4 Have Frugivores Influenced the Evolution of Fruit Traits in New Zealand?

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Introduction

Fruit-eating animals tend to consume many species of fruit and, likewise, the fruits of plants tend to be consumed by a wide range of animals (Herrera and Jordano, 1981; Wheelwright et al., 1984; Pratt and Stiles, 1985; Charles-Dominique, 1993; Howe, 1993; Larson, 1996; Corlett, 1998; Herrera, 1998). Because of this, the relationship between fleshy-fruited plants and frugivores is diffuse rather than consisting of tight mutualisms (Janzen, 1980; Howe, 1984; Jordano, 1987; Charles-Dominique, 1993). It is thus not surprising that frugivore characteristics rarely appear to influence the evolution of fruit traits (Hedge et al., 1991; Mazer and Wheelwright, 1993; Rey et al., 1997). There is, however, clear empirical evidence that frugivores could exert selective pressure on fruit traits. Frugivorous birds, for example, show preferences related to fruit colour, presentation, accessibility, level of insect damage and fruit size (Moermond and Denslow, 1983; Gautier-Hion et al., 1985; Jordano, 1987; Hedge et al., 1991; Whelan and Wilson, 1994; Puckley et al., 1996; Sanders et al., 1997; Gervais et al., 1999), when selecting among fruits on a single plant, fruits of individuals of the same species or fruits of different species (Levey, 1987; Debussehe and Isenmann, 1989). However, even when preferences are clear, they may have no directional effect on the evolution of fruit traits, because the composition and abundance of the frugivore assemblage can vary significantly over time (Herrera, 1998). Instead, if frugivore preference influences the evolution of fruit traits at all, it would most probably be via general characteristics of the frugivore assemblage or of dominant guilds of frugivores.

Differences in feeding ability or preferences between guilds of frugivores (e.g. birds and mammals) have been linked to differences among fleshy-fruited species in fruit colour, size, odour, protein and lipid content and degree of protection. This has lead to the description of fruit syndromes associated with particular frugivore guilds (van der Pijl, 1969; Janson, 1983; Gautier-Hion et al., 1985; Howe, 1986; Debsushe and Isenmann, 1989). However, the concept of syndromes is problematic; the traits used to define them vary from study to study, as does the composition of frugivore guilds. Consider mammalian frugivores as an example: the classical mammal dispersal syndrome involves large, husked or protected, brown, green, orange or yellow fruit, which are often odoriferous and low in protein content.
However, mammals differ enormously in their size, visual acuity and ability to access and manipulate fruit (e.g. primates vs. rodents vs. elephants; Gautier-Hion et al., 1985). Thus, the classical mammal dispersal syndrome does not apply, in its entirety, to all mammals, and it is wrong to expect it to do so. Conversely it does not necessarily exclude some mammals (e.g. Fischer and Chapman (1993) erroneously associated the syndrome with diurnal mammals). A more constructive approach is to identify frugivore traits that should be logically associated with certain fruit traits, and vice versa. For example, fruits dispersed by terrestrial frugivores should fall at maturity; large, fleshy, single-seeded fruits should be consumed by large-gaped frugivores; fruits mainly dispersed by nocturnal frugivores are unlikely to be coloured but likely to be odoriferous; and husked fruits are likely to be consumed by a dexterous frugivore. Specifically testing for an association between, for example, green, odoriferous fruits and a nocturnal mammalian frugivore (Tamboia et al., 1996) is a much more productive way to examine the relationship between frugivores and fruit traits.

Another very productive approach to examining the influence of frugivores on the evolution of fruit traits is to make use of biogeographical variation in the composition of frugivore assemblages. In particular, studies of fruit traits on islands that lack, or have lost, particular guilds of frugivores (e.g. Fischer and Chapman, 1993; see also McConkey and Drake, this volume) can provide a wealth of insights. The aim of this study is to examine the New Zealand fleshy-fruited flora for traits associated with the features of the main New Zealand frugivore guilds. New Zealand has a flora with some unusual features and, because of its isolation, it also has, or had, an unusual frugivore assemblage. The next section describes the New Zealand flora and then identifies three frugivore guilds. These are then each examined in detail with reference to specific fruit traits to test whether these frugivores have influenced fruit evolution in New Zealand.

Characteristics of the New Zealand Fleshy-fruited Flora

Approximately 25% of New Zealand’s indigenous plant genera and c. 12% of its species produce fleshy fruits (we use ‘fruit’ in the functional, not structural, sense). The distribution of fleshy-fruitedness in the flora has a historical component; fleshy-fruitedness is more common among genera that have a pre-Miocene pollen record in New Zealand than among genera with more recent pollen records, perhaps because the fragmented nature of the New Zealand land mass during the early–mid-Tertiary selected for highly vagile taxa (Lord, 1999). In prehuman New Zealand, the majority of fruits would have been consumed by birds or reptiles, because, with the exception of two species of bat (see below), no mammalian frugivores were present.

The New Zealand fleshy-fruited flora has three interesting features:

1. Fruits tend to be small (Fig. 4.1) \(\bar{X} = 6.4 \pm 3.8 \text{ mm (sd), maximum} = 18.9 \text{ mm; length: } \bar{X} = 7.7 \pm 5.4 \text{ mm, maximum} = 33.5 \text{ mm} \). This is significantly less than the mean for 332 tropical and temperate bird-dispersed angiosperm species (diameter: \(n = 332, \bar{X} = 10.2 \pm 5.4 \text{ mm}; \) length: \(n = 266, \bar{X} = 11.9 \pm 7.2 \text{ mm} \); Jordano, 1995; two-sample T-tests: length, \(|T| = 4.2, \text{ d.f.} = 510, P < 0.001; \) diameter, \(|T| = 3.8, \text{ d.f.} = 576, P < 0.001\).

2. Fruits tend to become more elliptic in shape with increasing size (Fig. 4.2); when log (fruit width) is regressed on log (fruit length), following Herrera (1992), the slope is significantly less than 1 (reduced major axis regression, slope = 0.8342, 95% confidence interval = 0.7530–0.9235, \(n = 67\); methods on fruit dimensions provided in section on volant birds, below). This relationship between fruit size and shape is not a feature of all floras; fruit length and width scale isometrically in the flora of the Iberian Peninsula (Herrera, 1992) and among bird-dispersed plants in Malawi (Mazer and Wheelwright, 1993). Mazer and Wheelwright (1993) did find that fruit became more elliptic with increasing size within a single species, within the Lauraceae and among...
bird-dispersed species of lower montane forests in Costa Rica. The relationship between fruit size and shape in the New Zealand flora is not just a product of the taxonomic mix of species present; when the same analysis was applied to 32 temperate and subtropical Australian species in 21 New Zealand genera, the 95% confidence interval for the regression slope encompassed one. 

3. The distribution of fruit colours is unusual (all colours mentioned refer to the human visual spectrum). No species have green fruits at maturity and only two species have brown fruits (*Fremcetia baueriana, Pandanaceae – see discussion below of mammalian frugivory; *Peperomia urvilleana, *Piperaceae, minute brownish drupes). Species with white or pale blue to sky-blue fruits, simultaneous bicoloured fruit in which one colour is white or pale blue, or species polymorphic for fruit colour in which one morph has white fruit, make up 21.2% of the fleshy-fruited flora (Fig. 4.3, 9.8% white, 8.6% polymorphic or bicolour, 2.9% pale blue or sky-blue; henceforth, these colour classes will be referred to collectively as white- or blue-fruited). This is collectively a higher proportion than has been observed for other temperate floras (Iberian Peninsula: 2.7% white, 15.3% blue (Herrera, 1989); Florida: 7.9% white, 3.9% blue; Europe: 5.2% white,
7.3% blue (Wheelwright and Janson, 1985); note that ‘blue’ may involve different hues and brightnesses in these floras).

New Zealand Frugivore Guilds

New Zealand frugivores can be classified into three guilds differing in size and ability to access fruits. These guilds are: (i) flightless birds, many of which were large and most of which are extinct; (ii) volant birds, including both extinct and extant species; and (iii) lizards. Mammalian frugivory has probably not been important in New Zealand. The only land mammals native to New Zealand are three species of Microchiroptera. Two of these species, the lesser short-tailed bat (Mystacina tuberculata) and the greater short-tailed bat (Mystacina robusta), are known or thought to have eaten fruit; however, M. tuberculata is now uncommon and M. robusta became extinct in the 1960s (Daniel, 1976; King, 1998). Mystacina tuberculata is known to consume the fruits of Collospermum species, monocot epiphytes with small red or white berries, and F. baueriana, a monocot liana with large, cream, succulent bracts surrounding a brown, pulpy, infructescence (Daniel, 1976). In areas where M. tuberculata is locally extinct, F. baueriana bracts and fruits are apparently being eaten by the introduced marsupial Trichosurus vulpecula (Lord, 1991).

Flightless avian frugivores

Humans arrived in New Zealand approximately 1200 years ago. Since then, nearly half of the avifauna, including many flightless birds, have become extinct, either as a direct result of hunting or as a result of introduced predators, such as rats (Rattus rattus, Rattus norvegicus, Rattus exulans), cats (Felis catus) and stoats (Mustela erminea). Many extinct flightless birds are known (from subfossil gizzard remains) or thought to have eaten fruit (Burrows et al., 1981; Clout and Hay, 1989; Holdaway, 1989; Gill and Martinson, 1991). Among extant flightless birds, weka (Gallirallus australis) and kiwi (Apteryx species) are minor frugivores (Clout and Hay, 1989). Fruit can be a
seasonally important component of the diet of kakapo (*Strigops habroptilus*), but, like most parrots, this species chews and cracks larger seeds and so must be regarded primarily as a seed predator, although small seeds can be voided intact (Best, 1984; Clout and Hay, 1989).

If flightless birds were significant seed-dispersers in prehuman New Zealand, one would expect to find fleshy-fruited species that dropped their fruits at maturity. New Zealand has several large-fruited species that do so (e.g. *Elaeocarpus* spp., *Dysoxylum spectabile*, *Corokia carpus*), but insufficient information is available to determine the frequency of this trait in the flora and whether it is associated with large fruits. However, features of some species that drop their fruit suggest that conspicuousness rather than food value per se may play a role in attraction. *Dysoxylum* seeds are surrounded by a conspicuous, thin, orange aril. The drupes of *Elaeocarpus* spp. are purple-brown and have very little pulp (17.3% of fruit dry weight for *E. hookerianus*), but the fruit exocarp has a metallic sheen that is highly visible on the forest floor. *Sophora microphylla* (*Fabaceae*) is not fleshy-fruited, but has conspicuous, tough-coated, bright yellow seeds which drop to the ground when the pods rupture. Some extant flightless birds are known to consume objects with apparently little food value; Australian emus pick up conspicuous objects readily (Eastman, 1969, in McGrath and Bass, 1999), and brown kiwi (*Apertyx australis*) pick up fruit of *Elaeocarpus dentatus*, possibly as substitute gizzard stones (Clout and Hay, 1989).

**Moas as frugivores**

The group of extinct flightless birds about which we know the most are the moas (Aves: Dinornithiformes), which were ratites most closely related to South American rhea species (*Rhea americana* and *Pterocnemia pennata*) (Cooper et al., 1993). New Zealand had at least 11 moa species prior to the arrival of humans. These species ranged in body mass from approximately 15 kg to 270 kg and were distributed throughout New Zealand (Cooper et al., 1993). Among extant ratites, the Australian cassowary (*Casuarius casuarius*) is the most highly frugivorous. Its diet tends to include species with large fruits that are often black or yellow/orange (Crome, 1976; Wilsson et al., 1989). Emus (*Dromaius novaehollandiae*) and rhea species also consume fruit, although their diets are composed mainly of grasses and herbs (Davies, 1978; Martella et al., 1996; Quin, 1996).

**WERE MOAS MAJOR OR MINOR FRUGIVORES?** Gizzard samples retrieved from swamps in South Island, New Zealand, representing 19 individuals in three moa genera (16 *Dinornis*, one *Eurapteryx* and two *Emeus*) (Falla, 1941; Gregg, 1972; Burrows et al., 1981), contain a wide variety of fruit, often in substantial amounts. The most complete gizzard sample described to date contains 851 seeds representing 16 fleshy-fruited species, in 4250 cm$^3$ (420 g) of plant material, with a further 2200 cm$^3$ (5.6 kg) of gizzard stones (*Dinornis* 12B, Pyramid Valley) (Burrows et al., 1981). A second, probably complete, gizzard sample from the same location contains 2216 seeds, representing 12 fleshy-fruited species in 1500 cm$^3$ of plant material (*Dinornis* XI) (Burrows et al., 1981). These samples suggest that fruit was an important component of the diet of some moa species.

**DID MOAS EXHIBIT FEEDING SELECTIVITY WITH REGARD TO FRUITING SPECIES OR FRUIT SIZE?** The majority of the gizzards described to date (16 of 19) originate from one site, Pyramid Valley Swamp, and those that have been radiocarbon-dated are between 3450 and 3740 years old (Gregg, 1972; Burrows et al., 1981). Collectively, these 16 individuals had ingested the fruits of 20 species of shrubs, small trees and lianas, including all but three fruiting species known to be present at the site from pollen and macrofossil evidence (Moar, 1970; Burrows et al., 1981). The three fruiting species not consumed (two species of canopy tree, *Dacrydium cupressinum* and *Dacrycarpus dacrydioides*, *Podocarpaceae*, and a mistletoe, *Tulipia antarctica*) were probably not accessible to moas, as fruits of these species tend to persist on the plant and are consumed by volant frugivores. Some fruits do seem to have been favoured by moas, as individual birds appear to have concentrated on particular fruits in a feeding bout. In two of the 13 individuals...
with more than 50 seeds in their gizzard, *Corokia cotoneaster* (shrub with berries 7.2 mm × 6.3 mm) accounted for 60% and 70% of seeds. *Coprosma* species accounted for more than 75% of seeds in seven of these 13 individuals. The berries of *Coprosma* species can be moderately large (12 mm × 7 mm, *C. lucida*), but the only species definitely known to have occurred at the site are small-fruited species (berries 3.5–6.5 mm × 3.5–4.1 mm). Only three gizzard samples contained seeds from moderately large fruits. In two individuals with more than 50 seeds in their gizzard, *Prumnopitys taxifolia* (drupes 9 mm × 5 mm) accounted for 75% and 87% of seeds. The largest fruit found thus far in gizzard samples is *E. hookerianus* (drupes 10.8 mm × 7.1 mm), represented by one seed in each of two samples (Burrows et al., 1981).

**DOES THE FLORA CONTAIN ‘ANACHRONISMS’ THAT COULD BE RELATED TO MOA DISPERSAL?** ‘Anachronistic’ or puzzling characteristics of extant plants have been used as evidence for selection pressures exerted by extinct herbivores and frugivores (Janzen and Martin, 1981; Givnish et al., 1994), although the existence of tight coevolved mutualisms between fruits and frugivores has been questioned on numerous occasions (e.g. Howe, 1984; Jordano, 1987, 1995; Herrera, 1998). Herbivory by moas has been suggested as the selective pressure behind the evolution of heteroblasty and the divaricating growth form (densely interlacing tough stems, with small sparse leaves) in New Zealand (Greenwood and Atkinson, 1977; Cooper et al., 1993; Givnish et al., 1994). The role of moas as frugivores might also be judged by an examination of the New Zealand flora. Are there species with apparently ‘anachronistic’ fruits? The obvious distinguishing feature of moas is size; the largest moa species would have been capable of swallowing fruits > 5 cm in diameter (Clout and Hay, 1989). However, the New Zealand flora contains no extant species with very large fruits; as mentioned in the previous section, New Zealand fruits are characteristically small and the largest fruits are well below the gape size of the largest moa species (*C. laevigatus*, *Corynocarpaceae*, drupes 33.3 mm × 17.6 mm; *Beilschmedia* spp., *Laura- ceae*, drupes 33.5 mm × 18.9 mm). If there were species specialized for moa dispersal, it is unlikely that they would have completely disappeared in the short time since moas were extirpated. Moa species were plentiful until about 1000 years ago (Cooper et al., 1993), which is within the lifetime of the longest-lived New Zealand tree species and no more than a few generations for many other fleshy-fruited species. Also, no unusual plant remains, such as very large seeds, have been reported from subfossil deposits or moa gizzard contents.

**Conclusion: frugivory by flightless birds**

New Zealand’s extinct flightless birds may have been important in the dispersal of seeds from fallen fruit. However, information on fruit impersistence is lacking and present-day studies of fruit fate could be regarded as ambiguous – the fruit of extant fruiting species that were once consumed by volant birds may now fall to the ground uneaten, due to the loss of bird species and reduction in numbers of extant frugivorous species. However, it is likely that the extinct flightless avifauna, in general, played a role in seed dispersal simply because of their abundance. Fruit was undoubtedly an important component of moa diets, and *Dinornis*, at least, appears to have selectively consumed fruits of certain shrubby species. There is little evidence that large fruits were selectively consumed. The lack of information on diets of moas in the North Island is a problem, as the three largest-fruited species in the flora occur mainly on the North Island. These species do occur in the northern third of the South Island but not at any of the sites from which gizzard contents have been described. As the flora contains no obvious fruit ‘anachronisms’ suggestive of specialization to moa dispersal, it seems that moas were not sufficiently selective or important to influence the evolution of, at least, fruit size. This does not mean, however, that moas were unimportant for seed dispersal; like the Australian emu, they would have been capable of carrying large numbers of seeds over large distances (McGrath and Bass, 1999) and probably played an important role in the maintenance of regional plant biodiversity in New Zealand.
Characteristics of volant New Zealand frugivorous birds

Clout and Hay (1989) list 17 volant indigenous birds that consume or consumed fruit. They have gape sizes ranging from < 0.5 cm to 1.5 cm (Fig. 4.4), and are small-bodied compared with Australian volant frugivorous birds (Fig. 4.5) (one-way analysis of variance (ANOVA): $F_{1, 70} = 6.18, P < 0.05$). Of these 17 species, two are extinct (huia, *Heterolocha acutirostris*, gape size 1.5 cm; piopio, *Turnagra capensis*, gape size 1.1 cm) and many others are severely reduced in numbers and distribution (Clout and Hay, 1989). The largest extant volant frugivore is the New Zealand woodpigeon (*Hemiphaga novaeseelandiae*, gape size 1.4 cm) (Clout and Hay, 1989). Birds introduced by European settlers have become important frugivores in New Zealand.

Fig. 4.4. The relationship between gape width (data from Clout and Hay, 1989) and body mass (data from Dunning, 1993) for 13 extant volant indigenous New Zealand frugivorous birds.

Fig. 4.5. A comparison of body masses of extant volant frugivorous birds in New Zealand (solid bars) and Australia (open bars). Information on bird diet from Clout and Hay (1989) and MacDonald (1973). Body-mass data from Dunning (1993).
(Ferguson and Drake, 1999) and some, such as the blackbird (Turdus merula), song thrush (Turdus philomelos) and starling (Sturnus vulgaris), have gape sizes similar to extinct or rare indigenous passerines (e.g. piopio; saddleback, Philesturnus carunculatus) (Clout and Hay, 1989). However, the degree to which introduced frugivores can replace extinct or rare indigenous frugivores is debatable; introduced frugivorous birds in New Zealand may preferentially consume the fruit of introduced plants (Williams and Karl, 1996). All extant volant frugivorous birds in New Zealand are non-migratory generalists that eat a wide range of fruits (Lee et al., 1991).

Birds with broader gapes generally eat larger fruits and, conversely, large fruits are generally consumed by large frugivores (Wheelwright, 1985; Pratt and Stiles, 1985; Debusche and Isenmann, 1989; Williams and Karl, 1996; Corlett, 1998). Birds also select among fruits on the basis of size, even in a single feeding bout; they are more likely to reject or mishandle larger fruits (Levey, 1987; Rey et al., 1997). Theoretically, then, the gape-size distribution of the frugivore assemblage could act as an agent for selection on fruit size. Fruit size appears to be more sensitive to disperser-driven selection than other fruit traits; in a study of phylogenetic conservatism in fruit traits, Jordano (1995) found that fruit diameter showed recent evolutionary divergence correlated with disperser type. However, the probability that a fruit will be swallowed is not simply a function of its size, but also of its shape. For a given volume, spheri- cal shapes will be less easily swallowed than elongated shapes, as the maximum diameter will be larger for the former. This leads to the prediction that, if gape size has influenced the evolution of fruit shape, then, for a flora dispersed by a common set of frugivores, larger-fruit species should be more elongate than smaller-fruited species (Levey, 1987; Herrera, 1992; Mazer and Wheelwright, 1995).

The difference in body-mass distribution and, by implication, gape size between New Zealand and Australian volant frugivorous birds provides an opportunity to test for an effect of frugivore size on the evolution of fruit size. Body mass is certainly correlated with gape size, at least among New Zealand frugivorous birds for which data are available (Pearson’s $r = 0.956, n = 13$) (Fig. 4.4). New Zealand and Australia share many fleshy-fruited plant genera; 63 out of 93 fleshy-fruited New Zealand genera also occur in Australia (though represented by different species). If frugivore size, particularly gape size, acted as a selective pressure on the evolution of fruit size, one would expect that fruit of New Zealand species in these genera would be smaller than fruit of congeneric Australian species.

**Within-genus contrasts between New Zealand and Australian species**

For 20 genera, representing 18 families, that occur in both New Zealand and Australia, five to 20 fresh, ripe fruit (depending on accessibility and availability) were collected for New Zealand and temperate–subtropical Australian species (Tasmania and New South Wales). None of the Australian species had brown or green fruit – a trait often associated with dispersal by mammals. Fruit length and width were measured to the nearest 0.1 mm with vernier calipers and averaged for each species. Paired $t$-tests showed that fruits of New Zealand (NZ) species were significantly smaller overall than their Australian congeners (NZ width − Australian width: mean diff. = $-2.780$, $T = -3.00$, d.f. = 19, $P < 0.01$; NZ length − Australian length: mean diff. = $-3.009$, $T = -2.94$, d.f. = 19, $P < 0.01$).

**Conclusion: frugivory by volant birds**

The difference in size between New Zealand and Australian fruits and the general small size of fruits in New Zealand (Fig. 4.1) are consistent with the prediction that the smaller-sized volant avian frugivore assemblage in New Zealand has acted as a selective pressure on the fruit size of New Zealand fleshy-fruited species, both in respect of related species in Australia and across the flora as a whole. Also, the fact that fruit species in the New Zealand flora become significantly more elongated with increasing size (Fig. 4.2) suggests that selection has acted on fruit shape to maintain ‘swallowability’, despite increased fruit mass.
Frugivory by lizards

Studies of frugivory by lizards are relatively uncommon, but the phenomenon has been noted in many areas, including South Africa (Whiting and Greeff, 1997), the Bahamas (Iverson, 1985), the Canary Islands (Valido and Nogales, 1994; Nogales et al., 1998), the Balearic Islands (Traveset, 1995), New Caledonia (Bauer and Sadlier, 1994) and Central and South America (Traveset, 1990; Figueira et al., 1994; Willson et al., 1996). Whitaker (1987) lists four gecko species (Gekkonidae) and nine skink species (Scincidae) as fruit consumers in New Zealand. Many of these species are restricted to open grassland or shrubland habitats; however, lizards are also relatively common in forest habitats. Lizards would have been more widespread and abundant throughout New Zealand prior to the introduction of mammalian predators. For extinct species, we have no way of reconstructing diet. Hoplodactylus delcourtii, at 370 mm snout–vent length with a head width of 87 mm, was the largest gecko in the world. It is known from a single, poorly preserved, specimen in the Musée d’Histoire Naturelle de Marseille, France (Bauer and Russell, 1986). Extant members of the genus, which is restricted to New Zealand, consume fruit regularly (Whitaker, 1987). We shall never know the role of H. delcourtii as a frugivore, but it may very well have consumed large fruits and dispersed seeds.

What seed-dispersal services might a lizard be able to provide a fruiting plant that a bird could not? Lizards might be more abundant in certain habitats than birds and able to access fruits in dense growth, where the fruits are inaccessible to birds. Also, lizards might deposit seeds in more suitable microsites than would birds (e.g. crevices) (Valido and Nogales, 1994; Traveset, 1995; Wotton, 2000). Fruit preferences have been documented among frugivorous lizards. Gallotia galloti (Lacertidae) on the Canary Islands shows feeding selectivity with regard to fruiting species (Valido and Nogales, 1994). The Cape Flat lizard (Platysaurus capensis, Sauria, Cordylidae) has been shown to discriminate between figs on the basis of ripeness and colour/brightness, choosing red- over white-painted figs (Whiting and Greeff, 1997). A different colour preference has recently been demonstrated in two common New Zealand skinks, Oligosoma macannii and Oligosoma nigriplantare (J. Marshall, unpublished data). In replicated trials under controlled conditions, captive skinks showed a clear preference for white or blue Coprosma (Rubiaceae) berries (C. cheesemani white morph, C. aff. parviflora sp.’t’, C. propinqua, C. rugosa) over red berries (C. cheesemani red morph, C. decursa, C. robusta), when simultaneously offered fruit of each colour. An association between fruit colour and consumption by lizards is also apparent from field observations in New Zealand: eight of the 16 fleshy-fruited species listed by Whitaker (1987) as visited by lizards are blue- or white-fruited. This is more than would be expected based on the prevalence of these fruit colours in the fleshy-fruited flora as a whole (21.5%; \( \chi^2 = 7.6496, \text{d.f.} = 1, P < 0.01 \)). Chemosensory response is also important to lizard feeding behaviour, and has been shown to shift with corresponding changes in diet (Cooper, 2000). The Coprosma fruits used in the colour preference trial described above also appear to differ in volatile compounds, which may underlie lizard preference patterns. Initial trials with gas chromatography–mass spectrometry suggest that blue and, to a lesser extent, white fruits contain resinous compounds (e.g. terpenes), whereas red fruits contain fruity and sulphurous volatiles (J.-P. DuFour and J.M. Lord, unpublished data).

We suggest that lizard dispersal, in general, should be a feature of densely growing shrubs in which fruit is borne towards the interior of the plant and which occur in an arid environment in which seed deposition in a humid microsite is important to germination. The relationship between fruit size and colour and dispersal by lizards is likely to vary between countries, depending on the size and colour sensitivity of the herpetofauna. In New Zealand, we predict that a densely growing shrub growth form and open habitats should also be associated with small, white or blue fruits, given the colour preference described above for two common frugivorous skinks and given that the frugivorous New Zealand lizards...
listed by Whitaker (1987) are generally small (maximum snout–vent length ranges from 77 to 160 mm). New Zealand has a particular abundance of densely growing shrub species, termed ‘divaricates’. Divaricates are shrubs that have a high branching angle, twiggy interlacing growth and small, sparsely distributed leaves (Greenwood and Atkinson, 1977; Kelly, 1994). The fruits are often borne on the undersides of the branches, where they are relatively inaccessible to birds (although the small native passerine *Zosterops lateralis lateralis* (A.S. Markey, 1999, personal observation)). Lizards, on the other hand, can move easily through divaricate shrubs. These shrubs may also provide relatively protected basking sites, as the shrub *Larrea divaricata* (*Zygophyllaceae*) does for a species of Argentinian lizard (Deviana et al., 1994). The divaricating habit is also associated with exposed or dry habitats (McGlone and Webb, 1981). In such environments, lizards may deposit seeds in more sheltered microsites than would birds (Wotton, 2000). Lord and Marshall (2002) tested for an association between fruit colour, fruit size, growth form and distribution, first using the flora as a whole and then using various subsets of the flora, such as divaricate species, shrubs and subshrubs, and the genus *Coprosma*. They found that white or blue fruit colours were more common than expected among divaricate species, and among shrubs and subshrub species. White and blue fruits were also more common in open habitats and were associated with small fruit size, both among all fleshy-fruited species and among fleshy-fruited shrubs.

Many of the divaricating species in New Zealand are in the woody Australasian–Pacific genus *Coprosma* (*Rubiaceae*). *Coprosma* in New Zealand is highly variable for fruit colour; many species have red or orange fruit, but all colours, from white, pink and yellow to deep wine and purple-black, are represented among the approximately 55 species. Thus, the genus provides an opportunity to test for an evolutionary association between fruit colour, growth form, leaf size and habitat. Fruit colour in *Coprosma* is known to be related to both leaf size and habitat. Lee et al. (1988) found that red fruits were more common among large-leaved *Coprosma* and at higher altitudes and provided a greater colour contrast in leafy environments (Lee et al., 1994). Small-leaved *Coprosma* species at lower altitudes tended to have blue, white-cream or dark purple-black fruits.

A recently constructed molecular phylogeny for *Coprosma*, based on the ITS (internal transcribed spacer) region of nuclear ribosomal DNA (A.S. Markey and S. Wichman, unpublished data), indicates that fruit, leaf and growth form traits are all highly labile. A relationship between plant traits and fruit colour is, however, apparent among closely related groups of species. In two well-supported terminal clades containing both red- and white- or blue-fruited species and with a large-leaved, red-fruited, probable ancestor, the white- and blue-fruited members of the clade have small leaves, smaller fruits and are of smaller stature and most have a divaricate growth form, suggesting that these traits evolved in concert.

**Conclusion: frugivory by lizards**

White and blue fruit colours are non-randomly associated with divarication, small fruit size, open habitats and a shrub growth form in the New Zealand flora as a whole, in various subsets of the flora and among related *Coprosma* species. This is consistent with the prediction that frugivory and seed dispersal by lizards with a preference for certain fruit colours may have been important in certain environments in New Zealand.

**General Summary**

Three features of the New Zealand fleshy-fruited flora are of interest; the general small size of fruits, the strong tendency for fruits to become more elongated with increasing size and the number of white- and blue-fruited species. We suggest that these features may have evolved partially in response to frugivory by two of the three main guilds of frugivores. The prevalence of small-gaped volant frugivorous birds is logically related to the small size of fruits and the tendency for fruits to become more elongate with increasing size, as would be expected if selection was acting to keep fruits within a swallowerable size range.

**Influence of Frugivores on Fruit Traits**

Three features of the New Zealand fleshy-fruited flora are of interest; the general small size of fruits, the strong tendency for fruits to become more elongated with increasing size and the number of white- and blue-fruited species. We suggest that these features may have evolved partially in response to frugivory by two of the three main guilds of frugivores. The prevalence of small-gaped volant frugivorous birds is logically related to the small size of fruits and the tendency for fruits to become more elongate with increasing size, as would be expected if selection was acting to keep fruits within a swallowerable size range.
independent of selection on fruit or seed mass. The frequency of white- and blue-fruited species and especially the non-random association of these fruit colours with small fruit size, open habitats and a shrubby growth form imply that frugivory by lizards may have influenced the evolution of fruit traits in New Zealand. There is ample evidence that extinct, large-bodied, flightless birds were important frugivores and showed some selectivity; however, there is no evidence from the fruit size distribution of the extant flora for tight mutualisms between extinct frugivores and New Zealand fruiting species.

**Implications for Conservation**

Judging from the fruit size distribution of the extant flora, no fruiting species has been left without a disperser, despite the large number of New Zealand frugivorous birds that have been driven to extinction in the last 1000 years. It is, of course, possible that any fruiting species closely dependent on dispersal by, for example, moa species, has already become extinct. However, it seems unlikely that such a species would disappear without a trace in such a short space of time. The extinction of and decline in the numbers of effective dispersers have left New Zealand’s largest-fruiting species (fruit diameter > 1 cm) very vulnerable, as these species are now virtually totally dependent on one avian frugivore, *H. novaeseelandiae*, for seed dispersal. This species is arguably the most important seed-disperser in New Zealand forests (Clout and Hay, 1989; Lee et al., 1991). The growing realization of the importance of lizards as frugivores in New Zealand also raises conservation concerns. Four of the 16 currently described gecko species, and nine of the 27 currently described skink species are classified as endangered (International Union for the Conservation of Nature (IUCN) definition), and most species have restricted distributions. Many of them are also highly susceptible to environmental disturbance from various forms of land development (Pickard and Towns, 1988; Gill and Whitaker, 1998). The loss or reduction in numbers of frugivorous skinks in open habitats may have adverse effects on the regeneration of many shrub species, especially those with a divaricate growth form that limits avian access to fruit.

**Avenues for Future Research**

Too little use has been made of biogeographical comparisons among floras in different parts of the world. New Zealand, like many islands, offers a wealth of possibilities in the field of frugivory, because of the limited range of animals naturally present and because of recent extinctions and introductions. For example, the absence of native terrestrial mammals affords an opportunity to test for the loss of protective mechanisms against seed predation, and for a shift in fruit traits within lineages. The reduction in numbers of frugivores and the loss of species are likely to have had an impact on the population structure and regeneration of fruiting species. The introduction of new frugivores could be altering the distribution and abundance of native and introduced fruiting species. The way forward is not, however, in analyses of whole floras for the occurrence of ‘syndromes’. Best use can be made of natural ‘experiments’ like New Zealand by testing predictions based on the characteristics of specific groups of frugivores and fruiting species.

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**References**


