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First report of 'mining' as a feeding behaviour among Australian manna-feeding birds

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The Forty-spotted Pardalote *Pardalotus quadragintus* is an endangered songbird endemic to the forests of Tasmania, Australia. Forty-spotted Pardalotes forage predominantly in the foliage of White (or Manna) Gums *Eucalyptus viminalis* for invertebrates, lerps (the protective coverings produced by psyllids) and manna, a crystallized exudate produced by certain *Eucalyptus* species. Although many Australian birds feed on manna, this study reports the first observations of birds actively stimulating manna production rather than feeding on it opportunistically. In light of these observations, we also compared rates of manna production across tree species and sizes, and quantified the relative importance of manna in nestling diet. Adult Forty-spotted Pardalotes stimulated manna production by clipping leaf stalks with their bills, creating small incisions in the stem surface. We experimentally mimicked this behaviour and found that, in 53.7% of incisions of *E. viminalis*, manna flow was released within 3 days. However, none of the other three common tree species at our sites produced manna in response to the same experimental damage. There was no effect of tree size on manna production by *E. viminalis*. To determine the importance of manna and other food sources in nestling diet, we videotaped provisioning trips by adults to nests and surveyed food availability in *E. viminalis* foliage within territories. Manna was the most important food item, comprising 84.2% of identified food items provided to nestlings, and it was selected over 50 times more frequently than expected given its relative availability in the foliage. As a manna miner, the Forty-spotted Pardalote is the first Australian bird to join the small number of bird species that mine sap or other exudates of trees. Their preference for manna as a food source, especially in nestling diet, provides an explanation for the species' specialization on *E. viminalis*, the only manna-producing tree at our sites. Our results suggest that *E. viminalis* forests provide critical food supply for developing nestlings, and that restoration of *E. viminalis* forests will be critical to the long-term viability of Forty-spotted Pardalote populations.

Keywords: diet specialist, food selection, manna gum, specialization, Tasmania, white gum.

INTRODUCTION

Habitat and diet specialists are disproportionately represented among threatened species globally, and are vulnerable to environmental change (Clavel *et al.* 2011, Ducatez *et al.* 2015). Food availability can limit the reproductive success and population abundance of birds, and is of particular importance for endangered habitat specialists (Martin 1987, Arcese & Smith 1988). The Forty-spotted Pardalote *Pardalotus quadragintus* is a globally threatened songbird endemic to Tasmania, Australia, where it specializes on forest and woodland habitat containing White (or Manna) Gums *Eucalytpus viminalis* (Rounsevell & Woinarski 1983). It is a foliage gleaner and feeds on invertebrates, lerps (the protective coverings produced by psyllids) and manna, a sugary exudate of some *Eucalyptus* species. Although historically distributed throughout eastern Tasmania, their distribution contracted with forest clearing and fragmentation following European settlement (Rounsevell & Woinarski 1983). Currently, the Forty-spotted Pardalote is restricted to two islands and several small mainland patches in southeastern

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Tasmania, and Flinders Island in the northeast (Bryant 2010). During the past 18 years, its population has further declined by 60% within existing habitat, coinciding with a decade of drought in Tasmania (Bryant 2010). The species is now listed as Endangered by the International Union for Conservation of Nature (IUCN). Although this decline is likely to be the result of drought-induced food limitation, Forty-spotted Pardalote feeding strategies and food selection preferences are uncertain. Additionally, Forty-spotted Pardalotes forage selectively in *E. viminalis* and breeding pairs are most abundant where *E. viminalis* is the dominant tree species. However, the reasons for this relationship are not well understood (Rounsevell & Woinarski 1983).

Some food resources require particular behavioural or morphological adaptations of the consumer (Robinson & Wilson 1998). Thus, food specialists may develop unique foraging strategies that enable them to exploit resources in unusual ways. For example, North American sapsuckers *Sphyrapicus* create sap-wells in food trees and return to these sites to harvest the sugar-rich sap (Eberhardt 2000). Similarly, an endangered Hawaiian honeycreeper, the Akiapolaau *Hemignathus munroi*, drills into Ohia *Metrosideros polymorpha* trees to stimulate the release of sugary sap (Pejchar & Jeffrey 2004). In addition to sap, Australian *E. viminalis* trees also produce sugar-rich 'manna', which is exuded from damaged leaves and leaf stalks and crystallizes as white clumps in the foliage (Fig. 1) (Basden 1966). During our study of their breeding biology, we observed Forty-spotted Pardalotes incising leaf stalks and using their notched bills (Fig. 2) to stimulate manna production by *E. viminalis* trees, mining the foliage to obtain valuable food resources (Fig. 3).

Manna is a food source for many canopy-dwelling Australian birds, mammals and invertebrates (Paton 1980, Steinbauer 1996). Although not systematically studied, it appears to be produced by just a small subset of *Eucalyptus* and *Angophora* species, including *E. viminalis*, and is secreted from damaged surfaces of leaves and twigs (Basden 1966, Steinbauer 1996). Manna is composed primarily of sugars (60%), including raffinose, melibiose, stachyose, sucrose, glucose and fructose (Basden 1966). Of the dominant eucalypt species in Forty-spotted Pardalote habitat, *E. viminalis* produces the highest volume of manna and supports the highest

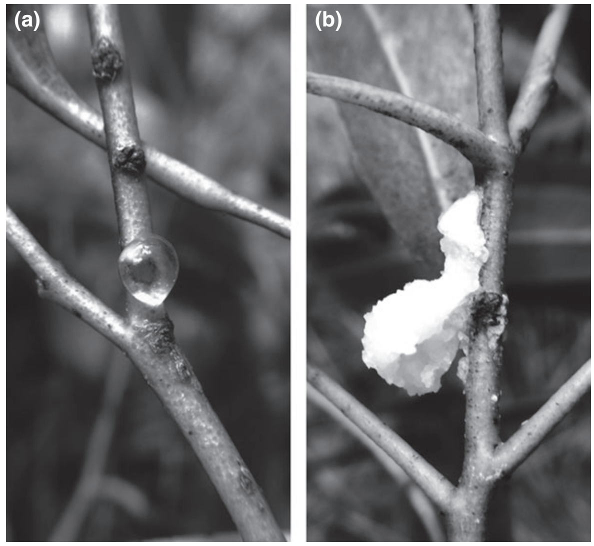

Figure 1. Examples of manna exuded from leaf stalks of *Eucalyptus viminalis* trees in southeastern Tasmania. (a) Liquid state of manna that may be exuded before crystallization. Fresh damage to the leaf stalk is visible below the manna droplet, and two older wounds are visible above the droplet. (b) Crystallized form of manna exuded from damage beneath the petiole.

Figure 2. Bill of the freeze-dried Forty-spotted Pardalote specimen used to inflict damage upon stem surfaces of *Eucalyptus viminalis*.

abundance of arthropods (Woinarski & Bulman 1985). Thus, the Forty-spotted Pardalote's preference for *E. viminalis* may be driven by the tree's high abundance and diversity of food items or, alternatively, by its unique production of manna.

Manna is an important part of nestling (and possibly adult) diet, and comprised around 75% of

Figure 3. Forty-spotted Pardalote foraging or manna mining on a *Eucalyptus viminalis* leaf stalk in southeastern Tasmania. Extensive damage to leaf stalks is visible upon the stem surfaces. Photograph by Alfred Schulte.

food items provisioned to nestlings in one study at North Bruny Island (Woinarski & Bulman 1985). However, its production, availability and selection by Forty-spotted Pardalotes are uncertain. The objectives of this study were to describe manna mining by Forty-spotted Pardalotes as a strategy for stimulating food production, to compare rates of manna production across tree species and sizes, and to quantify the importance of manna in nestling diet relative to the availability of manna and other food sources in the environment.

METHODS

Study area

Forty-spotted Pardalotes are confined to < 4500 ha of habitat, with the largest populations concentrated in southeastern Tasmania on Maria Island (*c*. 974 individuals) and Bruny Island (*c*. 450 individuals), and the largest mainland population at Tinderbox Peninsula (*c*. 46 individuals) (Bryant 2010). We conducted fieldwork at one site (17 ha) on Maria Island (42.654°S, 148.045°E) and two sites (25–29 ha) on Bruny Island (43.101°S, 147.36°E). Sites comprised dry, coastal woodland managed by the Parks and Wildlife Service (Maria Island), and the Indigenous Land Corporation and private landowners (Bruny Island). The Maria Island site (Isthmus) was flat and sandy, dominated by *E. viminalis*, with *Eucalyptus obliqua* and *Eucalyptus globulus* components. One Bruny Island site was hilly woodland surrounded by sheep paddock, and dominated by *E. viminalis* with *Eucalyptus pulchella* and *E. globulus*. The other was mixed forest including *E. viminalis*, *E. pulchella*, *E. globulus* and *E. obliqua*. See Edworthy (2016) for further site details.

Foraging observations

We used climbing ropes and ladders to access the canopy and closely observe foraging behaviour, including manna mining, when adults were foraging nearby. These observations were opportunistic and often occurred when we were doing other work at nest-cavities, which allowed us to observe Forty-spotted Pardalotes foraging at close range throughout the breeding season.

Nest monitoring

We located nests, monitored breeding and observed adult behaviour between August 2014 and January 2015. We found nests in natural cavities by searching known territories and previously used nest-cavities and by following birds back to their nest-sites. All nests on Maria Island were in natural cavities, whereas nests on Bruny Island were in both natural cavities and nestboxes installed in 2008. Nests were accessed using ladders or climbing ropes. We monitored nests every 4 days to determine nestling age and brood size by inspecting nest contents directly or by using a video camera on a flexible stalk. Inaccessible cavities were monitored from the ground for parental activity every 4 days to determine the start of incubation and hatching and to estimate nestling age.

Artificial damage experiment

To assess whether bird-like damage to leaf stalks stimulated manna production, we first mimicked bird damage using the bill of a freeze-dried Forty-spotted Pardalote specimen (Fig. 2). After succeeding in stimulating manna production using the bird's bill, we used a utility blade, which created similar incisions, to avoid damaging our specimen.

Table 1. Summary of experimental damage applied to common *Eucalyptus* species at our sites in southeastern Tasmania in January 2015. Values in the manna column represent the number of damage sites that produced manna between 1 and 3 days after incision date and the number in parentheses indicates the number of individual trees that produced manna.

Tree species	No. of trees sampled	Dbh range (cm)	No. of experimental damage sites	No. of damage sites (no. of trees) that produced manna
Eucalyptus viminalis	19	5.4–100.6	67	36 (13)
Eucalyptus pulchella	13	5.1–140.1	36	0 (0)
Eucalyptus globulus	12	10.5–157.6	33	0 (0)
Eucalyptus obliqua	10	6.0–31.5	22	0 (0)

To quantify manna production across tree species and size classes, we created incisions in leaf stalks of the common tree species at our sites, including *E. viminalis* (*n* = 19 trees), *E. pulchella* (*n* = 13), *E. globulus* (*n* = 12) and *E. obliqua* (*n* = 10), and measured diameter at breast height (dbh; 1.3 m above the ground) (Table 1). We selected trees at our two 10–15-ha study sites on Bruny Island, including all trees with foliage accessible from the ground (foliage at ~2 m), within known Forty-spotted Pardalote foraging territories. We also searched Pardalote territories bordering our study sites to increase our sample sizes of *E. pulchella*, *E. globulus* and *E. obliqua* to at least 10 trees. Incisions were made to leaf stalks at *c.* 2 m above the ground, with one to 10 stem subsamples per tree. All damage was applied near the base of a petiole using a single surface incision across the width of the stem, mimicking bird-inflicted damage. To avoid subsequent interference by insects, birds or weather, we enclosed damaged stems and associated foliage in re-sealable zipper storage bags with cut corners for ventilation. We checked damage sites for the presence of manna once a day for up to 3 days following the date of incision and measured the length, width and height of each manna clump to estimate the volume produced.

Nestling diet and food availability

We recorded nestling provisioning by parents using digital video cameras placed outside cavity and nestbox entrances. We recorded in daylight for at least 1 h per observation, and we obtained a total of 20 videos from 12 breeding pairs (three at Maria Island and nine at Bruny Island). To investigate changes in diet across nestling age-classes, we recorded six pairs early in the nestling period (0 to 9 days old), two pairs in the middle of the nestling period (10–18 days old) and five pairs late in the nestling period (>18 days old); nestlings fledged at 25–32 days old (Bulman *et al.* 1986, A. Edworthy unpubl. data). For each provisioning event, we recorded food type and food-load size relative to bill length. Invertebrates were identified to the finest taxonomic level possible given the image quality, usually to Order. Differentiating between manna clumps in clusters was difficult because of their white colour and mouldable shape. Thus, manna clusters were treated as single food items for analysis. In cases where manna and an invertebrate were fed together (*n* = 5), we counted each item separately.

To determine food availability in each territory, we sampled foliage shortly after nests were filmed, during daylight hours. For each pair we selected the three *E. viminalis* trees that were closest to the nest tree, within the territory, and had accessible foliage. One to three subsamples of at least 28 leaves each were taken per tree at a height of 5–7 m, using pruning shears on an extendable pole. Immediately after samples were cut, we searched all stem and leaf surfaces carefully for manna and invertebrates, excluding leaf galls and moulted exoskeletons as these were not considered food sources for Pardalotes. Forty-spotted Pardalotes forage at the full range of canopy heights but, because our pruners were limited to heights of up to 7 m, we used the 5–7-m height range to standardize sample height. As a result, most samples came from the lower canopy and may have contained a biased sample of invertebrates. However, Woinarski and Cullen (1984) found that sample height does not correlate with abundance or composition of invertebrate orders in eucalypts of southeastern Australia, and thus any bias in our invertebrate samples was likely to have been small.

Data analysis

To quantify the importance of manna vs. invertebrates in nestling diet composition and to test for changes with nestling age, we used a linear mixed-effects model with proportion of manna in diet as the response variable, nest stage (early, middle or late) as a fixed effect and nest identity (ID) as a random effect to account for repeated sampling of individual nest pairs across nestling age-classes. We arcsine transformed the response variable (proportion of manna in diet) to meet assumptions of normality and to even variance of residuals.

To assess whether manna or invertebrates were selected preferentially compared with their availability in tree foliage, we used a linear mixed-effects model with territory as the replicate to test whether the proportion of manna differed between nestling diet and availability in foliage. The response variable was proportion of manna (arcsine transformed for normality), modelled as a function of origin (provisioned to nestlings vs. sampled in foliage), with nest ID as a random factor. Proportions of manna and invertebrates in nestling diet were calculated as the total number of feeding events containing the food type divided by the total number of food items recorded. Food availability was calculated as the proportion of the total number of food items found in the foliage samples that were either manna or invertebrates. All analyses were performed using the statistical program R version 3.2.0 (R Development Core Team 2015), with packages 'lme4' (Bates *et al.* 2015), 'AICcmodavg' (Mazerolle 2015) and 'ggplot2' (Wickham 2009).

RESULTS

Manna feeding by Pardalotes

By climbing into the canopy, we were able to observe Forty-spotted Pardalotes foraging at close range, and saw them incising stem-surface tissue where no invertebrates or manna was visible. In areas where Forty-spotted Pardalotes were actively foraging, there were extensive horizontal incisions on stem surfaces (Fig. 3), as well as larger wounds that appeared to be maintained and widened over time (Fig. 1). When we found manna in our foliage samples, it either was exuded from damage or had dripped down from higher in the canopy. On occasion, we also saw Spotted Pardalotes *Pardalotus punctatus* engaging in similar behaviour, but the prevalence of this foraging strategy across other species is uncertain.

Artificial damage experiment

Of the four tree species investigated, *E. viminalis* was the only species to produce manna from our experimental incisions. Of 67 incisions made in leaf stems of 19 *E. viminalis* trees, 53.7% resulted in manna flow, and 13 of the trees (68%) produced manna flow (Table 1). From incisions that produced manna, the average manna volume on the day after incision was 2.1 mm^3 (n = 24). Some damage sites did not produce manna until 2 days after incision (n = 4). Of manna-producing samples monitored for at least 2 days (n = 32), 43.8% of samples showed continuous growth of the volume of manna exudate from the date of incision. The greatest volume estimated was 48 mm^3, much larger than the size of naturally occurring manna clumps in foliage which were typically < 8 mm^3. During hot weather, manna was sometimes secreted as, and remained, a viscous liquid (n = 3; Fig. 1a). Manna often continued to flow from the incision after a crystallized granule (Fig. 1b) detached. Manna easily detached from the stem in the presence of wind, rain or researcher disruption, which limited days of observation.

Eucalyptus viminalis trees with diameters ranging from 5.4 to 100.6 cm produced manna from our incisions, and there was no trend in the probability of manna production across tree diameter (χ^2 = 2.21, P = 0.14), which suggests that young and old trees were equally capable of producing manna.

Nestling diet and food selection

Our video recordings captured 172 food items provisioned by 12 pairs. Manna was the dominant food item provisioned to nestlings, making up 84.2% of nestling diet (standard error (se) range = 75.9–91.0%). Invertebrates occurred infrequently, comprising 15.8% of nestling diet (se range = 9.0–24.1%) (Fig. 4). Of 17 invertebrates identified, four were flies, four were spiders, one was a hymenopteran and one was a caterpillar. Manna was often fed to nestlings as a cluster of multiple clumps. The mean length of manna clump provisioned to nestlings was 7.4 mm (n = 135 clumps of manna). We did not detect either a change in food-load size across age ($F = 1.44$, $P = 0.41$) or a change in the proportion of manna in nestling diet across nestling age ($F = 2.44$, $P = 0.11$). Birds entered the nest rapidly and often food items were not visible on camera (e.g. obscured by the bird or blurred beyond recognition). In six of our original 18 pairs, the camera angle and nest orientation prevented us from identifying any food items, and hence we did not use these pairs in data analysis. We recorded 461 feeding events in total, and of these 172 (37%) had visible food items, all of which were identified as either manna or invertebrate. In 52% of feeding events the bill was obscured or blurred, and in the remaining 11% there was a clear image of the bill, but no food was visible. Thus, small food items (e.g. < 2 mm) may have been underrepresented if not protruding from the bill during feeding, and we are uncertain whether these small items might have been biased towards either manna or invertebrates. Nevertheless, we were able to classify food items in most images that contained visible food items, which were likely to be representative of nestling diet.

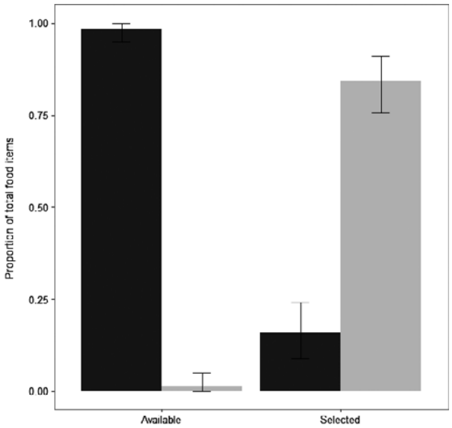

Figure 4. Comparison of proportions of invertebrates (dark grey) and manna (light grey) in foliage within foraging territories (available) and in nestling diet (selected) of Forty-spotted Pardalotes (12 breeding pairs) in southeastern Tasmania from August 2014 to January 2015. Estimates shown are back-transformation of the model output (originally arcsine-transformed). Error bars represent standard error.

We sampled food availability in the foliage of 18 territories, and identified 815 arthropods in these samples (Table 2). In contrast to nestling diet, invertebrates were the dominant item available in the foliage (98.5%, se range = 94.9–100.0%). The proportion of food items in the foliage that were manna was just 1.5% (se range = 0.03–5.1%) (Fig. 4). Thus, Forty-spotted Pardalotes strongly selected manna relative to its

Table 2. Arthropods identified from foraging territories of active breeding Forty-spotted Pardalote pairs ($n = 18$ pairs) at sites in southeastern Tasmania from August 2014 to January 2015. Blank cells indicate that the identification was unknown. Order totals are in bold.

Order	Family	Genus and species	Common Name	Frequency	Proportion
Lepidoptera	Geometridae			1	0.00
Lepidoptera	Nolidae	*Uraba lugens*	Gum Leaf Skeletoniser	577	0.71
Lepidoptera	Tortricidae			82	0.10
Lepidoptera				11	0.01
Total Lepidoptera				**671**	**0.82**
Hemiptera	Psyllidae	*Creiis* spp.		14	0.02
Hemiptera	Psyllidae	*Cardiaspina* spp.		1	0.00
Hemiptera	Psyllidae	*Glycaspis* spp.		7	0.01
Hemiptera	Psyllidae			80	0.10
Total Hemiptera				**102**	**0.13**
Hymenoptera	Formicidae			36	0.04
Total Hymenoptera				**36**	**0.04**
Coleoptera	Cantharidae	*Chauliognathus* spp.		1	0.00
Coleoptera	Curculionidae	*Gonipterus scutellatus*	Gum Tree Weevil	1	0.00
Coleoptera				1	0.00
Total Coleoptera				**3**	**0.00**
Arachnida				2	0.00
Total Arachnida				**2**	**0.00**
Diptera				1	0.00
Total Diptera				**1**	**0.00**
Grand Total				**815**	**1**

availability in the foliage. The most abundant invertebrate order was Lepidoptera (as caterpillars), comprising 82.3% of identified invertebrates (n = 815), and, of these, Gum-Leaf Skeletoniser *Uraba lugens* was the most abundant (70.8% of identified invertebrates) (Table 2).

DISCUSSION

Our results show that Forty-spotted Pardalotes mine manna from *E. viminalis* by puncturing stem tissues with their bills. This behaviour stimulates the production of manna by the tree over several days, and is thus a form of resource mining, rather than simply foraging for available food resources. We also show that manna is a highly selected food item during the nestling period and that, within active territories, manna is produced exclusively by *E. viminalis*. Together, these results suggest that manna, a high-quality food source, is the key link between Forty-spotted Pardalotes and their specialized foraging habitat, *E. viminalis* trees. This study is the first, to our knowledge, to experimentally produce manna flow. This new technique allows detailed study of manna production, as manna is released within several days, and fresh damage sites can be protected by bagging. Additionally, if the Forty-spotted Pardalote population declines to the extent that captive breeding becomes necessary, our method for inducing manna flow might be effective in obtaining food for nestlings.

Manna is an important food resource for many Australian birds, including nectarivores and insectivores such as honeyeaters and silvereyes (Recher *et al.* 1996, Steinbauer 1996, Gartrell 2000, Wilson & Recher 2001). It is also a food resource for mammals, such as the Yellow-bellied Glider *Petaurus australis*, Sugar Glider *Petaurus breviceps* and Leadbeater's Possum *Gymnobelideus leadbeateri* (Smith 1982, 1984, Goldingay 1986). Insect damage is thought to release manna flow and manna is also a food resource for some ant species (Basden 1966, Steinbauer 1996). Because many species feed on manna, but few stimulate its release from trees, manna-mining species may serve as ecosystem engineers for communities of manna-feeding birds, mammals and invertebrates. In southeastern Tasmania, we observed Striated Pardalotes *Pardalotus striatus* and Spotted Pardalotes frequently entering Forty-spotted Pardalote territories to forage. Forty-spotted Pardalotes spent a substantial amount of time chasing these intruders away, probably defending their manna supply. Larger competitors such as the Black-headed Honeyeater *Melithreptus affinis* and New Holland Honeyeater *Phylidonyris novaehollandiae* also gleaned foliage within Forty-spotted Pardalote territories, and were tolerated. Thus, the extent to which manna miners serve as ecosystem engineers by increasing manna availability as opposed to monopolizing and defending these valuable food resources is an area ripe for further research.

Mining for tree exudates is a rare foraging behaviour among bird species. Other tree exudate miners include the North American sapsuckers and the Akiapolaau, an endangered Hawaiian honeycreeper (Ralph & Fancy 1996, Eberhardt 2000, Pejchar & Jeffrey 2004). Sap from their preferred tree species, the Ohia, provides an important resource for the Akiapolaau during times of low insect availability (Pejchar & Jeffrey 2004). Likewise, sapsuckers are freed from dependence on dead trees which other woodpeckers require as a source of insects. These mining birds also select trees for characteristics including the volume, sugar content and toxin load of sap produced (Eberhardt 2000, Pejchar & Jeffrey 2004). In Australia, Yellow-bellied Gliders are the only vertebrate known to employ a similar foraging strategy to the pardalotes: they actively stimulate sap production by creating incisions in the bark of eucalypts (Goldingay 1986, 2000).

Eucalyptus viminalis was the only tree at our sites to produce manna, although in other parts of Australia at least 15 species of *Eucalyptus* and *Angophora* are known to produce the exudate (Steinbauer 1996). The importance of *E. viminalis* as a key manna source in Tasmania explains the strong specialization of Forty-spotted Pardalote on this single tree species. *Eucalyptus viminalis* is also a common forage tree for marsupial browsers in Australia, and the relative nutritional value and toxin load are key factors determining selection of tree species and individuals (Moore & Foley 2000, Jensen *et al.* 2015). A recent study of *E. viminalis* leaf chemistry found that the species has high levels of available nitrogen compared with other eucalypts, which may explain the ability of Forty-spotted Pardalote nestlings to persist on a high-manna, low-invertebrate diet (Wallis & Goldingay 2014). Nitrogen in the form of amino acids can be a limiting nutrient for frugivorous and nectar-feeding birds (Bosque & Pacheco 2000). However, if the available nitrogen found in *E. viminalis* leaves is also present in manna, the tree may be providing a rich source of both sugars and the building blocks of proteins. Further analysis of manna and the selection of individual *E. viminalis* trees by Forty-spotted Pardalotes is needed to address this question.

In songbirds, dependence on a single plant species for food supply is rare and often associated with unique behavioural and morphological adaptations (Parchman & Benkman 2002, Hess *et al.* 2014). For example, the Palila *Loxioides bailleui*, an endangered Hawaiian finch, has a stout bill which is specialized for opening *Sophora chrysophylla* (māmane) seed pods but this limits its ability to forage efficiently for other food sources (Hess *et al.* 2014). Additionally, crossbills *Loxia* have evolved crossed mandibles used for opening the cones of specific coniferous species (e.g. Parchman & Benkman 2002). The Forty-spotted Pardalote has an elongated bill tip (Fig. 2), a morphological adaptation that aids in incising stem surfaces. This trait varies among individuals and might wear from use. While many species of honeyeaters *Meliphagidae* (a dominant group of Australian passerines) and two other pardalotes consume manna, this feature of the bill is only present in the Forty-spotted Pardalote and, to a lesser extent, the Spotted Pardalote (Paton 1980, Woinarski & Bulman 1985). The honeyeaters and Striated Pardalote lack a notch entirely, which may be related to their more generalist diets (Woinarski & Bulman 1985). As seen in both the Forty-spotted Pardalote and Palila, specialists on a single food species are highly vulnerable to depletion of their required food source.

Forty-spotted Pardalote habitat, dominated by *E. viminalis*, was historically much more common throughout eastern Tasmania, but has become highly fragmented as a result of land clearing. Additionally, Tasmanian *E. viminalis* has undergone dieback, atrophy and poor sapling recruitment during a recent decade of drought (Bryant 2010). As climate change results in more frequent drought events in Tasmania, it will be important to understand how manna production is influenced by climate and forest health. Because manna easily detaches from the foliage in wind, rain or heat, climate change may have a strong impact on its availability. Encouragingly, our results show that even very young *E. viminalis* trees provided manna. Our smallest experimental tree (dbh = 5.4 cm) exuded manna at every incision site (n = 3). However, older trees have larger canopies and may provide a more abundant supply of manna. Not all available *E. viminalis* habitat is occupied by Forty-spotted Pardalotes and an investigation of variability in manna production across occupied and unoccupied forests might help to explain their occurrence patterns (Bryant 2010). Overall, our results show that manna is a surprisingly important resource for this endangered species. Thus, restoration of *E. viminalis* habitat is a critical conservation strategy for the Forty-spotted Pardalote, specifically targeted to conditions optimal for manna production. In the context of increasingly frequent and intense drought, a better understanding of the soil and microclimate variables that regulate manna production by *E. viminalis* will enable managers to identify areas best suited for planting seedlings as a future manna resource. Additionally, further research into manna mining species as ecosystem engineers and into interspecific competition for manna would greatly improve our knowledge of Australian foliage-gleaning communities.

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