

Patterns of invertebrate food availability and the persistence of an avian insectivore on the brink

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Abstract Globally, insectivorous birds are at high risk of decline. One explanation of this relates to changes in invertebrate resources due to anthropogenic pressures. The northern population of the eastern bristlebird (*Dasyornis brachypterus*) relies heavily on invertebrate food resources, and has experienced an 80% population reduction over the past 40 years. We investigated invertebrate abundance and nutritional quality across 23 currently and historically occupied northern bristlebird sites to determine whether extant territories were associated with more, or more nutritious, invertebrate resources. Pitfall and leaf-litter invertebrate sampling were done in both breeding and non-breeding seasons from 2014 to 2016. There was no difference in abundance, biomass or nutritional value of invertebrates between occupied and abandoned territories; however, within territories invertebrate abundance and nutritional value did correspond to the habitat characteristics with which bristlebirds are associated. Nutritional value of invertebrates increased with proximity to rainforest, while the abundance of macro-invertebrates (>1 mm) was correlated with grass height. Bristlebird territories are often close to rainforest margins, and these ecotones may provide more nutritious mesic-associated invertebrates. Higher abundances of large invertebrates in tall grasses may also contribute to the known association of bristlebirds with tall grasses. Maintenance of tall grass adjacent to rainforest through appropriate fire and grazing management is likely to be important for northern bristlebird recovery and long-term persistence of the population.

Key words: Australia, eastern bristlebird, grassy forest, insects.

INTRODUCTION

Insectivorous birds are sensitive to land use change, habitat loss, degradation and fragmentation (Bennett & Watson 2011; Watson 2015). This is particularly true for ground-feeding insectivorous birds, which are experiencing some of the greatest declines globally (Benton *et al.* 2002; Antos & Bennett 2006). Anthropogenic disturbances within grassy native vegetation, such as land use change, habitat fragmentation, introduction of exotic species and changes to natural fire regimes can have a strong influence on local habitat conditions and subsequently the invertebrate communities they are able to support (Andersen 1988, 1991; Didham *et al.* 1996; Chambers & Samways 1998; Zanette *et al.* 2000; Swengel 2001; Pryke & Samways 2012). Some research has suggested that changes in prey availability or accessibility within native ecosystems may be a leading contributor to insectivore decline (Watson 2011; Rioux Paquette *et al.* 2014; Razeng & Watson 2015).

The eastern bristlebird (*Dasyornis brachypterus*) is an endemic small, cryptic, cover-dependent passerine of Southeast Australia with limited flight ability

(Hartley & Kikkawa 1994). The northern population (henceforth referred to in this paper simply as the ‘northern bristlebird’), is critically endangered and isolated (>800 km) from the southern populations, occurring only along the border of New South Wales and Queensland in eastern Australia (OEH, 2012; Fig. 1b). The northern bristlebird occupies patches of grassy sclerophyll forest on basaltic ridges and slopes, typically embedded within rainforest, and (now) often bordered by cleared land (Holmes 1989; Lamb *et al.* 1993; Rohweder 2000). This contrasts markedly with the southern populations of the eastern bristlebird, which occupy coastal heath (Baker 1997, 1998, 2009; Baker *et al.* 2012).

The northern bristlebird has declined by an estimated 80% in the last 40 years (Grant *et al.* 2004). The decline of the species in general (i.e. both northern and southern populations) has been attributed to habitat loss and fragmentation, introduced predators and inappropriate fire regimes (Bain *et al.* 2008; Baker 1997; OEH 2012). The 2016 annual census (the most recent undertaken) of the northern bristlebird estimated the current wild population at 40 individuals, with just five confirmed breeding pairs (Wildsearch Environmental Services, 2016).

Although eastern bristlebirds are considered omnivorous, consuming a range of invertebrates and

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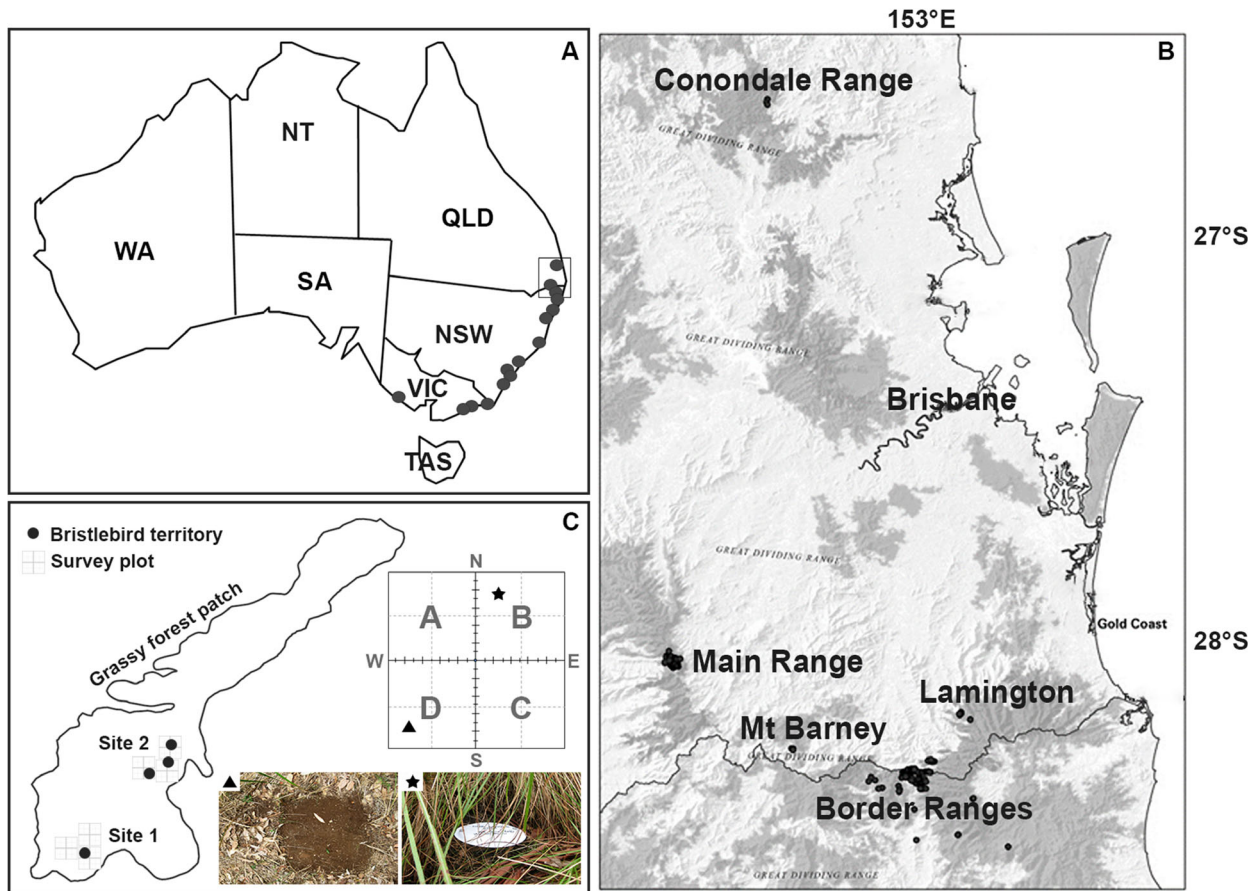


Fig. 1. Clockwise from top left: historic locations of the eastern bristlebird; all known locations of the northern population of the eastern bristlebird in Queensland and northern New South Wales; example of plot layout for two sites within a single grassy habitat patch where vegetation and invertebrate sampling were conducted, the former along two transects at right-angles to each other, the latter within randomly sampled plot subdivisions (pitfall traps = circles, leaf litter samples = crosses).

seeds (Gibson & Baker 2004; Gubler *et al.* 2016), faecal analysis and observations of foraging birds indicate their diet is predominately invertebrates (Gibson & Baker 2004). The major invertebrate groups consumed in the southern population studied by Gibson & Baker were Coleoptera (beetles), Hymenoptera (ants), Diptera (flies) and Mantodea (mantids), with a lower incidence of Arachnids (spiders). Anecdotal observations of northern birds in the field and in captivity indicate their diet is similar.

Omnivorous bird species often increase their dependence on insect prey during the breeding season as insects provide important nutrients necessary for successful breeding (Razeng & Watson 2015). As a result, breeding success and recruitment can be influenced by the availability of invertebrates (Bryant 1975; Martin 1987; Eeva *et al.* 1997; Robb *et al.* 2008). Knowing whether the decline in the northern bristlebird is at least partly a response to a decline in food availability in grassy sclerophyll forest patches would aid managers in determining management

actions to maintain high-quality habitat for the northern bristlebird. This was the rationale for this study, in which we compare invertebrate resources between current and historically occupied northern bristlebird sites, and between the microhabitats found within habitat patches, in an attempt to determine whether disappearance of northern bristlebirds may be in part a response to fewer invertebrate resources.

Specifically, we first tested whether northern bristlebird presence in patches was correlated with invertebrates. If northern bristlebird disappearance from a site is associated with insufficient food, we might expect historically occupied (i.e. abandoned) sites to have lower abundance, biomass or nutritional value of invertebrates or different invertebrate community composition, compared to currently occupied sites.

We also tested whether invertebrate patterns within habitat patches were related to particular vegetation structural attributes or patch characteristics. Northern bristlebird presence has been shown to be associated with larger, more densely grassy patches (Stone

et al. 2018). If this association is a response to prey availability, then we might expect patches with taller, thicker grass structure to have more prey. We also tested whether invertebrate abundance or composition differed between breeding (spring) and non-breeding (autumn) times of year, to see whether currently occupied sites had a higher, or more nutritious, invertebrate profile during the breeding season than historically occupied sites.

METHODS

Study area

Fieldwork was carried out across all known territories where grassy habitat still exists and is currently, or has historically been, occupied by northern bristlebirds. Sites were defined using the point territory locations of Holmes (1989) and the annual New South Wales Office of Environment & Heritage monitoring. Because the Holmes (1989) territory locations represent points at which birds were detected, we grouped points occurring within 500 m of one another to represent a single site, likely to correspond with a single territory (Fig. 1c). Bristlebird sites are generally isolated from one another by denser forest, with regional clusters of sites found in and around Conondale, Main Range and Lamington national parks in Queensland and Border Ranges National Park in NSW (Fig. 1b). The climate in the study area is subtropical-temperate, with warm, wet summers and mild, dry winters (Stern *et al.* 2000). Rainfall in the Border Ranges averages 1500 mm year⁻¹, most of which falls during the summer, and maximum air temperatures averaging 29°C in summer and 21°C in winter (based on local landowner data at Grady's Creek, Border Ranges). Sites are found clustered within small areas in and adjacent to the above-mentioned parks, largely on upper slopes or exposed ridgelines where rainforest gives way to open, grassy eucalypt forest or woodland. Much of the grassy eucalypt woodland found on lower slopes in the study region has been extensively cleared for agriculture, while rainforest is the dominant vegetation at higher altitudes.

Northern bristlebird presence and absence

Northern bristlebird presence and absence were determined using the data from the annual monitoring by the New South Wales Office of Environment & Heritage (Sandpiper Ecological Surveys, 2012; Wildsearch Environmental Services, 2015a,b,c, 2016). These annual surveys consist of an initial 5-min listening period followed by a 5-min period broadcasting northern bristlebird recordings, and then a 20–25 min listening period to pick up responses. Once birds respond, the survey ceases. Sites in which birds have not been detected for 5 years are classified as unoccupied (D. Charley, pers. comm., 2017). Since 2013 this standard monitoring has been supplemented by use of a specially trained detector dog at the NSW sites. The dog has been shown to be able to detect as little as a single bristlebird

feather or the scent of an occupying bird, even if the bird is not present at the time. This detector dog confirmed that the absence of birds at historically occupied sites recorded by the annual monitoring is indeed true absences (and not just a lack of detection or lack of calling). The combination of monitoring techniques allows a high degree of confidence in the presence/absence records, despite the cryptic nature of the northern bristlebird.

Invertebrate sampling

Invertebrate samples were collected at 23 of the 38 known currently and historically occupied northern bristlebird sites. While vegetation assessments were undertaken at all 38 sites, access constraints and planned burns meant that some sites were inaccessible during some invertebrate sampling periods. As a consequence, we include in this analysis only the 23 sites that were available for all sampling periods. Of the 23 sites, nine sites were currently occupied, while the remaining 14 were sites in which northern bristlebirds used to occur but have not been detected for many years, and are considered abandoned. The number of plots surveyed at each site varied depending on site size. Northern bristlebird territory locations can be focussed on specific areas within a habitat patch or be spread over a larger area of the habitat patch (Fig. 1c). Larger sites had more survey plots: there were 4–6 plots at each site depending on size. To account for variation in the number of plots, trapping effort ('trap nights' = number of traps × number of nights) per site was calculated and included as a predictor in models.

A random sampling approach was used to locate invertebrate survey plots within sites, with each site defined in ArcGIS (ESRI, 2016). Each plot covered an area of 20 × 20 m and was randomly placed within 200 m of the current or historic northern bristlebird territory location within a site (the point detections of Homes (1989)). Each plot was further subdivided into sixteen 2.5 × 2.5 m subplots, of which two were randomly chosen for pitfall and leaf litter sampling for any given sampling occasion (Fig. 1c).

Eastern bristlebirds forage by gleaning from and turning leaf litter with little to no digging below the surface (Gibson & Baker 2004). To reflect this, invertebrates were collected using methods that target epigeic (surface active) invertebrates: pitfall traps and leaf litter sampling (Sabu & Shiju 2010). Sampling was conducted in 2015 and 2016 in May–June and September–October. These times were chosen to sample the non-breeding winter period (May–June) and the onset of breeding activity (September–October; (Gubler *et al.* 2016).

Pitfall trapping

For each sampling period, one pitfall trap was centrally placed within a single randomly located subplot (i.e. there was one pitfall trap per plot, giving a total of 4–6 per site per sampling period). Because of the presence of northern bristlebirds and other small threatened vertebrate species, wire bird netting with a 1.3 cm hex aperture was placed over each trap to avoid non-target bycatch. While this may

have had some influence on the abundance of larger macro-invertebrates captured, the invertebrates eaten by the eastern bristlebird are considered to be mostly smaller than this (Gibson & Baker 2004) and this method was deemed necessary to avoid vertebrate mortality.

Each trap consisted of two round straight-sided plastic containers approximately 8 cm in diameter and 12 cm deep, one placed inside the other, the interior one with a removable lid. The use of nested containers allowed for removal of samples without disturbing the surrounding soil. Traps were dug in so the rim was flush with the surrounding soil. Containers were left sealed for 1 week prior to sampling to reduce digging-in effects (Greenslade 1973). Pitfall traps were then opened and filled with approximately 3 cm of a diluted propylene glycol fluid (1:3 parts water) and detergent to remove surface tension (Jud & Schmidt-Entling 2008). A cover approximately 18 cm in diameter was positioned 10 cm above each trap to protect it from rain and flooding. Traps were then left open for seven consecutive nights after which they were removed and sealed. The contents of the traps were transferred to 70% ethanol to preserve them until sorting.

Leaf litter samples

At each sampling occasion, a single leaf litter sample was also taken in each plot at a randomly predetermined subplot (excluding the pitfall trap subplot). This meant there was a minimum of 5 m between the pitfall trap and leaf litter sample, to avoid interactions (Ward *et al.* 2001). Each litter sample was obtained by gathering leaves, litter and loose humus from a 50 × 50 cm quadrat dropped in the centre of the target subplot. Samples were collected quickly and carefully stored in fine weave cotton bags to prevent the escape of invertebrates. Leaf litter samples thus sampled the upper organic litter layer plus the loose humus layer that bristlebirds forage in. No underlying compact soil was included. Litter samples were passed through 5 cm wire sieves to separate larger litter material (i.e. sticks) and remaining material was emptied into a Berlese extraction apparatus (16.5 cm diameter, 18 cm height, 1.3 cm mesh, 25 W filament lamp) and left for 1 week, as described by Sabu and Shiju (2010). Large litter material was checked visually for macro-invertebrates that may have been missed. Collection jars were attached to the base of the Berlese apparatus and filled with 20 mL of 70% ethanol solution.

Invertebrate identification

Invertebrates captured from each site were sorted to order level using a dissection microscope (Leica EZ4HD) and the dichotomous key of Harvey and Yen (1997). Taxa were grouped and identified following the protocols of Razeng and Watson (2012). Because the diet of the northern bristlebird has been little studied but the available observations show they consume very small insects (A. Beutel, pers. comm., 2017), we counted invertebrates in both macro- (>1 mm) and micro- (<1 mm) size classes. We counted the total number of individuals ('total abundance') in each order per size class for each sample. Samples were then dried in a 60°C oven for 48 h to obtain the dry weight (biomass; accurate to the nearest 0.0001 g).

Habitat patch characteristics

To test whether vegetation structure influenced invertebrate abundance or composition, we measured grass height along two 20 m transects that crossed the centre of each survey plot (Fig. 1c). Cover (to the nearest 5%) was estimated for each species in the ground (0–1 m), shrub (1–3 m) and canopy (>3 m) vegetation layers for each 10 × 10 m survey plot quarter. These measurements provided estimates of individual species cover and were also used to calculate overall ground, mid-storey and canopy cover. The extent of suitable grassy habitat over the contiguous habitat patch in which a site is located) was mapped by visually delineating grassy patches using ADS40 aerial imagery (taken in 2009, the most recent available). This imagery has a resolution of 5 m. The distance from the centre of each survey plot to the nearest rainforest margin was also measured from the aerial imagery.

Statistical analysis

To describe the invertebrate community composition, we ran a non-metric multidimensional scaling (NMDS) ordination (stress = 0.16) using mean abundances from each combination of order and size class (micro- and macro-invertebrates) and used the scores for each plot on NMDS axes 1 and 2 to generate two new variables that expressed the main differences in the insect communities between the sites. This analysis used Bray–Curtis dissimilarities. After creating these new variables, we used them in our models as indices of variation in community composition.

Total abundance and biomass variables were calculated from the sum of both pitfall and leaf litter samples. The nutritional value of the invertebrates at each site was calculated using the total abundance of macro-invertebrates from five main invertebrate groups – Araneae, Coleoptera, Diptera, Hemiptera and Hymenoptera – multiplied by the crude protein and fat values (mg/individual) from Razeng and Watson (2015). Their study analysed the macro- and micro-nutrients for the 11 main invertebrate groups in open woodland forests in southern New South Wales. While this is not the same as the habitat as in this study, it is the closest available analysis of invertebrate nutritional composition, and represents the potential nutritional value available within a grassy, eucalypt-dominated habitat type. We included only the five mentioned invertebrate groups in our calculations because: they are known eastern bristlebird prey (Gibson & Baker 2004), they are known to be preferred prey for insectivorous birds more generally (Moorman *et al.* 2007; Razeng & Watson 2015), and they were abundant enough to be present in most of our samples (comprising 58% of the sampled macro-invertebrates abundance).

We used an information-theoretic approach to assess which aspects of invertebrate resources bristlebird presence was correlated with. Generalized linear mixed-effects models (GLMMs) were fitted with a logit link using the lme4 R package (R Development Core Team, 2017). All invertebrate and habitat predictors were standardised before including in models. Subregion (Main Range, Border

Ranges, Conondale and Lamington) was included as a random effect in all models to account for spatial clustering of sites across the northern region. We controlled for further spatial auto-correlation of northern bristlebird sites by incorporating an auto-covariate into each candidate model, including the null models (Crane *et al.* 2012). Variation in sampling effort between sites was controlled by adding the log of sampling effort as an offset in all models.

To compare current and historically occupied sites at different times of year, we tested whether there were any differences in invertebrate abundance, biomass or nutritional value between currently and historically occupied sites separately in each of spring and autumn using paired t-tests. For the t-tests, the data were averaged across all plots per site to account for variation in plot numbers. The t-test results were then used to compare differences in invertebrate community composition between either sites or seasons using an ADONIS multivariate analysis in the Vegan R package (Oksanen *et al.*, 2008), and tested for statistical significance by comparison against 1000 null permutations.

Finally, we tested whether invertebrate characteristics at sites were related to habitat attributes (regardless of their occupancy by the birds). Candidate models were chosen *a priori* to reflect four main hypotheses to explain bristlebird presence: (i) total invertebrate abundance, (ii) total invertebrate biomass, (iii) invertebrate community composition and (iv) invertebrate nutritional value. For these models, we fitted GLMMs with a Poisson error distribution for invertebrate abundance as a response variable against grass structure, mid-storey and canopy cover and habitat patch context. We also tested whether invertebrate biomass and nutritional value were influenced by these habitat predictors using GLMMs with a Gaussian error distribution and an identity link for biomass and nutritional value.

RESULTS

A total of 41 413 arthropods was collected from 23 historically and currently occupied northern bristlebird sites (Table 1). Collembola, Acarina, Hymenoptera and Coleoptera made up 76% of all (macro + micro) invertebrates sampled. The number of invertebrates per site ranged from 20 to 196 (77 ± 33 , $n = 23$) and total arthropod dry weight per site ranged from 0.20 to 1.07 g (0.53 ± 0.20 g, $n = 23$) per sampling period.

Bristlebird presence in relation to invertebrate resources

Northern bristlebird presence and absence were modelled as a response to various invertebrate predictors. Conditional and marginal R^2 values of the best models were >0.5 . However, within our candidate model set, while nutritional value was the best performing model, it was only slightly more parsimonious than the null model ($\Delta AICc = 0.101$; Table 2).

Overall, northern bristlebird presence was not found to be influenced by invertebrate resources with none of our alternative models substantially outperforming the null (Table 2).

Northern bristlebird presence also was not related to invertebrate community composition found at a site ($r^2 = 0.06$, $P = 0.06$; Fig. 2). ADONIS of NMDS scores found no significant differences in the composition of invertebrates available at occupied or historical northern bristlebird sites throughout the year ($P = 0.75$, 0.017) or during spring ($P = 0.21$, 0.55) and autumn ($P = 0.4$, 0.14) seasons. Omnivorous bird species can often rely more on invertebrate resources during breeding but we found no relationship between northern bristlebird presence and invertebrate abundance, biomass or nutritional value across breeding (spring) or non-breeding (autumn) seasons (Fig. 3).

Invertebrate patterns within bristlebird habitat patches

We found no relationship between northern bristlebird presence and invertebrate variables at the time of sampling, but invertebrates themselves were strongly influenced by habitat variables, particularly at the patch scale (Table 3). Patch context, particularly patch size had a strong influence on the nutritional quality of invertebrates with smaller sites having a higher nutritional value than larger ones (Table 3). Sites closer to the rainforest margin also had a higher abundance of invertebrates present than those further away. Overall, smaller sites closer to the rainforest margin appear to have abundant, more nutritious invertebrates.

Vegetation structure also had a strong influence on invertebrates. Canopy cover influenced invertebrate nutritional value, with invertebrates at sites with a more-open canopy and less shrub cover having higher invertebrate nutritional value. Grass structure had a strong influence on overall invertebrate abundance, with our grass structure model outperforming the null (Table 3). Invertebrate abundance increased at sites with taller grass height and thicker ground cover. While invertebrate abundance increased with increasingly complex grass structure, invertebrate biomass did not. None of the alternative models for predicting invertebrate biomass outperformed the null model (Table 3).

DISCUSSION

Food limitation, particularly by invertebrate resources, can be a key determinant of insectivore abundance and performance (Zanette *et al.* 2000;

Table 1. Number of invertebrates collected in pitfall traps and leaf litter samples within northern bristlebird habitat patches

Invertebrate order [†]	Common name	<i>n</i>	% of total captures	>1 mm (macro)	<1 mm (micro)
Acarina	Ticks, mites	10 162	24.83	276	9886
Araneae	Spiders	1083	2.65	805	278
Amphipoda	Amphipods	533	1.30	525	8
Blattodea	Cockroaches	166	0.41	163	3
Coleoptera	Beetles	4640	11.34	1862	2771
Collembola	Springtails	10 014	24.47	1963	8051
Dermaptera	Earwigs	235	0.57	234	1
Diplopoda	Millipedes	178	0.43	177	1
Diplura	Two-pronged bristletails	45	0.11	29	16
Diptera	Flies	1676	4.10	1145	531
Gastropoda	Snails	38	0.09	30	8
Geophilomorpha	Soil centipedes	99	0.24	99	0
Haplotaxida	Earth worms	85	0.21	85	0
Hemiptera	True bugs	793	1.94	327	466
Hymenoptera	Ants, bees, wasps	6338	15.49	5322	1016
Isopoda	Wood lice	1514	3.70	1192	322
Isoptera	Termites	4	0.01	4	0
Lepidoptera	Butterflies, moths	18	0.04	18	0
Lithobiomorpha	Centipedes	46	0.11	46	0
Mantodea	Praying mantis	5	0.01	4	1
Onychophora	Velvet worms	8	0.02	8	0
Orthoptera	Crickets, grasshoppers	69	0.17	68	1
Phthiraptera	Lice	1	0.00	0	3
Pseudoscorpionida	Psuedo-scorpions	462	1.13	45	417
Scolopendromorpha	Tropical centipedes	24	0.06	24	0
Scorpionida	Scorpions	51	0.12	51	0
Scutigerida	House centipedes	15	0.04	15	0
Siphonaptera	Fleas	4	0.01	4	0
Thysanoptera	Thrips	12	0.03	8	4
Unidentified larvae		2565	6.27	1660	905
Unidentified		44	0.11	15	29
Total		40 927		16 204	24 928

[†]Invertebrate orders based on Harvey and Yen (1997) classifications. The five orders that made up >80% of all invertebrate samples are highlighted in bold.

Watson 2011; Razeng & Watson 2015). However, we found no differences in invertebrate availability between historically and currently occupied bristlebird sites. Invertebrate abundance, biomass, nutritional value and community composition were all similar between sites in which northern bristlebird persists and those from which they have been lost. This suggests that chronic food limitation is not a key driver of birds not persisting in habitat patches. Main prey items such as Hymenoptera and Coleoptera (Gibson & Baker 2004) were similarly abundant across all sites, making up a quarter of all invertebrates, and almost half the macro-invertebrates present.

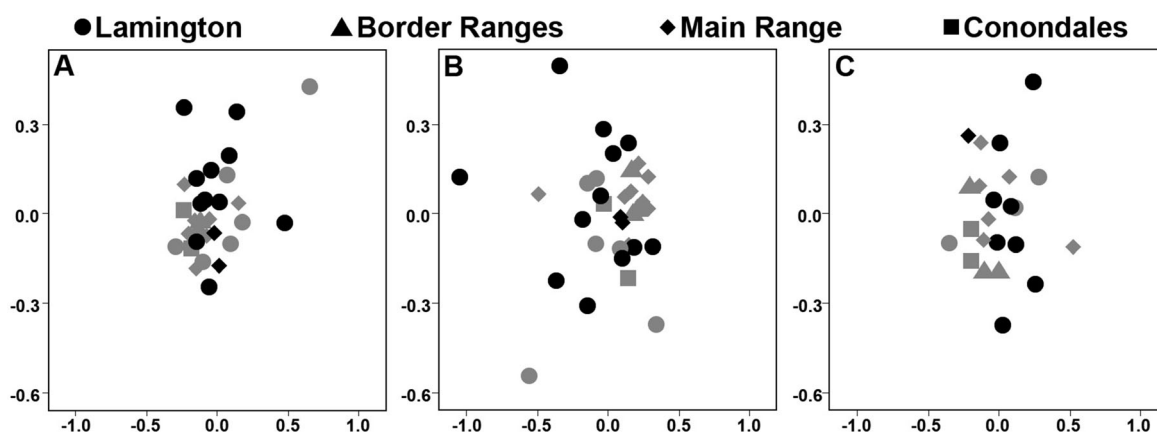
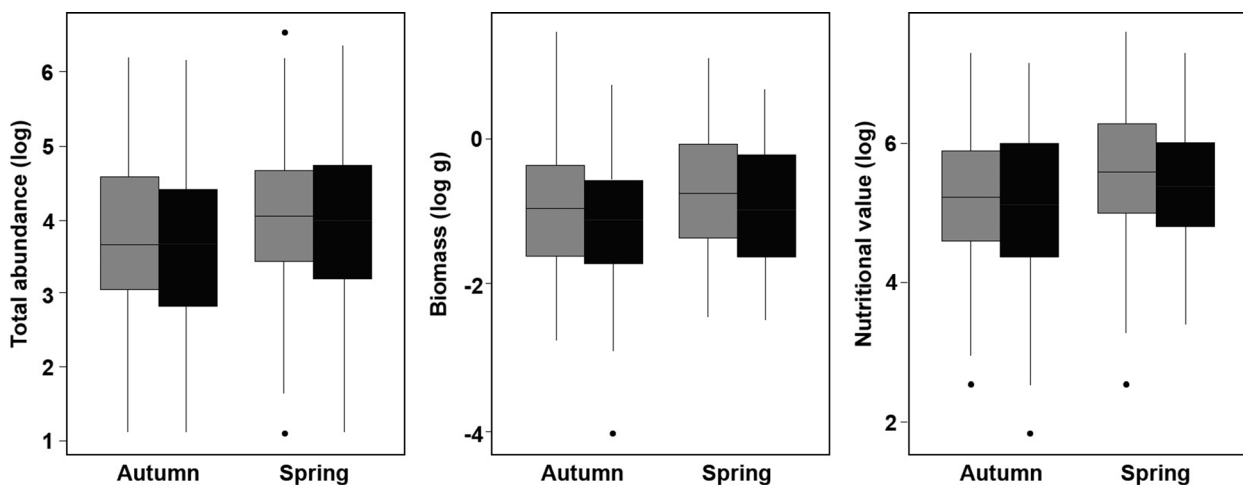
Despite the lack of relationship between invertebrates and bird presence, there were significant effects of site variables, particularly at the patch scale, on invertebrate patterns. Nutritional value of invertebrates was higher at sites closer to the nearest rainforest margin, and abundance was greater in habitat

patches with taller, thicker grass, both habitat features with which northern bristlebird persistence is associated (Holmes 1989; Lamb *et al.* 1993; Rohweder 1999; Stone *et al.* 2018).

We found no difference in invertebrates between non-breeding and breeding periods. Breeding is a highly energetically demanding activity and successful breeding is often determined by food availability (Martin 1987). For omnivorous birds, invertebrates often provide critical nutrients during the breeding season, and become a main dietary component at this time (Wilson *et al.* 1999). According to anecdotal evidence, northern bristlebirds form strong pair bonds during the breeding season, and males have a high energy investment at the commencement of breeding through territorial calling, nest building and feeding females throughout the courtship period (A. Beutel, pers. comm., 2017). The fact that there was no difference in invertebrates between seasons may suggest that fluxes in food availability that can

Table 2. Relative fit of alternative models testing northern bristlebird presence in response to invertebrate predictors in currently occupied and historically occupied sites

Model	Intercept	Total	Biomass	NMDS1	NMDS2	Nutrients	d.f.	logLik	AICc	Δ AICc	ω
Macro-nutrients	-3.818					1.302 (± 0.91)	4	-9.777	29.8	0	0.331
Null	-3.631						3	-11.307	29.9	0.101	0.314
Biomass	-3.746		-1.220 (± 0.92)				4	-10.240	30.7	0.926	0.208
Abundance	-3.625	-0.339 (± 0.51)					4	-11.086	32.4	2.619	0.089
Composition	-3.571			0.634 (± 0.57)	0.730 (± 0.65)		5	-9.872	33.3	3.498	0.058

Standard error for model coefficients included (\pm SE).**Fig. 2.** Two-dimensional ordination plots of (a) overall, (b) autumn and (c) spring invertebrate community composition for current (black) and historically occupied (grey) northern bristlebird sites classified by region.**Fig. 3.** Differences in invertebrate abundance, biomass and nutritional value between autumn and spring sampling seasons for all current (black) and historically occupied (grey) northern bristlebird sites.

support energetically demanding breeding behaviours are absent. Monitoring of invertebrate resources near known nest sites during the nesting period (not just

within the territory more generally), compared to non-breeding locations and historic sites, may be useful to definitively rule out any food limitations.

Table 3. Relative fit of alternative models testing invertebrate abundance, biomass and nutritional value response to habitat patch characteristics across currently occupied and historically occupied northern bristlebird sites

Model	Rank	Equation	d.f.	logLik	AICc	Δ AICc	ω
1. Invertebrate abundance							
Grass structure	1	$1.580 + (0.134 \pm 0.027 \text{ SE} \times \text{GrassH}) + (0.176 \pm 0.0327 \text{ SE} \times \text{GrassC})$	4	-176.13	362.48	0	0.55
Canopy cover	2	$1.595 + (-0.062 \pm 0.037 \text{ SE} \times \text{Shrub}) + (-0.201 \pm 0.028 \text{ SE} \times \text{Canopy})$	4	-176.33	362.87	0.40	0.45
Patch context	3	$1.618 + (0.010 \pm 0.043 \text{ SE} \times \text{Patch}) + (0.158 \pm 0.028 \text{ SE} \times \text{DistRF})$	4	-189.77	389.77	27.29	0
Null	4	1.596	2	-206.69	417.97	55.5	0
2. Invertebrate biomass							
Null	1	-2.242	3	-17.42	42.09	0	0.92
Grass structure	2	$-2.223 + (0.197 \pm 0.098 \text{ SE} \times \text{GrassH}) + (-0.128 \pm 0.093 \text{ SE} \times \text{GrassC})$	5	-17.57	48.67	6.58	0.04
Canopy cover	3	$-2.256 + (-0.153 \times \text{Shrub}) + (-0.126 \times \text{Canopy})$	5	-17.57	48.68	6.58	0.03
Patch context	4	$-2.177 + (0.195 \pm 0.145 \text{ SE} \times \text{Patch}) + (-0.020 \pm 0.112 \text{ SE} \times \text{DistRF})$	5	-19.13	51.79	9.70	0.01
3. Invertebrate nutritional value							
Patch context	1	$269.009 + (-38.480 \pm 19.68 \text{ SE} \times \text{Patch}) + (-11.406 \pm 10.68 \text{ SE} \times \text{DistRF})$	5	-121.6	256.74	0	0.62
Canopy cover	2	$269.009 + (-26.714 \pm 21.1 \text{ SE} \times \text{Shrub}) + (19.214 \pm 19.1 \text{ SE} \times \text{Canopy})$	5	-122.52	258.57	1.83	0.25
Grass structure	3	$269.765 + (-6.448 \pm 19.48 \text{ SE} \times \text{GrassH}) + (-14.200 \pm 12.34 \text{ SE} \times \text{GrassC})$	5	-123.16	259.85	3.11	0.13
Null	4	269.009	3	-131.21	269.69	12.95	0

Note that invertebrate abundance models were fit using a Poisson link function and so estimates produced using these equations should be back-transformed. Standard errors for model coefficients included (\pm SE).

Despite finding no differences in invertebrate resources between current and historically occupied sites, northern bristlebird occupy areas with specific habitat characteristics, in particular those that are close to rainforest margins (within 400 m) and where there are tall thick grass cover and a relatively open canopy (Lamb *et al.* 1993; Rohweder 2000). We found higher invertebrate nutritional value and abundance of macro-invertebrates in these areas.

Stone *et al.* (2018) found a strong influence of habitat patch size on northern bristlebird presence, with northern bristlebirds more likely to persist in large patches of contiguous grassy habitat. While we found no effect of patch size on invertebrate resources per unit area, by simple extrapolation, larger habitat patches should provide more invertebrate resources (since bird territories do not extend into the rainforest). Not only do large patches provide a greater area for foraging, they probably also have greater habitat heterogeneity (Karr & Freemark 1983). Habitat heterogeneity allows for a wider diversity of localised environmental conditions and produces more variation in spatio-temporal distribution of prey (Law & Dickman 1998). This may contribute to a higher overall year-round availability of invertebrate resources in large habitat patches (Ford *et al.* 2001). The mountainous subtropical region in which the northern bristlebird is found has substantial seasonal and year-to-year climatic variation: during

drought conditions summers may be very hot and dry, while more typical summers are warm and can have high rainfall due to the subtropical nature of the region. Having a greater range of microhabitats available within a patch and close to it may mean that large patches less often experience a food shortage than small patches. The observation that some birds have temporarily moved down into gullies within available habitat during extremely hot dry summers (Z. L. Stone, E. M. Tasker and M. Maron, pers. comm., 2017) supports this possibility.

Despite no relationship between northern bristlebird presence and nutritional value of invertebrates, sites closer to rainforest margins had a higher overall nutritional value of invertebrates than sites further from the margins. While our study was not designed to test the effects of ecotones on invertebrates, the almost universal tendency for northern bristlebird sites to be near to rainforest margins suggests this ecotone is important. Previous explanations have suggested rainforest may provide an important short-term refuge following fire events (Lamb *et al.* 1993; Rohweder 2000). Our results suggest the ecotone may also affects invertebrate resources, potentially from a spill-over effect (Rand *et al.* 2006; Lacasella *et al.* 2015).

Grassy habitats are often subject to strong fluctuations in temperature and moisture and higher anthropogenic disturbance (Matlack 1993). Invertebrates

are highly sensitive to environmental conditions (Kremen *et al.* 1993): vegetation composition and structure, microclimate, physical and chemical soil properties, topography and disturbance occurring within habitat patches all play a role in shaping the invertebrate communities found within them (Curry 1994). Higher soil nutrients, soil moisture and leaf litter along forest-grassland boundaries (Turton & Sexton 1996) and diverse vegetation structure (Berg & Pärt 1994) may contribute to higher abundances and quality of invertebrates. Lacasella *et al.* (2015) found that forest dwelling arthropod species were less sensitive than grassland species to edge effects, with many forest species found 'spilling over' into the ecotone area. By remaining close to rainforest margins, northern bristlebirds may be able to utilise rainforest for short-term refuge and prey resources during dry periods. Few studies have looked at invertebrate patterns across natural rainforest-grassy forest ecotones, with most focussing on disturbed agricultural or closed forest-grassland edges (Kotze & Samways 2001; Durães *et al.* 2005). The few studies that have been carried out at natural forest-grassland edges have found them to have higher numbers of predatory invertebrates (Ingham & Samways 1996), carabid beetles and amphipods (Heliölä *et al.* 2001; Kotze & Samways 2001; Yu *et al.* 2007). Differences in invertebrate resources between the rainforest and grassy forest may provide complementary nutritional resources which can be consumed at different periods depending on energetic needs (Law & Dickman 1998).

We found no significant differences in invertebrate community composition between sites or sampling periods. This may be as a result of only identifying specimens to order level. This level of identification was based on the generalist feeding patterns of bristlebirds observed by Gibson and Baker (2004), however there can often be significant within-order variation in invertebrate responses (Pik *et al.* 1999; Timms *et al.* 2013) even if no pattern is shown at a higher taxonomic level. Within order, there can be variation in the composition of families, genera and species in relation to, for example, habitat type, environmental conditions and disturbance (Andersen 1991; Andersen & Müller 2000; Orgeas & Andersen 2001; Radford & Andersen 2012).

Tall, thick grass has been previously identified as a critical component of northern bristlebird habitat (Holmes 1989; Lamb *et al.* 1993; OEH 2012; Rohweder 2000; Stone *et al.* 2018). In this paper, we found more invertebrates in grass with greater height and cover. Plant density, vegetation diversity and patch attributes can significantly affect patterns of invertebrates (Denno & Roderick 1991). Greater invertebrate abundance in taller grass may reflect this, and may be partially contributing to the

importance of tall grass for northern bristlebirds. Increased abundances of invertebrates could allow less foraging effort, likely to be particularly important during nesting (which occurs in tall grass tussock patches).

Whilst Gibson and Baker (2004) found that seeds made up only a small proportion of bristlebird diet, their study was on the southern population which lives in heathland. It is possible that seed resources may be more important to northern birds. In grassy forest habitat, seeds – which are less likely to have a hard, dormant seed coat or be stored in woody cones – may be more important to bristlebirds. Future research on the actual diet of the northern bristlebird would help confirm the relative importance of seed and invertebrates at different times of the year, though the cryptic, ground-dwelling nature of bristlebirds, as well as their rarity, make this difficult. An indirect way to accomplish this could be to compare seed availability between occupied and abandoned sites to see whether there are differences.

The results of this study suggest that altered invertebrate assemblages are unlikely to be a major determinant of current northern bristlebird distribution. We found no direct evidence to suggest currently occupied northern bristlebird sites have greater abundance, biomass, nutritional value or diversity of invertebrate prey per unit area. However, distance to rainforest and understorey vegetation structure may play more significant roles for northern bristlebird persistence, and this may be partly through their effects on food availability. In contrast, continued loss of northern bristlebird habitat and deterioration in grass condition due to inappropriate fire are a higher priority for management (Stone *et al.* 2018).

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