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# Plant structural defences against browsing birds: a legacy of New Zealand's extinct moas

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Browsing by large vertebrates has been a major force in the evolution of terrestrial plants but Holocene extinctions of the browsers have left a legacy of broken biotic partnerships. Ratite birds were the largest herbivores in several regions, such as the moas of New Zealand. Many woody plants there have a distinct form of branching, described as "divaricate", with thin, wide angled, branches intertwining to form a tangled canopy. Divaricate branching has been interpreted as a form of protection against climate extremes or as an anachronistic defense against the extinct moas. Here we report the first experimental evidence that many of these plants are defended against extant ratite browsers. In feeding experiments on two tree species with different (heteroblastic) juvenile and adult branch morphology, emus and ostriches obtained adequate feeding rates from adult shoots but sub-maintenance feeding rates from juvenile shoots with the ratite-resistant traits. Divaricate juvenile shoots suffered 30–70% less biomass removal to the birds than adult shoots. Ratites browse by a distinctive clamping and tugging action. Structural defence traits that exploit the limitations of this feeding mode include narrow, strong, elastic branches that resist being torn off, wide branching angle ("divaricate") that makes shoots difficult to swallow, and small, widely spaced leaves. This novel plant architectural defence has developed in at least 20% of the native woody flora of New Zealand, including 10 heteroblastic tree species that exhibit the ratite-resistant strategy until they reach ca 3 metres height. It is also a major axis of variation amongst homoblastic woody shrub species. The defences are useless against mammalian browsers that shear shoots, contributing to marked decreases in the abundances of ratite-resistant species in New Zealand after the introduction of mammals.

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Many large vertebrates have become extinct over the last 50 000 years (Martin and Klein 1984, Roberts 2001) largely due to human impacts. The extinctions are so recent that they have left a legacy of surviving plant species with traits that evolved in response to extinct partners. Some fruits, for example, no longer have dispersing mammals and others have spines that protect against extinct mammalian browsers (Janzen and Martin 1982, Barlow 2000). In New Zealand, 12 species of flightless ratites (moas, Worthy 1990) were extirpated within a few centuries of human settlement less than a thousand years ago (Anderson 1989, Holdaway and Jacomb 2000). Although these were the dominant terrestrial vertebrate herbivores in New Zealand (Worthy and Holdaway 2002), it is uncertain how these animals may have influenced the evolution of plant species, especially regarding defences against browsing.

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New Zealand has over 50 endemic woody plant species, representing 16 families of angiosperms, having a distinctive "divaricate" branching structure with wide-angled, thin, interlaced shoots bearing small leaves (Wardle 1991, Kelly 1994). The most striking group of divaricate plants is a polyphyletic group of heteroblastic trees. These have divaricate juvenile branches with small leaves below 2–3 m, and acute-angled adult branches with larger leaves above this height (Greenwood and Atkinson 1977, Poole and Adams 1990, Fig. 1). The divaricate growth form has long been interpreted as an adaptive response to features of the climate, including wind, cold, and abrupt changes from frosty nights to sunny days (McGlone and Webb 1981, Howell et al. 2002). An alternative hypothesis is that the densely intertangled branches acted as a cage-like barrier protecting the plants against browsing by moa (Greenwood and Atkinson 1977, Atkinson and Greenwood 1989). The herbivore defense hypothesis has been strongly contested by proponents of climate alternatives (McGlone and Clarkson 1993, Howell et al. 2002). The problem, as with any attempt to identify an evolutionary anachronism, is that the putative selective agent is extinct.

Fortunately extant relatives of the moas still survive. Here, we report the first experimental study of the hypothesis that divaricate and other architectural traits of New Zealand plants function as structural defences against ratite browsing. We conducted feeding trials on divaricate and non-divaricate plants with emus and ostriches, extant ratite relatives of the extinct moas. We analysed diverse plant traits to determine which were most effective in reducing losses to bird browsing.

Our aims were:

1) To observe feeding behaviour of ratites. Arguments on the defensive function of divaricates have been based on inferences on the mode of moa browsing without reference to extant ratites.
2) To compare feeding rates of emus and ostriches on different branch architectures to see whether some forms slow feeding rates in a manner analogous to spines (Cooper and Owen-Smith 1986, Belovsky et al. 1991).
3) To compare leaf and branch loss to browsing among different branch types.
4) To analyse those plant traits most effective in reducing losses to browsing.

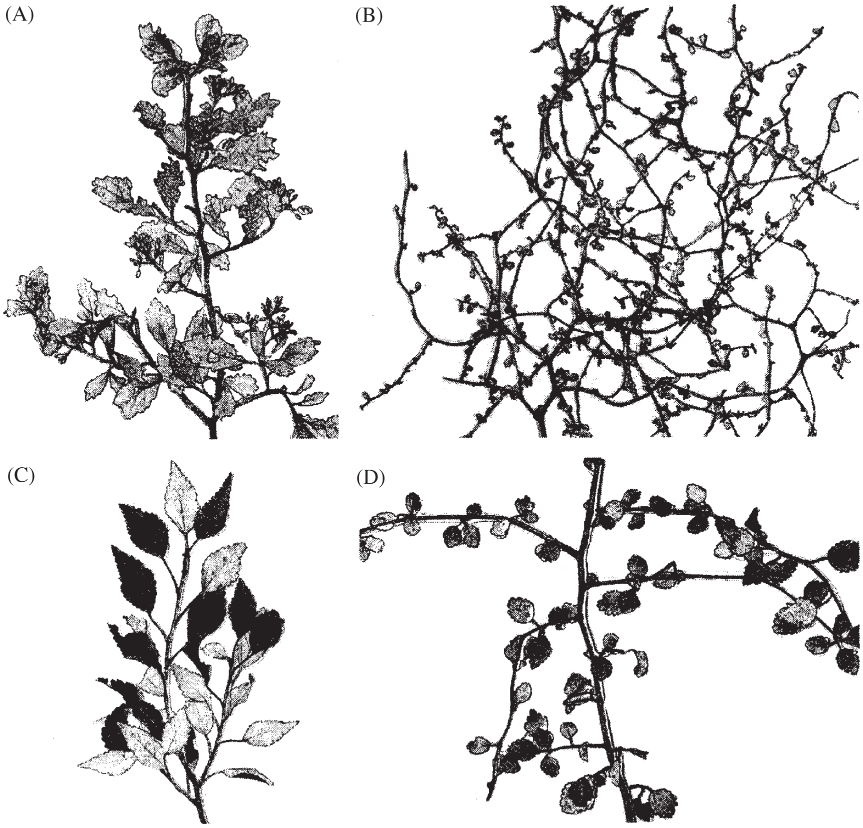

Fig. 1. Branching patterns in shoots of *Pennantia corymbosa* (A) adult (B) ratite-resistant juvenile, and *Plagianthus regius* (C) adult, (D) ratite-resistant juvenile. All plants are drawn at the same scale.

## Methods

### *Feeding studies*

We observed feeding behaviour and food intake rates of emus (*Dromaius novaehollandiae*) and ostriches (*Struthio camelus*) on adult and juvenile shoots of two common heteroblastic tree species: *Plagianthus regius* (Malvacae) and *Pennantia corymbosa* (Icacinaceae) (Fig. 1). *P. regius* was eaten by Dinorthid moas (Burrows 1980), which browsed at heights from $<1$ m to 3 m or more (Atkinson and Greenwood 1989). Emus have a body weight (35–55 kg) similar to the smaller emeid moas (Worthy and Holdaway 2002), and feed up to 2 m, while ostriches are larger (90–110 kg) and reach to 3 m. Emu and ostrich beaks are somewhat longer for their breadth and much less robustly constructed than similar sized moa species (Anderson 1989).

All emu and ostrich studies were with a flock of between 7 and 21-yr-old birds kept in a grass paddock and fed pelleted rations. For feeding rate experiments, freshly cut shoots ca 0.5 m long were offered to animals for 3 min after the first bite. We recorded fresh weight and total branch length of each shoot immediately before and after each feeding trial, except in the ostrich trial where leaves were counted instead of weighed. Weight losses were adjusted for water losses from control shoots. We timed bite rates with a stopwatch for a single animal. Each treatment (adult and juvenile shoots of both species, cut leaves of adult shoots, and feeding trials with a goat) was replicated six times. From oven dried material, the fresh weight to dry weight conversion for a typical bite is: *Plagianthus* adult 0.33, juvenile 0.37; *Pennantia* adult 0.28, juvenile 0.30.

To compare mammal browsing with ratite browsing, we fed shoots of *Plagianthus* to a tethered goat under the same conditions as for the emu and ostrich experiments.

### *Plant traits*

We measured a number of plant traits on the two heteroblastic tree species and the additional woody species used in the cafeteria experiment (described below) to determine key traits contributing to variation in losses to emu and ostrich browsing. Since branch losses to emus and ostriches appeared to vary depending on tensile strength, we measured forces exerted by emus on shoots and resistance of branches to a pulling force. Forces exerted by emus when feeding were measured by attaching shoots to a BLC Load cell connected to a Campbell logger for a total of 15 minutes of feeding. The maximum force recorded was 30 Newtons. Branch failure rates were recorded on shoots attached to rooted plants using a modified vice grip attached to a dynamometer and clamped on lignified shoots, avoiding soft current year's growth. The equipment was pulled slowly until shoot failure or until the maximum capacity of the dynamometer (80 Newtons) had been reached. Trials where twigs broke at the clamp were discarded. The method does not simulate the dynamic load exerted by the whiplash feeding action of ratites and is only an index of plant strength. Failures were often structural, at branch joints, rather than in the shoot material of the internodes.

For 7 heteroblastic tree species (juvenile and adult shoots separately) and 49 homoblastic shrubs, we quantified a series of functional traits to determine their contribution to the results from feeding shoots from representative species to emus and ostriches. Samples (terminal 50 cm of branches) were collected from the botanical garden of Dunedin, New Zealand in January 2001. For each branch, we determined the average width and length for 3–5 exterior leaves and interior leaves. We also measured the number of clusters of leaves, the total number of leaves on the branch, the length of the branch, the amount of length $<3$ cm in diameter, average internode distance, and the angle between branches at each node. For multiple leaves (10–20), we determined the average area of an individual leaf and its specific leaf area (SLA; $\mathrm{cm}^2\ \mathrm{g}^{-1}$). Branches were segmented into approximately 10-cm lengths, generally between nodes to determine tensile strength, measured by recording the force required for the branch to break.

Plants may develop chemical defences that limit the digestibility of plant material (e.g. tannins) or have a toxic effect on organ systems after absorption into the blood stream (e.g. alkaloids, Iason and Van Wieren 1999). To help determine possible chemical components of defences against browsing, we sampled leaves and stems taken from growth less than 2 years old, collected from 3 representative juvenile and adult shoots of seven heteroblastic species (Table 2), oven dried (70°C) until constant weight, and ground with a Cyclone sample mill (Udy Corp, Ft. Collins, CO, USA). Following a Kjeldahl digest with sulphosalicylic acid (to include nitrate N) and sodium sulphate, nitrogen and phosphorus were determined colorimetrically by a continuous flow analyser, and potassium, calcium, and magnesium by atomic absorption spectrometry. Condensed tannins and total phenolics were determined colorimetrically (Broadhurst and Jones 1978, Day 1998) after extraction from the plant material with 50% acetone. Fibre, cellulose, and lignin were determined using an acid-detergent technique (Price and Butler 1977).

### *Cafeteria experiments*

We conducted cafeteria-style experiments with emus to test the importance of different plant traits in determining loss to browsing. Nine species of nursery-raised potted woody plants were firmly staked in the ground within reach of browsing animals for 24 h. We estimated branch length ($<3$ mm diameter) of each plant before and after the feeding trials. Species included: *Coprosma* *areolata*, *Coprosma propinqua*, *Coprosma rugosa* (Rubiaceae), *Myrsine divaricata* (Myrsinaceae), *Sophora microphylla* (juvenile form) (Fabaceae), all considered divaricate by Greenwood and Atkinson (1977), and *Sophora molloyi*, *Coprosma lucida*, *Coprosma rotundifolia* and *Myrsine australis*, representing non-divaricate forms.

## Results

Both emus and ostriches removed browse by clamping the beak over a branch and/or leaf and pulling the head back with a force that ranges from a strong tug to a whip-lash action of the head. The birds peck at single leaves, strip leaves from branches, or tear off whole sections of branch. Both emus and ostriches never sheared shoots like mammal browsers with hinged jaws. If the birds did manage to tear off a large, multi-branched shoot, it was dropped and left on the ground after futile attempts to re-position the shoot for swallowing.

### *Feeding studies*

In the replicated feeding trials with heteroblastic trees, emus obtained smaller bite sizes, similar but slightly lower bite rates, and much lower feeding rates from juvenile shoots of both tree species (Table 1). Ostriches, with a larger gape width, obtained larger bite sizes and higher feeding rates than emus. Like emus, they had smaller bite size, lower bite rate, and much lower feeding rates on juvenile compared to adult shoots of *Plagianthus regius* (Table 1).

Juvenile plants lost less foliage than adult plants when fed on by emus and ostriches. Adult shoots lost two to three times more leaf mass to emus than juvenile shoots and four to five times more branch length (Table 1). The shoots were frequently reduced to small leafless stubs but divaricate branches survived more or less intact. Similar differences were found in shoots of *Plagianthus* fed to ostriches. Adult shoots lost nearly ten times more shoot length than juveniles (Table 1) and four times more biomass. For both emus and ostriches, juvenile shoots lost far less biomass than adult shoots and retained most of the framework of branches.

### *Plant traits*

Adult and juvenile shoots differed in their functional traits. Among juvenile and adult branches of 7 heteroblastic species, an average juvenile leaf is 79% smaller, has 11–24% higher nutrient concentrations (except K) and 43% less acid detergent fibre than adult leaves (Table 2). The woody portions of juvenile branches have 12–52% lower nutrient concentrations and 123% greater fibre than adult branches. The lower levels of secondary compounds in juvenile branches and leaves compared to adults indicate that the ratite-resistant strategy of heteroblastics does not rely on these carbon-based chemicals. Juvenile branches also have more stem length $< 3$ mm diameter with wider branching angles that result in three times higher displacement when pulled (Table 2). Associated with the higher structural fraction in the juvenile branches, at all diameters measured, juvenile branches required more force to break than adult branches (Fig. 2).

Compared at the mean diameter (1.95 mm), juvenile branches require more than twice as much force to break as adult branches ($57.5 \pm 2.3$ N vs $26.3 \pm 2.0$ N, $F = 106$, $p < 0.001$).

Similar patterns of traits exist among 49 homoblastic species representative of endemic New Zealand woody shrubs that grow to heights below the reach of the biggest moas. Measuring many of the same traits as measured for heteroblastics, we ran a principal components analysis to test for the relationships among traits without any a priori assumptions about relationships. The second axis of the PCA of the traits of homoblastic

Table 1. Feeding behaviour and plant losses in feeding trials with ratite-resistant (juvenile) and non-ratite-resistant (adult) shoots of *Plagianthus regius* and *Pennantia corymbosa*. Values given are means (and standard deviation) for 6 replicates of standard feeding bouts each lasting 3 minutes. Adult shoots of each species were significantly different from juvenile shoots ($P < 0.05$) for all variables shown in the table except bites/minute in *Pennantia* (Mann-Whitney U-test).

| Species | Shoot type | Bite size (g) | Bites/min | Feeding rate (g/min) | % reduction in shoot weight | % reduction in shoot length |
|---|---|---|---|---|---|---|
| Emu | | | | | | |
| *Plagianthus* | adult | 0.20 (0.04) | 33.7 (8.4) | 6.7 | 69.4 (13.4) | 63.7 (19.8) |
| | juvenile | 0.06 (0.02) | 25.2 (5.5) | 1.5 | 29.3 (11.1) | 11.9 (7.8) |
| *Pennantia* | adult | 0.25 (0.05) | 29.9 (9.4) | 7.5 | 75.2 (8.9) | 70.8 (22.8) |
| | juvenile | 0.04 (0.01) | 24.6 (6.9) | 1.0 | 23.8 (5.3) | 15.0 (7.3) |
| Ostrich | | | | | | |
| *Plagianthus* | adult | 0.33 (0.06) | 32.8 (5.5) | 10.8 | 88.5 (4.1) | 41.5 (9.0) |
| | juvenile | 0.11 (0.08) | 28.2 (10.2) | 3.1 | 18.4 (10.6) | 4.7 (3.2) |
| Goat | | | | | | |
| *Plagianthus* | juvenile | 0.34 (0.11) | 18.4 (3.4) | 6.3 | 36.5 (8.6) | 46.2 (11.1) |

Table 2. Differences in functional traits between juvenile and adult shoots of heteroblastic species (*Carpodetus serratus*, *Elaeocarpus hookerianus*, *Hoheria angustifolia*, *Plagianthus regius*, *Pennantia corymbosa*, *Sophora microphylla*, *Streblus heterophyllus*). For comparisons of signs that do not add up to 7, some species had the same value for juvenile and adult shoots.

| Factor | Leaves | | | | Stems | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean juvenile trait value | Mean difference (juv. − adult) | Greater vs less | $p > \|t\|$ | Mean juvenile trait value | Mean difference (juv. − adult) | Greater vs less | $p > \|t\|$ |
| %N | 1.93±0.41 | +0.24 | 6/1 | 0.24 | 0.82±0.10 | −0.25% | 0/7 | 0.02 |
| %P | 0.20±0.30 | +0.02 | 5/2 | 0.29 | 0.12±0.01 | −0.04 | 2/5 | 0.11 |
| %K | 0.98±0.02 | −0.22 | 1/6 | 0.02 | 0.84±0.14 | −0.24 | 2/5 | 0.20 |
| %Ca | 2.22±0.13 | +0.38 | 6/1 | 0.02 | 0.74±0.08 | −0.81 | 1/6 | 0.04 |
| %Mg | 0.41±0.36 | +0.08 | 7/0 | 0.002 | 0.22±0.02 | −0.03 | 2/5 | 0.25 |
| Tannin (meq $mg^{-1}$) | 22.30±1.78 | −1.46 | 0/3 | 0.18 | 48.54±2.38 | −0.46 | 0/3 | 0.08 |
| Phenolics (meq $mg^{-1}$) | 12.81±1.61 | −2.24 | 1/6 | 0.08 | 28.84±1.45 | −1.94 | 0/7 | 0.02 |
| % fibre | 11.38±3.15 | −8.44 | 6/0 | 0.12 | 19.25±2.74 | +10.6 | 7/0 | 0.002 |
| SLA ($cm^2$ $g^{-1}$) | 113.8±9.2 | +2.17 | 3/3 | 0.77 | | | | |
| Area/leaf ($cm^2$) | 1.09±0.31 | −4.03 | 0/6 | 0.01 | | | | |
| Length $<3$ mm (cm) | | | | | 168.5±34.87 | +124 | 7/0 | 0.002 |
| Displacement (cm) | | | | | 12.81±2.51 | +8.78 | 7/0 | 0.01 |
| Displ/length (cm $cm^{-1}$) | | | | | 0.09±0.05 | −0.07 | 2/5 | 0.22 |
| Branch angle (°) | | | | | 84.9±7.7 | +21 | 7/0 | 0.01 |
| Internode length (cm) | | | | | 33.06±8.73 | +3.65 | 4/3 | 0.56 |

species separates the species in a manner similar to the differences between juvenile and adult shoots (Table 3). The eigenvectors of homoblastic axis 2 are significantly correlated with heteroblastic axis 2 ($r^2 = 0.94$, $p < 0.001$), which separated juveniles and adult (paired t-test, mean difference juvenile-adult = 1.62, $p < 0.001$). As in the paired t-test, juvenile branches and juvenile-like homoblastics are distinguished by high lateral displacement, high tensile strength, large branching angles, a large amount of branch length $<3$ mm in diameter and the tendency to have smaller leaves.

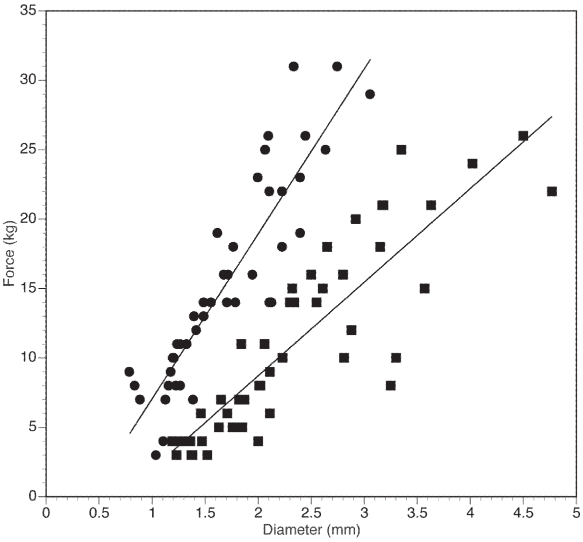

Fig. 2. Relationship between the diameter of a branch segment and the force required for juvenile (●) and adult (■) branches to break, using seven heteroblastic species. (Adult: $y = -3.47 + 5.87x$; juvenile: $y = -3.80 + 10.9x$)

The first axes of the PCA's of the traits of homoblastic species and heteroblastic species are well-correlated ($r^2 = 0.90$, $p < 0.001$) and separate species with few large leaves from those with more numerous, smaller leaves (Table 3). Differences along heteroblastic axis 1 were not significantly associated with differences between juvenile and adult foliage ($p > 0.1$) and we believe represent differences between fast-growing species of lowland nutrient-rich habitats and slow-growing species of upland, nutrient-poor habitats.

### *Cafeteria experiments*

The high tensile strength and elasticity of branches were key features in reducing the loss of stem and leaf material to ratite browsing. Branch loss to emus in nine species offered in the cafeteria-style experiment ranged from $<10\%$ to 100% and was closely related to failure rates of shoots under tension equivalent to the forces applied by emu feeding. For both emus and ostriches, there was significantly higher browse losses from species with high failure rates ($>85\%$, Fig. 3). Tensile strength (here, proportion of fractures at 80 Newtons) was the only significant structural trait retained in a multiple regression with branch loss as the dependent variable (adjusted $r^2 = 0.88$; $F = 30.771$, $P < 0.001$). The five species with low branch strength lost, on average, 80% of their branches to emus compared with the four species with high tensile strength that lost only 16% ($F = 66$, $P < 0.001$). This is the first report of the importance of high tensile strength of branches in reducing losses to browsers that feed by tugging.

Although smaller leaf size is part of the ratite-resistant set of traits, smaller leaf size alone does not limit the browsing of leaves by emus and most likely requires both

Table 3. PCA results for 49 homoblastic species (homoblastic axis) and 7 heteroblastic species – listed in Table 2 – (heteroblastic axis). Bold type indicates that the factor was correlated with the axis at $p < 0.05$.

| | Axis 1 | | Axis 2 | |
|---|---|---|---|---|
| | Homoblastic | Heteroblastic | Homoblastic | Heteroblastic |
| Leaf width (inside) | **+0.85** | **+0.96** | **−0.43** | −0.16 |
| Leaf length (inside) | **+0.77** | **+0.91** | **−0.50** | **−0.35** |
| Leaf width (outside) | **+0.83** | **+0.96** | **−0.44** | −0.20 |
| Leaf length (outside) | **+0.78** | **+0.89** | **−0.53** | **−0.37** |
| No. clusters | **−0.57** | −0.32 | −0.24 | −0.21 |
| No. leaves | **−0.71** | **−0.56** | −0.03 | **−0.41** |
| Branch length | **+0.39** | +0.18 | **+0.46** | **+0.60** |
| Branch length $< 3$ mm | **−0.42** | −0.23 | **+0.60** | **+0.75** |
| Displacement | −0.02 | −0.24 | **+0.88** | **+0.84** |
| Tensile strength | −0.18 | −0.09 | **+0.68** | **+0.89** |
| Branch angle | −0.03 | +0.03 | **+0.80** | **+0.69** |
| Internode length | **+0.34** | −0.31 | 0.00 | −0.08 |

changes in distances between leaves and leaf size. We trimmed each leaf of six adult branches of *Plagianthus* to an equivalent area as the leaves of juvenile *Plagianthus*. Emus removed almost all of the adult leaves, whether reduced in size or not, during a 3-min exposure to emu feeding with biomass loss rates equivalent among adults, and adults with smaller leaves, as compared to juvenile branches with small leaves.

### *Mammal browse*

Mammal browsers have strong teeth, a jaw structure that can shear stems, and a tongue and lips that can manipulate the position of food in the mouth. The goat fed on juvenile branches of *Plagianthus* by shearing off a short segment of the shoot, repositioning the shoot in its mouth with its tongue and lips, and shearing off another segment. Under the same experimental conditions as emus and ostriches, the goat removed four times more branch biomass than emus (Table 1). Although the tensile strength of the juveniles is higher, there are only slight differences in the shear force required to cut adult and juvenile shoots of *Plagianthus* ($r^2 = 0.96$, juvenile: $y = 10.0x - 1.56$; adult: $y = 15.1x - 16.70$; differences in slopes and intercepts represents 4% of total explained variation).

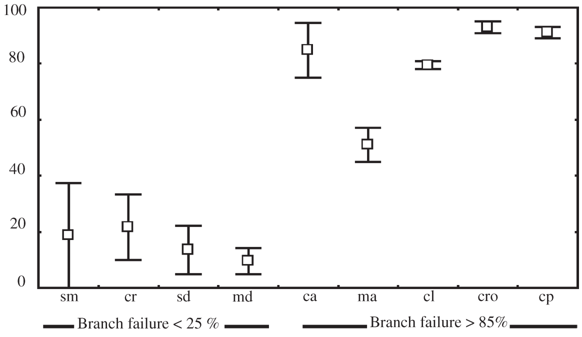

Fig. 3. Branch failure versus branch loss of plants eaten by emu in a cafeteria-style experiment. Branch failure was measured as the proportion of lateral shoots that broke when subjected to a force of 80 N. Branch loss is the % change in total length of branches of potted plants after emu feeding. Species were: ca *Coprosma areolata*, cl *C. lucida*, cp *C. propinqua*, cr *C. rugosa*, cro *C. rotundifolia*, ma *Myrsine australis*, md *M. divaricata*, sd *Sophora microphylla* (juvenile form), ss *S. molloyi*. Two points are shown for each species indicating results of two separate experiments.

## Discussion

The results of this study support the hypothesis that a group of New Zealand plants has evolved a distinctive wiry, small-leaved morphology that helped defend them against browsing moas. The feeding trails on two heteroblastic tree species show both that juvenile branches reduce ratite feeding rates and that they survive browsing with lower losses of leaves, and much lower losses of shoots, than adult branches. There are remarkable analogies with the function of spines as structural defences against mammal browsing, despite the very different morphology.

Spines of African acacias can reduce feeding rates of mammal browsers below maintenance levels (Cooper and Owen-Smith 1986). We assessed daily energy intake in relation to daily energy needs for ratites browsing on juvenile vs adult branches using the data in Table 1 and equations developed from field measurements of ostrich metabolism (Williams et al. 1993). An ostrich with a body weight of 100 kg could meet its daily energy needs by feeding for 14 h on adult shoots of *Plagianthus* but would starve on juvenile shoots since it would need 40 h of feeding for equivalent intake. Similarly, an adult emu with a body weight of 40 kg could meet its daily needs by feeding on adult shoots (for 9 h) but would starve on juvenile shoots (36 h required). Browsing moas with beaks of equivalent size to emus or ostriches probably took larger bite sizes because moa beaks were more robustly constructed, and the birds probably tugged with greater force, having more substantial neck muscles (Anderson 1989, Atkinson and Greenwood 1989, Worthy and Holdaway 2002). However moas also had relatively larger body sizes requiring higher food intake. Because juvenile shoots reduce feeding rates of ratites to starvation levels, foraging birds would be more likely to move in search of more rewarding plants after sampling a shoot. Spines act in an analogous manner in African ecosystems (Cooper and Owen-Smith 1986), reducing feeding rates of mammal browsers to below maintenance levels and forcing them to move on.

The anti-ratite strategy is also analogous to spines in being more effective in reducing loss of branches than loss of leaves (Gowda 1997). Protection of branches would be an essential prerequisite for juveniles of heteroblastic trees to escape above the browse zone and grow to maturity. However, despite these functional analogies with spines, structural defences against ratite browsing work in an entirely different manner, exploiting features of birds that are quite different from mammals. Ratite birds browse in a different manner from mammals and structural traits that defend plants against ratites reflect these differences. Ratites are not as susceptible to spines as mammals because of their hard beaks. The birds feed by clamping a branch and/or leaf with the beak and pulling the head back with a force that ranges from a strong tug to a whiplash action of the head. The high tensile strength of the narrow branches reduces breakage, while the widely spaced, small leaves increase the energy and time required to acquire leaf biomass. It was clear during our trials that the complex three-dimensional structure of the shoots, a product of “divaricate” branching, made swallowing of the branches considerably more difficult. Extant herbivorous ratites ingest food by a “catch and throw” mechanism similar to fish-eating birds (Zweers et al. 1997, McQueen 2000, W. J. Bond, pers. obs. for ostriches, D. Westcott, pers. comm. for cassowaries). With no teeth, cheeks or prehensile tongue, the birds have to ingest food whole, manipulating the branch in a manner similar to a heron swallowing a fish. The largest browseable unit is limited to the smallest dimension that can fit into the gape of the beak. Bulky branches cannot be swallowed. Divaricate branches are extremely awkward food items for ratite browsers to handle and ingest.

Observations of gizzard contents of Dinorthid moas led to the suggestion that moas fed by shearing shoots with their beak, as do mammals with hinged jaws (Burrows et al. 1981). Several shoot fragments, including some from divaricate species, in the moa gizzards appear to have been cut, rather than torn off. In our view it is highly unlikely that the extinct moa were able to cut shoots. Beak shapes varied among moa species but none had deep, blade-like opposing edges suitable for shearing (Anderson 1989). Worthy and Holdaway (2002) interpret bill morphology to suggest a range of feeding modes, from tugging to cutting, but indicate that the latter may have been restricted to a few moa species. Positioning the plant material for swallowing is more difficult for the birds than mammals. Ratites lack a prehensile tongue and cannot use appendages, especially feet, to position the shoot for swallowing. The “catch and throw” ingestion mechanism (Zweers et al. 1997) prohibits swallowing of large sheared shoots in the manner illustrated by Burrows et al. (1981). We think that a more likely explanation for apparent cut-shoot ends in moa gizzards is mechanical breakage at branch insertions of mature shoots (within browse reach of the large dinorthid moas, Beismann et al. 2000) or slicing of shoots by gizzard stones.

Alternative hypotheses for the functional significance of divaricate branching are that it confers tolerance to wind and frost (McGlone and Webb 1981, McGlone and Clarkson 1993), that boundary layer effects produce warmer more humid conditions in the shrub interior (McGlone and Webb 1981, Kelly and Ogle 1990), or that light interception is enhanced to promote carbon gain (Day 1998) or reduced to limit photoinhibition (Kelly 1994, Howell 2002). Divaricate shrubs have been shown to offer some shelter from frost damage but other tests have yet to find significant climate-related benefits of the branch architecture (Kelly and Ogle 1990, Darrow et al. 2001). The recent discovery of inner canopy foliage sensitivity to cold-induced photoinhibition in several divaricates (Howell 2002) fails to demonstrate processes different from those that occur in non-divaricate species (Lusk 2002). It is also hard to see how carbon gains from shading of leaves by a dense network of branches can outweigh the carbon costs of constructing the branches. A general difficulty with these hypotheses is why the growth form occurs in both sheltered and exposed environments within New Zealand and why it is rare elsewhere in the world (Atkinson and Greenwood 1989, McQueen 2000). None of the current alternative hypotheses predicts high tensile strength in response to climate.

We estimate that approximately 20% of the woody trees and shrubs endemic to New Zealand exhibit the ratite-resistant strategy. We suspect that, upon testing, this will include most (but not all) of the divaricates listed by Greenwood and Atkinson (1977). For example, nursery-grown plants of the divaricate *Coprosma propinqua* had low tensile strength and suffered high shoot loss by feeding emu (Fig. 3). Other species, not considered divaricates (particularly *Carmichaelia* in the Fabaceae), also appear to demonstrate ratite-resistant features. The structural defence may be more obvious in New Zealand than elsewhere because this was the only place where ratites occurred in the absence of browsing mammals. It is unknown to what degree the ratite-resistant strategy is expressed in other systems that has or had ratites as the dominant terrestrial herbivores (e.g. elephant birds, Madagascar and associated islands). In regions where mammalian and ratite herbivores co-existed (e.g. Australia; emus, Africa; ostriches, South America; rheas), the ratite-resistant strategy may be rare due its ineffectiveness against mammals. Co-existence may have promoted greater divergence in feeding modes between ratites and mammals elsewhere, compared with ratite-dominated systems such as New Zealand. However, this could only be tested if we were able to determine more precisely feeding modes from the scarce gizzard and beak fossil remains of moa.

Although the leaves and stems of the juvenile branches of heteroblastic species have lower concentrations of tannins and phenolics than adult shoots, it is difficult to reconstruct the importance of plant chemical defences against ratites. In our experiments emu and ostrich feeding appeared unrelated to plant chemistry, though *Prumnopitys taxifolia* (Podocarpaceae) was relatively unbrowsed and we suspect that it contains high concentrations of secondary compounds. Chemical ratite-resistant strategies are likely to exist in the New Zealand flora but more research is necessary to determine patterns.

Our experimental evidence suggests that in New Zealand woody species without the ratite-resistant strategy would have been disadvantaged relative to ratite-resistant plants. Extinction of the moas might have triggered ecological release of broadleaved plant species which could out compete ratite-resistant species because of their faster growing, undefended shoots. Ratite-resistant plants suffer an additional burden because their costly allocation to structural defences is useless against invasive mammal browsers. Although our experiments involving mammals were limited to the goat, field observations indicate that results can be extrapolated to nearly all the large domestic and feral mammals in New Zealand. We believe that recognition of broken evolutionary partnerships, such as those between moas and plants defended against them, is important not only for understanding the current ecological status of species but also for predicting the wider consequences of impending species extinctions. By our estimates, ratite-resistant species are currently more than twice as likely to be threatened or declining in New Zealand as all other endemic species (de Lange et al. 1999). Interestingly, there are a few ratite-resistant shrubs (e.g. *Melicytus alpinus*, *Myrsine divaricata*) that in non-forest habitats have thick stems ($>3$ mm diameter) and densely caged canopies that are currently widespread and appear preadapted to mammalian browsing. Unfortunately, there are currently no wild areas in New Zealand where ratites have been introduced in the absence of mammals in order to examine the response of the vegetation to ratite browsing. There is also little work outside of New Zealand examining ratite-resistant strategies in plants where ratites were or are abundant, potentially limiting our understanding of the ecology of these regions and the conservation of their florae.

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