier immediately outside the forest.

2) We accept that mammalian predators are an important factor in the decimation of native birds, and hence in the success of exotic birds, in mainland forest. However, predators are not the whole answer: exotics penetrate the forests of Lady Alice and Mauitaha despite these islands being as predator-free as Hen and more so than Little Barrier.

3) Two observations suggest that the effect of browsing on mainland forest structure is also an important factor. First, Little Barrier's forest avifauna differs from that of the mainland not only in the absence of exotic species but also in the altered relative abundances of native species, and these alterations are mostly ones expected from lack of browsing. Second, alterations in forest structure due to succession have allowed exotic bird species to enter forest on Lady Alice, and even more on Mauitaha. The changes in relative abundances of bird species, as one proceeds from Little Barrier or Hen to Lady Alice to Mauitaha, are qualitatively similar to the changes observed along a similar successional gradient on the mainland, where exotic bird species are most dominant in the most disturbed habitats (*16*).

In short, we infer that exotic bird species were not able to achieve their present penetration into New Zealand forest until the forest structure had been disturbed by browsing and logging, or until native species had been decimated by predation, disease, and these habitat changes. (The relative importance of these two factors remains unknown.) This conclusion suggests that control of introduced mammals is crucial to the future of New Zealand's surviving avifauna in native forest.

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15. Absence of browsers results in more abundant, less disturbed leaf litter on the ground, denser lower and middle stories, and fewer openings, as well as in more food plants for birds. The denser forest is related to the increased abundance of *M. albicilla*, which gleans on foliage and limbs, and to the decreased abundance of *G. igata*, which prefers disturbed forest with openings. The honeyeaters *A. melanura* and *P. novaeseelandiae* exploit native plants for fruits and nectar. Nests of *P. novaeseelandiae* and possibly *M. albicilla* are especially vulnerable to mammalian predators.
16. Does the varying penetration of exotic species into island forest depend on the varying local number of native forest bird species? This interpretation is refuted by two facts: mainland forest has about as many native bird species as Little Barrier, and Lady Alice has about as many as Hen; yet, in each case exotic species are common in forest on the first-named island of the pair but virtually absent on the second. Hence we infer that the dependence is instead on abundance of native bird species, which depends in turn on forest structure.
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## Associative Learning in *Aplysia*: Cellular Correlates Supporting a Conditioned Fear Hypothesis

Abstract. *Aversive associative learning in* Aplysia californica *survives restraint of the animal and surgical exposure of the central nervous system. The learning is expressed in the intracellularly recorded activity of identified motor neurons mediating three different defensive behaviors: escape locomotion, inking, and siphon withdrawal. In each case, animals that had previously received paired training showed significant facilitation of synaptic input to motor neurons during test stimulation in the presence of the conditioned stimulus. Animals without such training showed no facilitation of input to the motor neurons. Resting potential and input resistance appeared unaffected by conditioning and were not altered by application of the conditioned stimulus. These results show that the conditioned facilitation of defensive responses cannot be explained by subthreshold actions of the conditioned stimulus on the motor neurons and support the hypothesis that* Aplysia *learn to associate the conditioned stimulus with a fearlike central state.*

Aversive conditioning of *Aplysia californica* produces a learned response resembling conditioned fear in vertebrates. After a chemosensory conditioned stimulus (CS, shrimp extract) is paired with an aversive unconditioned stimulus (US, head shock) the CS becomes capable of enhancing defensive responses and reducing at least one appetitive response (*1*). Although one defensive behavior (head withdrawal) is directly elicited by the CS after training, three other defensive behaviors (escape locomotion, inking, and siphon withdrawal) are not elicited by the CS, yet they are significantly facilitated if they are elicited by other

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