The Editor Sir

## Response to R. Holdaway

We would like to thank Holdaway (this issue) for his comments concerning our article (Rhodes et al. 2009). Holdaway points out the absence of groundnesting cavity nesters and those that nest "under cover" in our analysis of the potential roles of predation, microclimate, and cavity abundance in the evolution of tree-cavity nesting in New Zealand. We considered these beyond the scope of our paper, although we did note ground-nesting cavity species in our Fig. 1. Eliminating ground cavity-nesting birds from our analysis was done in part because few authors that study secondary cavity-nesting forest birds examine ground cavity-nesters. In many forested habitats, ground cavities are uncommon, and are utilized in much lower percentages compared to tree cavities, especially by smaller bodied forest birds (Camprodon et al. 2008). While ground cavities may seemingly offer attributes similar to tree cavities, the 2 types of sites differ in terms of quality (e.g. abundance, exposure to flooding, or nesting success; Robertson 2009). This is not to say that "covered nests" or "ground cavities" do not possess advantages, but for comparative purposes with the international cavity-nesting literature we chose to concentrate only on tree cavity nesting birds. We recognize that investigations into the use of ground nests or "covered" nests of cavity-nesting forest birds have been lacking, and we welcome any future investigations. Regardless, including ground cavity or "covered" nesting species would likely not change the overall conclusions of our paper, and if anything, they might suggest an even higher dependence on "cavities" generally compared to other places in the world.

We believe that Holdaway has misinterpreted our Fig. 1 as a phylogenetic analysis. His comments related to systematic relationships of some native birds we refer to are correct. However, our intention was to simply list the nesting habits of New Zealand's land birds. We did not intend for any other relationships to be inferred from our Fig. 1 beyond the names of taxonomic groups.

We acknowledge that understanding predation pressures in pre-human New Zealand is likely to be complex. Our aim was not to project past predation rates, but to convey that predation pressures were potentially *different* in a pre-human New Zealand (largely avian predatory guild) compared with continental habitats. Mammalian and reptilian predators (e.g. snakes) possess advantages over birds when preying on cavity nests, in part because of their well developed sense of olfaction. Most birds possess a limited sense of olfaction, and must detect prey visually or through sound, which is more difficult when nests are normally not visible and nesting birds can remain motionless or not call to avoid generating sound. Even if a cavity nest is located, larger bodied birds (e.g. New Zealand falcon) cannot enter cavities with the ease or frequency of small bodied mammals or predatory reptiles. However, Holdaway's statement that there was likely "little or no predation" on closed nests in pre-human New Zealand (presumably because many predatory birds are unable to access small cavities) may be inaccurate as some bird species are still able to prey on cavity nesters as they exit the nest or by reaching inside (Sedgeley & O' Donnell 1999). Even with the much greater abundances of potential avian cavity nest predators in the

past (e.g. morepork, long-tailed cuckoo), what is important to note is that the frequency and nature of predation was likely different [e.g. predatory mammals are more likely to kill incubating adults (O'Donnell *et al.* 1996)] from continental systems that possess abundant mammalian and reptilian guilds as well as avian predators.

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