Individual variation in the foraging behaviour of two New Zealand foliage-gleaning birds

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Abstract: The foraging behaviour of two foliage gleaning birds, rifleman and grey warbler (henceforth warbler), was studied at Kowhai bush, Kaikoura, with the aims of exploring behavioural variation by individual pairs, and broader patterns of foraging behaviour for each species. Data on six foraging variables were collected from individually identifiable birds of known breeding status at the time of sampling. A total of 1,632 samples were taken during the spring/summer period of 1987/8. Data analysis explored foraging behaviour in relation to species, sex, and breeding stage. Individual pairs of riflemen exhibited significant variation in behaviour, indicating behavioural specialisation that I term a "foraging personality" identified as an emergent characteristic of each pair. Riflemen showed greater within-pair variation than warblers. The similarities and differences in foraging behaviour between the two species are described and are linked to their behavioural ecology. Analyses are presented in relation to the problem of data independence when repeated samples are taken from one individual.

INTRODUCTION

Behavioural flexibility in relation to current environmental conditions, varying physiological demands or morphological variation makes evolutionary sense, and presumably influences survival. Flexibility in foraging behaviour by bird species has been found in a wide range of contexts. Two bark-foraging species, nuthatch (*Sitta europaea*) and Eurasian tree creeper (*Certhia familiaris*), showed significant between-year variation in the proportion of time spent foraging on beech (*Fagus sylvatica*) (Adamik & Korňan 2004). Coal tits (*Parus ater*) and common starlings (*Sturnus vulgaris*) adjusted their foraging behaviour in relation to the presence or absence of snow (Maccarone 1987; Brotons 1997), and wind for the coal tits

(Lens 1996). Gustaffson (1988) linked individual differences in foraging behaviour of coal tits to size, wing morphology and age. Foraging behaviour of gray-breasted jays (*Aphelocoma ultramarina*) is affected by age, dominance status, and learning opportunities (McKean 1990). Mixed-species flocks of migrant North American warblers and non-migrant Australasian warblers both adjusted their foraging behaviour in relation to drought (Bell & Ford 1990; Newell *et al*. 2014), and forest type (Tarbox *et al*. 2018). Numerous other examples are documented in these papers. Most relevant here is that these examples are reported in relation to species or populations; flexibility in foraging behaviour by individual passerine birds is only rarely reported (e.g. Greenberg 1990; Whelan 2001; Aplin *et al*. 2014) and is presumably rarely studied. However, as a principle, behavioural flexibility has been reported across a wide variety of taxa, and is

clearly an important factor influencing behavioural outcomes (Lea *et al*. 2020).

The theoretical context of most research on bird foraging has been variously described as niche (or resource) partitioning, guild structure, foraging specialisation, ecological (or behavioural) plasticity, or species flexibility (e.g. Holmes & Robinson 1988; Bell & Ford 1990; Greenberg 1990; Martin & Carr 1990; McNally 1994; Somasundaram & Vijayan 2008; Mansor & Mohd Sah 2012). More recent research has shifted towards the conservation/applied science context, where birds are used as bioindicators (e.g. Virkkala 2016). Recognising that individual variation is a key factor underlying all of this research, researchers have recently begun to use the notion of personality when referring to the expression of different behaviours under the same conditions (Aplin *et al*. 2014). By extension, some authors now refer to personality as an emergent property of groups of animals (e.g. Planas-Sitjà *et al.* 2015).

Using an experimental approach with three closely-related species of American warblers, Whelan (2001) described what he called "distinct foraging microhabitats". Under controlled conditions, each species foraged from different surfaces within the artificial forest and adjusted their foraging behaviour in relation to current foraging location. Whelan showed that leaf dispersion has the strongest influence on prey capture location, and distance to prey determines prey capture manoeuvre. A key finding is that he demonstrated significant variation in the location and behaviour of individual birds of the same species foraging under the same conditions. Furthermore, Whelan (1989) showed that the learning rate of warblers varies at both individual and species levels. These (wild-caught) birds therefore demonstrated individual preferences, different learning outcomes, and behavioural specialisation, in a standardised context. Those results are entirely consistent with the notion of personality as used in recent literature, although Whelan (1989) did not use the word.

It therefore seems likely that individual behavioural variation makes a fundamental, albeit rarely studied, contribution to the patterns documented in many ecological studies of passerine birds. Understanding that variation should help to explain the broader patterns of behaviour described in much research on foraging behaviour (Martin & Carr 1990; Lea *et al*. 2020).

Research designed to explore phenotypic variation in behaviour necessarily requires long-term data gathered from identifiable individuals, usually as a series of samples. A statistical issue that immediately arises is independence of data. Multiple samples taken from one individual increase the final sample size considerably, potentially making the data more representative of behaviour and enabling more fine-scaled analyses if reasonable independence of samples can be assumed. The issues for birds have been addressed in detail in Bell *et al.* (1990), Heijl *et al*. (1990), and Recher & Gebski (1990). Multiple samples were taken in this study, which includes two analyses addressing the question of whether the data can be treated as independent measures for statistical analysis.

An additional analytical problem is that sampling of bird behaviour almost inevitably results in a mix of continuous (e.g. height) and categorial (e.g. perch type) variables, complicating any attempt to combine variables into a single analysis that captures the diversity of foraging behaviour for comparative purposes. Treating variables separately can result in multiple statistical analyses, and associated type II errors. The present study was descriptive, and the approach taken was therefore to use exploratory quantitative techniques to search for broad patterns in the data, and use a minimum of inferential analyses to test trends apparent in the data.

This study explored the foraging behaviour of two foliage gleaning bird species in relation to sex, stage of breeding, and individual variation. The aims were: i) to explore behavioural differences within and between breeding pairs, ii) to document behavioural variability during different stages of the nesting cycle, and iii) to compare the behaviour of the two species.

METHODS

Birds were studied in a small, mostly isolated, forest, 7 km inland from the small coastal tourist town of Kaikoura, eastern South Island, New Zealand (173°37′E, 42°23′S). The forest was mostly *Kunzea ericoides* (kanuka, Myrtaceae) existing as secondary re-growth on a flood plain adjacent to a small river (a more detailed description is in Gill 1980b). The original forest was cleared for farming, and then allowed to revert to forest for flood control purposes about 30 years before this study. Most of the trees were similar in height at 5–7 m, which is a mature size for this early-stage forest coloniser, although it can grow considerably taller (http://www.nzpcn.org.nz/flora_details. aspx?ID=885). The canopy was closed but not dense, and the relatively low and consistent canopy height supported human observation of these tiny birds. The area was occasionally grazed by cattle, ensuring minimal undergrowth and easy access for researchers throughout the forest. There was little leaf litter or fallen branches on the forest floor, allowing researchers to move silently in any direction. Both bird species are relatively tolerant

of human presence and tend to move through the forest at a speed approximating a human walking pace. Thus, individual birds could usually be followed reliably for 10–30 minutes, enabling repeated sampling of foraging and reliable finding and monitoring of nests. The main study area of about 1 km^2 was marked out in a 25x25 m grid, enabling easy monitoring of location, although marked birds (and researchers) sometimes moved beyond the gridded area.

The data reported here were collected in the (southern) spring and summer of 1987/8. The data were lost in a computer crash in 1989. However, paper records were retained and were recently re-entered. For most analyses, the data were linked to breeding stage, identified as BL (building/laying), IN (incubation), FN (feeding nestlings), and FF (feeding fledglings). Each of these stages was about three weeks long, although nests could fail at any time, and re-nesting could begin while fledglings were still being fed. Data collection began in late August and continued until mid-January. Breeding stage for every pair was checked at least weekly.

Study species

Rifleman (A*canthisitta chloris*, titipounamu, Acanthisittidae) and grey warbler (*Gerygone igata*, riroriro, Acanthizidae, henceforth warblers) are the two smallest bird species in New Zealand (Anderson, 2013; Withers, 2013). Both are endemic species, with the rifleman being one of two surviving species in an endemic suboscine family. Warblers are the only mainland New Zealand representative of an Australasian group (including the Philippines, Thailand, Indonesia, and New Guinea) containing the gerygones (about 20 species), thornbills (about 12 species), and some others (https://carolinabirds.org/index.html).

Male riflemen are 10–15% smaller by weight than female riflemen and both warbler sexes. Both species are active foliage gleaners, thus are easily located due to continuous movement and regular calling (riflemen) or singing (male warblers). Demographic and behavioural detail for both species are summarised in Table 1 (references therein, and personal observations). Riflemen are dimorphic (males are green, females are brown), but sex in warblers can only be distinguished by behaviour: female warblers sing rarely, do all nest building and incubation, and are generally much quieter and less conspicuous than males. Female and male riflemen are similarly conspicuous and vocal, routinely giving contact calls as they forage. Mate guarding behaviour by males of both species early in the breeding season allowed pair-identification, and sex assignment for warblers. During the BL phase of the breeding season, male warblers sit 1.0–1.5 m below females as they forage, and move wherever the female goes (= guarding). Other male activities include singing patrols (moving and foraging as they sing), occasional intensive chase interactions with other males, and accompanying the female when she is off the nest during incubation. Once eggs hatch, males provision nestlings and fledglings (Gill 1982a), including doing all provisioning if the female initiates a new nest. Male riflemen participate fully at all stages of the breeding cycle, including provisioning females to support egg production, and doing most nest building (Sherley 1985, 1989). One study of foraging of non-breeding riflemen identified differences in perch use by males and females, but no differences in activity budget or prey capture rate (Lill 1991). Gill (1980b) reported that non-breeding warblers fed mostly in the upper part of the forest, they were always upright when perched, and 40% of their foraging behaviour was hover gleaning.

Most birds were individually colour-banded. Capture was primarily with mist nets, although a few riflemen were captured using a hand net near a nest box. No birds were injured during capture and banding, and no nests were abandoned as a result of our activities. Content of nests was only checked if it was known that no bird was present, with most determination of nesting stage achieved using bird behaviour (e.g. carrying nest material or food; returning to the nest secretively and without food). The species studied form long-term pair bonds and are sedentary (Gill 1982a; Sherley 1985), thus, any unbanded birds could be identified by their association with a mate and/or a nest. I did not record foraging data from unbanded birds that could not be linked to a nest and/or a banded mate at the time of sampling.

Research methodology was approved by the Animal Ethics Committee of the Department of Zoology at Canterbury University. Bird banding was conducted under licence from the Department of Conservation.

Warblers build an enclosed pendulous nest, generally in a dense clump of vegetation in the upper half of trees in this study area. Riflemen are hole nesters, building a ball nest with a side entrance. In this study, most rifleman nests were in nest boxes. Thus, riflemen nests were protected from predators, but warbler nests were not. Warblers are also parasitized by the shining bronze cuckoo (*Chalcites lucidus*) (Gill 1982b; McLean & Rhodes 1991; Briskie 2007; Thorogood *et al.* 2017). Some of the data used here were from birds feeding a cuckoo chick, including one nest from which both a warbler and a cuckoo chick were successfully fledged (the female fed the warbler fledgling and the male fed the cuckoo fledgling).

Table 1. Demographic characteristics of rifleman and grey warbler

Characteristic	Rifleman[*][#]	Warbler[+][#]
Clutch size	4.4 $\pm$ s.d. 0.4	3–5 (mode 4)
Egg size	19% female weight	23% female weight
Laying rate	2-day intervals	2-day intervals
Incubation period	19.6 $\pm$ s.d. 0.8 days	17–21 (19.5) days
Nestling period	24.0 $\pm$ s.d. 1.2 days	15–19 (17.2) days
Female weight	7.0 $\pm$ s.d. 0.7, N=20	6.4 (combined gender)
Male weight	5.6 $\pm$ s.d. 0.3, N=33	6.4 (combined gender)
Male guards female	Yes	Yes
Male provisions female	Yes (pre-lay and lay only)	No
Male builds nest	Yes (> female)	No (may follow female)
Male incubates	Yes (> female during day)	No
Male feeds chicks	Yes (> female)	Yes
Helping behaviour	Yes (uncommon)	No
Male aggression	Yes (neighbour disputes)	Yes (neighbour disp.)
Female aggression	Yes (neighbour disputes)	No
Male territorial singing	No	Yes (very persistent)

[*]Rifleman: Sherley (1985, 1989, 1990a, 1990b)
[+]Warbler: Gill (1980a, 1980b, 1982a)
[#]Personal Observations

Sampling foraging

All data were collected when there was good weather with little wind and no rain. Movement and binoculars were essential for following birds closely, and rain, or movement of vegetation due to wind, made sampling too difficult.

After a bird was identified, I waited for it to peck at a food item and immediately started a stop watch. The bird was then observed continuously until the next peck in order to obtain the inter-peck time interval and the distance moved between peck locations, estimated as the pathway distance travelled in decimetre units. Recorded for the *second* peck site were: perch site, peck substrate, feeding behaviour, height of bird, and height of canopy directly over the bird (as estimates). Using the inter-peck interval data reported here, an average of 15 seconds would have elapsed from when the bird was first seen, and the data recorded for the first foraging event. A tree marked in metre units was used for training for height estimation; path estimation of distance moved was practiced using a measuring tape.

Height was analysed as relative height (bird/ canopy = relative position of the bird in the tree) rather than the more usual absolute height. Thus, the position of the bird in the tree was estimated very precisely, effectively by using top down as well as bottom up estimates for the two heights.

The birds moved continuously and could disappear from direct view at any time. To minimise bias towards short inter-peck time intervals, I continued the sample if the bird was out of sight for less than three seconds. If the bird was unseen for more than three seconds, no data were recorded and another timed sample was initiated from the next peck seen. If the bird was lost completely, the time and travel distance when it was lost were recorded and I recorded the foraging details of the *first* peck; no inter-peck rate was available for that record, but a distance moved was. I recorded up to five samples from one individual bird on one day. Minimum time interval between samples was initially set at five minutes, but was reduced to two minutes once preliminary data had been collected (peck rate for both species was around 6/min, birds were opportunistic in their use of feeding method and location, and birds could easily move through the entire height of the forest in two minutes). If working with a pair, individuals were alternated in order to maximise the time between samples taken from one individual. If <5 samples were obtained during one session with a bird, then the balance could be taken later in the day. A few instances of >5 samples from one bird in one day were found in the data (maximum 8); these were mostly due to two samplers working separately and encountering the bird at different times (all samples were accepted).

Peck rate and distance moved were recorded and reported as continuous variables. If a bird made multiple pecks at the substrate (e.g. due to finding a resting swarm of flying insects, or taking scale insects), the number of pecks was counted and divided into the inter-peck time interval. Peck rate was converted to pecks per minute. Movement rate was calculated using the distance moved and time interval between pecks, converted to metres/min; values >60 m/min were removed from the data as they indicated a fast flight not linked to foraging.

The two height measures were recorded as continuous variables, but reported as a discrete (ordinal) variable: proportion of total samples recorded at relative heights between 0 (ground) and 1 (top of canopy). Relative height was then analysed using six categories: 0–0.1, >0.1–0.3, >0.3–0.5, >0.5–0.7, >0.7–0.9, >0.9.

Perch substrate, peck site and feeding behaviour were recorded as categorical (nominal) variables. Categories were:

Perch substrate: i) Ground, Trunk (stem of tree from ground), ii) Large Branch (side branch off trunk with a thickness >25 mm), iii) Small Branch (side branch <25 mm but too thick for the birds to disturb), iv) Twig (branchlet with leaves directly attached, < 10 mm thick), v) Leaf (including leaf petioles), vi) Dead Wood.

Peck site: i) Ground (including ground vegetation such as low grass), ii) Litter (or other loose ground vegetation), iii) Moss (mostly on ground, occasionally on trees), iv) Lichen (on trees), v) Bark (bark on *K. ericoides* is loose and stringy and may strip off naturally to expose bare wood), vi) Dead wood, vii) Leaf (including leaf petioles), viii) Flower, Air, Web (spider), ix) Hole (cavity in the wood), x) Knot (site on trunk or large branch where a branch had been lost), xi) Trunk or Branch (large or small) were recorded only if there was no bark at the peck site.

Feeding Behaviour: A peck at the substrate (glean) was divided into: i) Upright glean (bird standing upright), ii) Downside glean (bird feeding on underside of perch; the distinction effectively gives the exposed and shaded sides of the substrate), iii) Hover glean (the bird hovers to inspect vegetation and takes a prey item off the substrate while hovering), iv) Probe (bird pokes its beak into a hole), or v) Lunge (the bird jumps or flies to grab a previously sighted resting prey item; it may stop at the peck site or continue on, but it does not hover and the prey item was on the substrate when taken). Non-gleaning behaviour included vi) Flush

(the bird's activities disturb a sedentary prey item that flies or falls, which is then taken in the air), vii) Hawk (the bird attacks a flying prey item that was not flushed), and viii) Provision (male feeds female).

If the bird caught flying prey that was not flushed (= Hawk), then the jump-off perch was recorded and the peck site was recorded as "Air".

Analysis
Data summaries
Levels of analysis supported by the data included: i) within and between-pairs, ii) between-breeding stage (both species), iii) between sexes (within species), and iv) between-species. To be included in i), a minimum of 5 samples was required for both members of the pair for all four stages of breeding (= minimum 20 total samples per individual). To be included in analyses for ii), iii), and iv), a minimum of three samples for an individual was required. For all analyses, each sample was treated as an independent measure of foraging behaviour.

Between-pair variation in behaviour: within-pair data
The aim of the between-pair analysis was to capture variation in the behaviour of individual birds working together as a pair. Hence each pair was treated as a nominal individual. For each behavioural variable, the data for females and males were collapsed to create one index value for each breeding stage that assessed the scale of behavioural difference within a pair for each breeding-stage/variable combination. To produce the index, all six behavioural variables were converted into categorical variables, each with exactly six categories. Some combining of minor categories was required for the three categorical variables (described in Results). For continuous variables, the categories were defined to ensure a reasonably even spread of data across categories. The data were indexed using the formula:

$$\Sigma I_{BS} = [(F_C/N_F)-(M_C/N_M)]*((N_F+N_M)/10)$$

Where I_{BS} = Index value for Breeding Stage
   F = Female, M = Male
   C = behaviour category count
   N_X = sample size for the breeding stage for the specified sex
   10 is a constant that reduces the scale of the final index to a number close to 1, without affecting its relative value.

A key characteristic of this formula is that behaviour categories with higher counts have a higher proportional representation in the final index value relative to categories with lower counts, compensating for the problem that categories with

low counts (and therefore lower reliability) could dominate the overall index when Ns are small. Low counts (including zeros) are expected for some categories due to the nature of the behaviour being sampled. Modelling indicated that those counts could bias the result if a simpler index such as a percentage was used (e.g. with a total N of 5, one observation enters the data as 20%; with a total N of 20, two observations enter the data as 10%).

Thus, for each pair, six indexed values (one for each sampled behaviour) were calculated for each of the four breeding stages. The formula delivers a value where 0 = no difference between female and male, positive values mean F>M, negative values mean M>F, and larger values indicate a bigger difference between female and male. The upper and lower bounds are open as they depend on sample size, but modelling indicated that they were likely to range between 3 and -3 in this data set: the biggest calculated index values were 2.08 for riflemen and 2.94 for warblers. The sum of the six values is always zero because females and males are contributing equally to the data, so negative values were converted to positive in the index. A final data set indexing the behavioural differences for a pair with complete data contained 24 values: (4 x breeding stage) x (6 x behaviour category). For riflemen, seven pairs had sufficient data; for warblers one pair had sufficient data. One rifleman pair with complete data in the first three stages, but data for only the male in the FF stage, was included by using an estimate of the missing female datum (thus total N = 8). N's per individual rifleman ranged from 35–60.

The complete analysis was therefore only possible for riflemen, but between-species comparison was achieved using a more limited data set. Ten warbler pairs had enough data for at least one stage of the breeding cycle to support a partial analysis, allowing a visual review but not a statistical analysis. To compare directly with riflemen, the complete indexed rifleman data set for eight pairs was subsampled to match the partial warbler data set. Exclusion of some rifleman data was achieved by matching pairs of warblers and riflemen using a randomly assigned pair number, and then eliminating any rifleman breeding stage result for which the equivalent warbler analysis was missing. For example, if five warbler pairs had data available for FN, then only the five matched indexed rifleman values for FN were used. Two warbler pairs with indexed results for only one breeding stage were eliminated to match the warbler N to the rifleman N of 8. Thus, for the between-species comparison of gender variation within pairs, sample size and data availability were equivalent for the two species, enabling use of ANOVA.

Sex and species comparisons: all data

All individuals with <3 samples were removed from the data set, leaving for riflemen: 16 females and 17 males, and for warblers: 15 females and 14 males. Variable structure was 2 x species, 2 x gender, 4 x breeding stage, and 6 x foraging behaviour (= 96 in total). Patterns in the data were initially identified visually, and then reviewed using hierarchical cluster analysis in SPSS to confirm the visual conclusions. The original plan to use follow-up statistical analysis to check the significance of major differences was abandoned when it became apparent that relationships amongst the many elements of the data were complex. There were few obvious differences and a great deal of overlap, potentially resulting in a large number of statistical tests. Thus, the analysis is primarily visual, with 95% confidence intervals plotted on the graphs wherever appropriate as an indication of statistical distinctiveness.

Independence of data

Two analyses were conducted to check whether a series of five samples taken from one individual at one time could be treated as (reasonably) independent in the overall analysis. The checks were conducted on continuous variables only (peck rate, distance moved, height), as these supported analyses that explored variance.

In the first analysis, I looked at mean and variance for each variable across the 5-sample sequence for all birds in the data set of each species. This analysis explores patterns in the sequence, with the prediction that if the birds are responding to the observer, then there will be detectable trends in the sequence (such as moving higher, moving more quickly, or pecking at a slower rate).

In the second analysis, I predicted that if the five samples taken from one individual were correlated (= not independent), then the variance of those samples should, on average, be smaller than the variance for five randomly chosen values from the full data set. Here, I extracted the first available sequence of five samples for all females in the BL breeding stage category (riflemen) and for all males in the FN category (warblers). For riflemen, 14 females satisfied the criterion, giving 70 samples; for warblers 12 males satisfied the criterion, so I included two repeat sets from two male individuals in order to match N with riflemen.

The two species were analysed separately. Samples ordered by bird were paired against themselves (i.e. two identical columns were created). Order of the second column was then randomised (with replacement), creating a paired data set where each sequence of five samples for one bird was paired with five randomly selected samples

from the full data set (of 70 samples). The mean/variance ratio of each sequence of five samples was then calculated, giving 14 pairs of ratios (individual:random). These 14 were compared using a paired t-test, where it was predicted that a ratio calculated using the data from one bird would, on average, be larger (because the variance of a set of correlated data should be smaller), than the ratio calculated from five samples chosen randomly from the same data set. The test was bootstrapped 20 times, giving 20 t values for each behaviour for each species (= 120 t-tests). The scale and distribution of the t values is of primary interest rather than their possible significance, although significant t values would support the prediction.

RESULTS
There are three sections in the Results. First, is an analysis of within-pair foraging behaviour of pairs of birds, using the summarising index that treats each pair as an individual. Second, is a broad descriptive analysis of the foraging behaviour of the two species using all of the data broken down by species, sex, and breeding stage. Third, is an analysis of the issue of data independence for multiple samples taken from the same individual bird. The acronyms for breeding stage codes are: BL (building/laying), IN (incubation), FN (feeding nestlings) and FF (feeding fledglings).

A total of 1,632 observations were obtained, of which 978 from 33 birds (riflemen) and 529 from 29 birds (warblers) with 3+ samples were accepted for the analysis of foraging behaviour. Sample range per rifleman was 3–60 (= 19.6 ± s.d. 10.7), and per warbler was 3–40 (= 17.5 ± s.d. 11.3). Actual sample sizes in some analyses were slightly reduced due to occasional missing elements in the data.

Within-pair variation in foraging behaviour
There was significant variation in within-pair behaviour among rifleman pairs (2-way repeated measures ANOVA, Fig. 1), with both behaviour (F_5 = 3.3, P = 0.007) and breeding stage (F_3 = 7.1, P < 0.001) being significant. The interaction was not significant (F_{15} = 1.5, P = 0.1). Sex differences were generally strongest during BL, whereas they were most variable during IN. Most similar in terms of pattern were pairs 14 and 1, and pairs 5 and 3 (the estimated value for FF for pair 5 was not plotted). Sex difference through the breeding cycle was least variable for pairs 13 and 6, indicated by strongly overlapping 95% confidence intervals; for all other pairs sex difference had non-overlapping 95% CIs.

The broad results from this analysis are, i) that each pair had a unique pattern of sex difference through the breeding cycle, and ii) there was considerable variability in foraging behaviour by individual pairs.
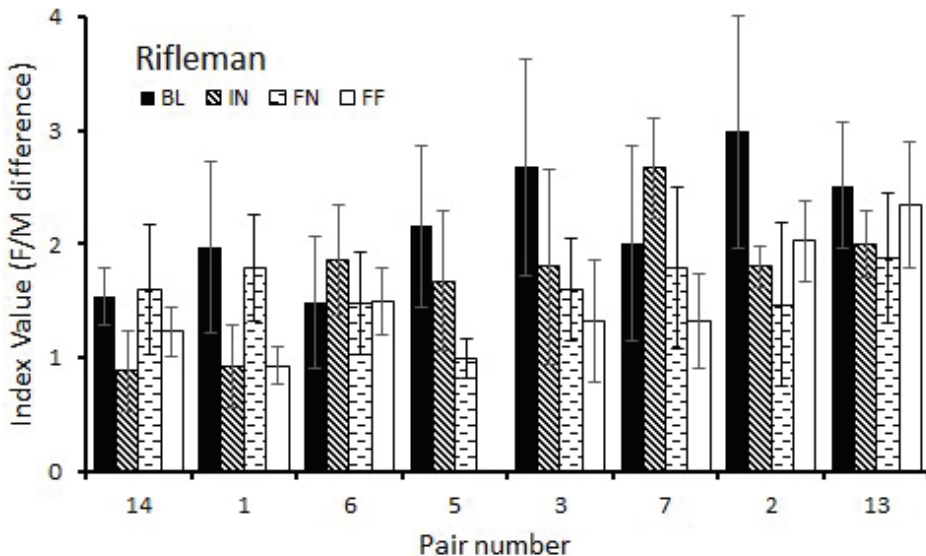

Figure 1. Difference in the foraging behaviour of paired female and male riflemen at four different stages of the nesting cycle (see Methods, paragraph 2), indexed using six standardised behavioural variables collapsed into one value for the pair (formula in Methods). Higher values indicate a greater difference in foraging behaviour within the pair. Bars are index means for the pair ± 95% confidence intervals (N per bar = 12 = 6 lumped behavioural variables for both sexes). The pairs are organised along the x-axis by increasing overall dissimilarity.

Because more limited data were available for warblers and bars were not as directly comparable as in Fig. 1, the warbler version of Fig. 1 was plotted as two separate graphs with the primary aim of comparing between species (Fig. 2a,b). Sex difference between warbler pairs was relatively small, with six of the ten pairs having very similar index values (black bars in Fig. 2a). The warbler data were matched with rifleman data (see Methods) to create a statistically comparable data set for eight pairs from each species. There was significant variation in sex difference between warblers and riflemen, both between species (2-way repeated measures ANOVA, $F_{11} = 9.9$, P = 0.003, Fig. 2a) and among the breeding stages ($F_3 = 6.4$, P = 0.001, Fig. 2b). The interaction was not significant. The main source of the between-species difference was in the BL and IN stages, with riflemen having bigger within-pair differences in behaviour at both stages.
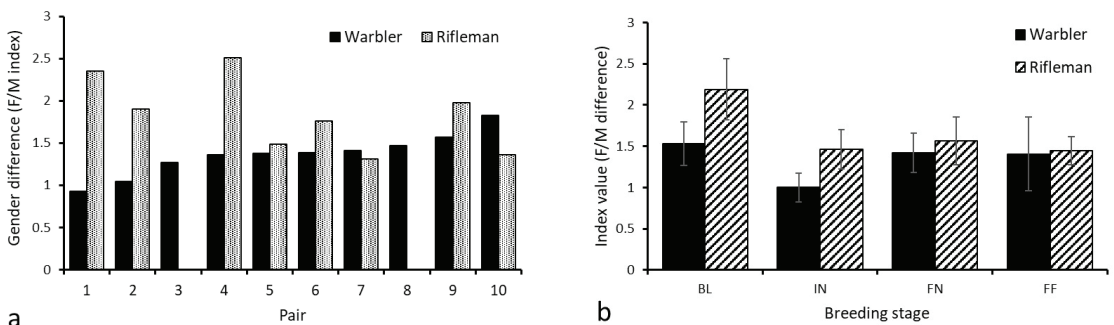
Comparative foraging behaviour
These summaries are based on visual inspection of the data and describe general comparative trends. Ns are warbler, female:male, BL, 77:88; IN, 32:42; FN, 86:110; FF, 49:61; rifleman, female:male, BL, 224:171; IN, 91:87; FN, 92:80; FF, 68:60. In the figures, Y axes were standardised for within-species sex comparison, but may be different between-species.

The most obvious differences between the two species were, i) the wider height range and associated differences in perch types and peck sites (especially use of trunks and bark) used by riflemen relative to warblers, ii) the exclusive and frequent use of hover gleaning by warblers, iii) provisioning of female riflemen by males during BL, and iv) the high peck and movement rates for female warblers during IN. The most obvious general similarity was the similar movement rates by both species.

Figure 2. Difference in the foraging behaviour of paired birds of two species in the breeding season indexed using six standardised behavioural variables averaged across available data for the pair (formula in Methods). Each warbler pair is matched to equivalent data from a randomly selected rifleman pair. Higher values indicate a greater difference in foraging behaviour within the pair. Bars are mean index values using all available data from any stage of the breeding season (a), or averaged across pairs with available data in each breeding stage ($\pm$ 95% CI) (b).

Height
Riflemen foraged throughout the full height distribution in the forest whereas warblers spent relatively more time in the upper part of the forest (Fig. 3). Female warblers foraged most frequently in the canopy, especially when IN and FF, and tended to forage lower during BL. Male warblers generally foraged lower than females, although they rarely used the bottom third of the forest, and they moved higher when FF. Rifleman males foraged more than females in the canopy when IN, FN and FF, whereas during BL males foraged more than females in the bottom half of the forest.
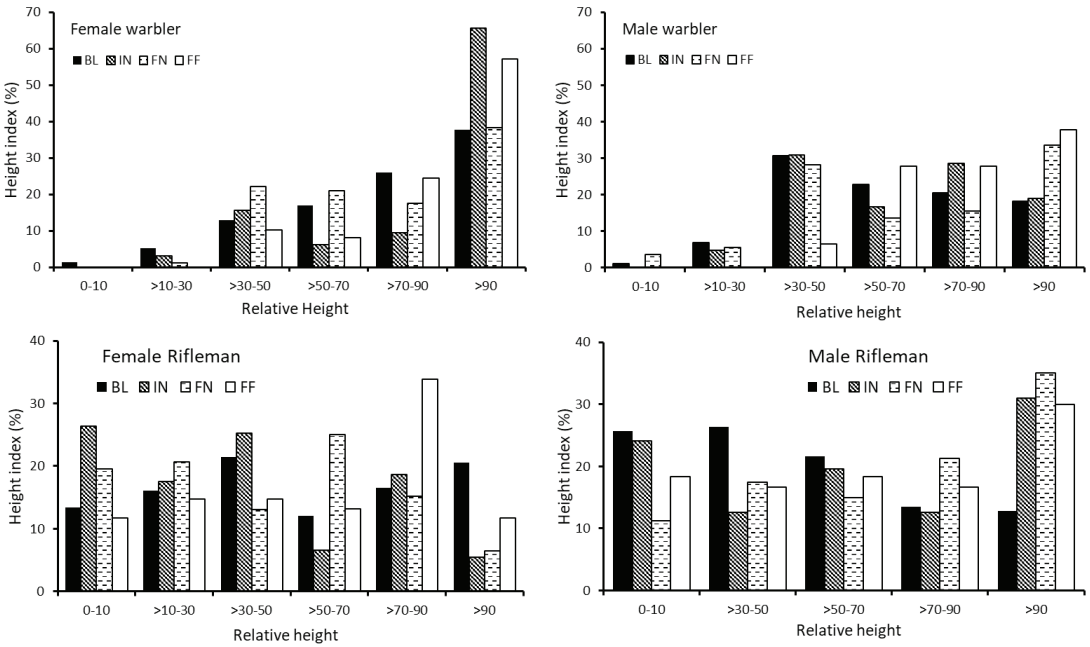
Figure 3. Relative foraging heights used by two bird species organised by sex and stage of the breeding season. Bars are frequencies of height index categories converted to %. Rifleman N = 978, warbler N = 529. BL = building/laying, IN = incubation, FN = feeding nestlings, FF = feeding fledglings.
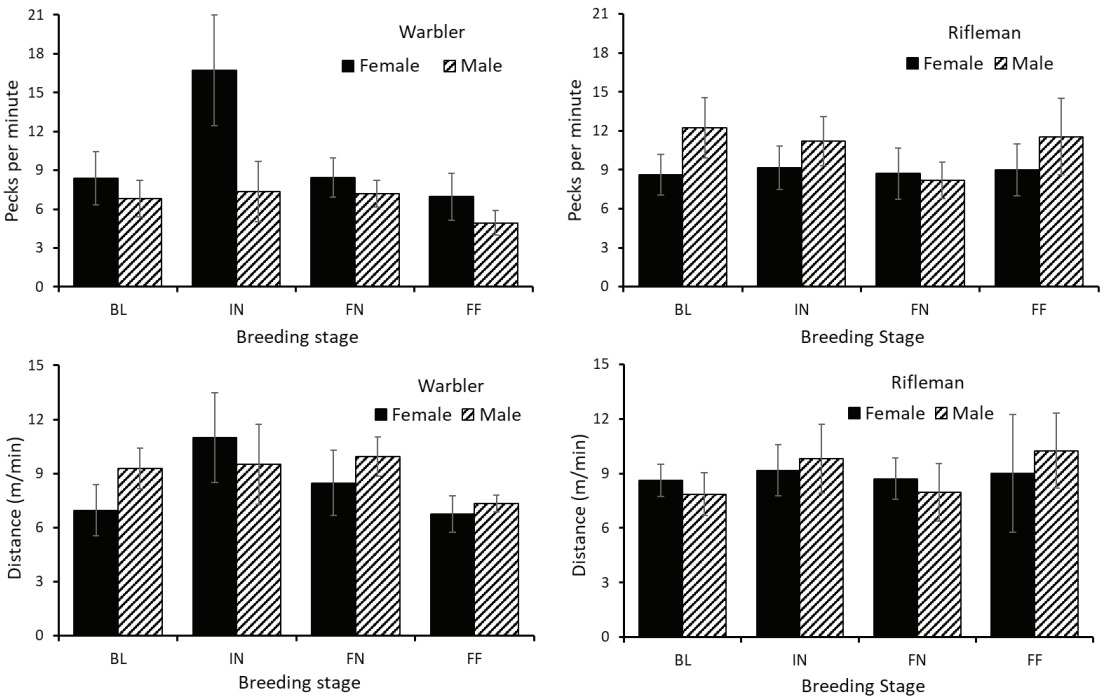

Figure 4. Pecking and movement rates of two bird species organised by sex and stage of the breeding season. Bars are mean ± 95% CI. See Figure 3 for sample sizes and acronyms.

Peck rate
With the exception of female warblers during IN, riflemen generally pecked at higher rates than warblers (Fig. 4). Female warblers pecked at higher rates than male warblers during all breeding stages, and at a very high rate during IN. Female riflemen pecked at lower rates than males during BL, IN and FF.

Movement rate
Both species moved at similar rates at all stages of the breeding cycle (Fig. 4). Variability was slightly higher for warblers than for riflemen both through the breeding cycle and between sexes, with female warblers moving at the slowest rate during BL and FF, and the fastest rate during IN.

Perch substrate
Riflemen used all available perch substrates, with an emphasis on trunks and twigs, whereas warblers used twigs and leaves almost exclusively (Fig. 5). Male riflemen used twigs more than trunks, whereas females used trunks more than twigs. Female warblers used twigs and leaves even more exclusively than males. Use of twigs increased and use of leaves declined through the breeding cycle for both species. Although neither species foraged frequently on the ground, riflemen used the ground more than warblers.

Peck site
Warblers pecked primarily at leaves, whereas riflemen pecked predominantly at bark (females) or equally at bark and leaves (males) (Fig. 6). Use of leaves increased through the breeding cycle for both species and genders. Male warblers used a more diverse array of peck sites than females (particularly bark), whereas both rifleman sexes used a similar array of peck sites. Female riflemen used leaves at a much lower rate than males in the BL stage.
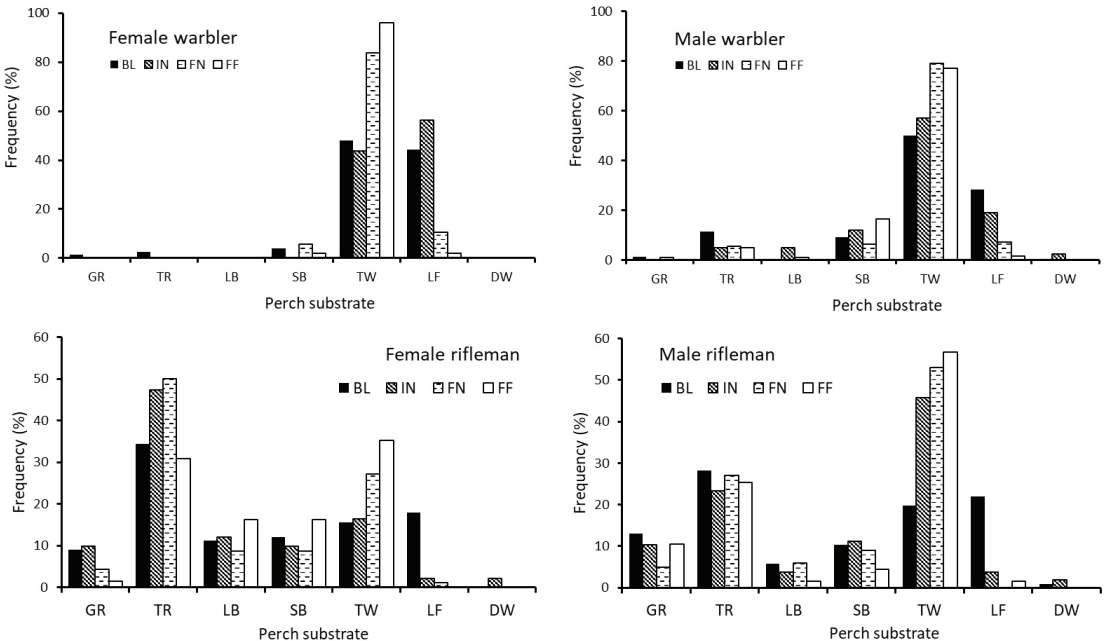

Figure 5. Perch substrates used by two bird species organised by sex and stage of the breeding season. Bars are counts for each category converted to %. GR = ground, TR = trunk, LB = large branch, SB = small branch, TW = twig, LF = leaf, DW = dead wood. See Figure 3 for sample sizes and acronyms.

Feeding method

Foliage gleaning was the primary foraging method for both species (Fig. 7). However, of the types of foliage gleaning identified, riflemen primarily used upright gleaning; they used lunging, downside gleaning and probing at relatively low frequencies, and used hover gleaning very rarely. For rifleman, courtship feed (5.4%, BL, females only) and flush (0.9% IN, 1.0% FN, males only) were left off the graph to maintain comparability with warblers. Warblers used similar frequencies of upright gleaning and lunging, slightly lower frequencies of hover gleaning, and did not probe or provision the female. Riflemen used downside gleaning more than warblers, whereas warblers used flushing more than riflemen. Both genders of both species used hawking at relatively low rates. In relation to the breeding cycle: during BL upright gleaning was the most used foraging technique by female and male riflemen and female warblers, whereas male warblers used lunging most; lunging and hover gleaning were used more frequently by female warblers during IN and to a lesser extent during FF; male riflemen used lunging and hawking more during IN and FF; male warblers used hover gleaning more when FN and FF.

Cluster analysis generates a dendrogram that represents the relative relationships between variables. Variables that are more similar in terms of standardised data will connect more strongly, identified by links and groupings in the diagram. Here, it was predicted that variables would cluster by species and sex (within species). No prediction was made for clustering by breeding stage. The predictions were incorrect with the reality being far more complex. The following general patterns were identified by visual inspection of the links in the dendrogram (Appendix 1):
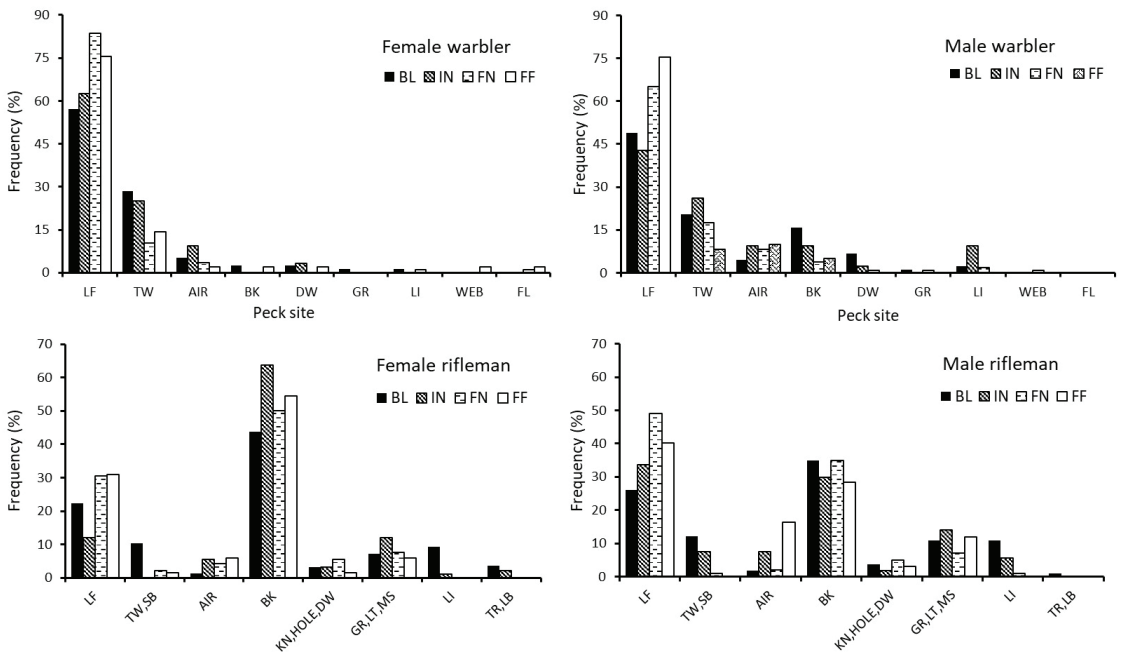

Figure 6. Peck sites used by two bird species organised by sex and stage of the breeding season. Bars are counts for each category converted to %. Some minor (and linked) categories were combined for rifleman. LF = leaf, TW = twig, BK = bark, KN = knot, DW = dead wood, GR = ground, LT = litter (on ground), MS = moss, LI = lichen (on trees), WEB = spider's web, FL = flower, TR = trunk, LB = large branch. See Figure 3 for sample sizes and acronyms.

- Peck rate for female warblers during IN clustered on its own as the variable most different from all others.

- Species did not cluster distinctively.

- Genders did not cluster distinctively.

- Breeding stage did not cluster distinctively.

- Most variables clustered together to some extent, usually with a few exceptions (such as peck rate for female warblers during incubation, as above).

- Relative height for both species clustered together very strongly.

- Perch substrate and peck site clustered together strongly (for both species).

- Travel rate and peck rate clustered together strongly (for both species).

Overall, the cluster analysis indicates considerable overlap in the foraging behaviour of riflemen and warblers. They were distinguished by specific breeding-stage/gender/species combinations summarised at the beginning of the results, such as feeding at lower heights (riflemen), using unique feeding methods (warblers - hover glean), or feeding predominantly on leaves in the canopy (female warblers). But none of the three independent variables clustered strongly together.

The three continuous variables (peck rate, movement rate, height) were further investigated using factor analysis to see if there were unique groupings (factors) in the data. No clearer outcome was found (analysis not presented), supporting the broader interpretations of the cluster analysis.

Independence of data in the 5-sample sequence
Analysis of the five-sample sequence indicated strong overlap and no clear trends when all data were inspected (Fig. 8). For riflemen: *pecking rate* increased for the first three pecks then decreased,
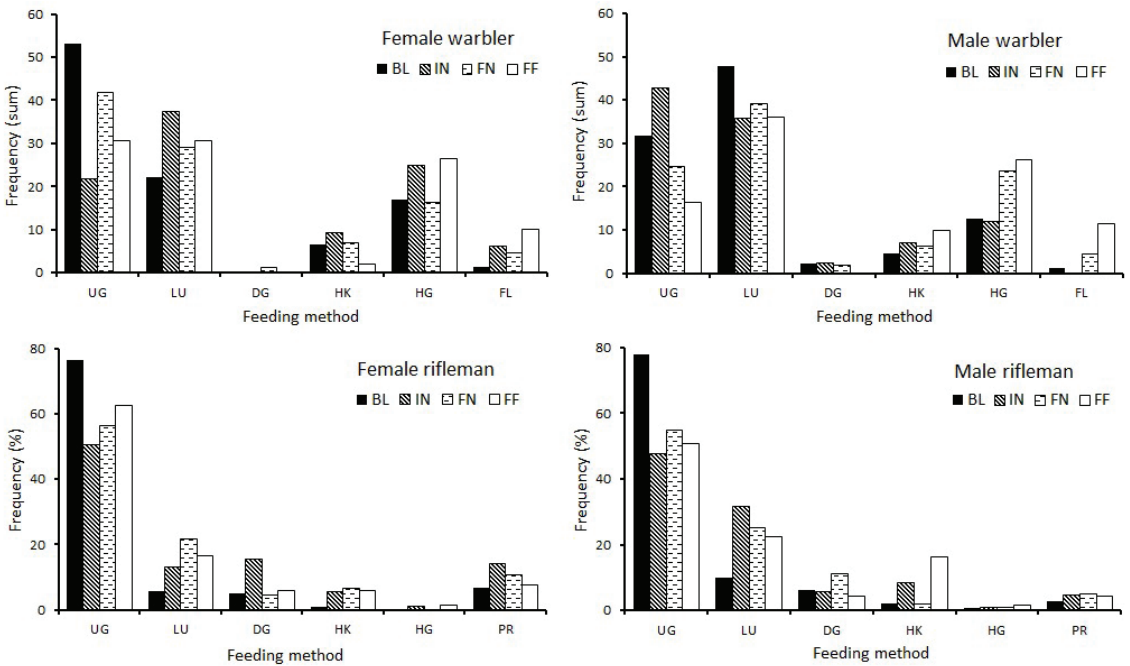

Figure 7. Feeding methods used by two bird species organised by gender and stage of the breeding season. Bars are counts for each category converted to %. UG = upright glean, LU = lunge, DG = downside glean, HK = hawk, HG = hover glean, FL = flush, PR = probe. See Figure 3 for sample sizes and acronyms.

with samples 3, 4 and 5 bracketing sample 1; *movement rate* decreased for the first three pecks then increased, although the first sample was slightly bigger than the other four; *height* had a slight trend downward. All 95% CIs overlapped strongly in all three graphs. Repeated measures, 2-way ANOVA using all three variables indicated no significant variation in the sequence of five samples (F_4 = 1.02, P = 0.4). For warblers: *pecking rate* decreased then increased; *movement rate* was very similar; for *height*, the first sample was lower than the others, with samples 2 and 3 higher and samples 4 and 5 intermediate. Height for warblers was the variable where 95% confidence intervals overlapped least, with the data suggesting that warblers moved higher after the first sample was taken. However, repeated measures, 2-way ANOVA using all three variables indicated no significant variation in the sequence of five samples (F_4 = 1.08, P = 0.38). While it is not appropriate to draw conclusions from non-significant results, the results for both species do not support a conclusion that there are trends or patterns in the 5-sample sequences of behaviour.

Six bootstrap procedures were run (giving 120 t values from three behaviours x two species x 20 runs). Small t values were found on all 120 t-tests, with no test approaching significance (at P = 0.05, t_{13} = 1.77). Warbler: *peck rate*, t range = 0.31–0.93,

median = 0.75; *movement rate*, t range = 0.03–0.79, median = 0.27; *height*, t range = -0.19–0.18, median = 0.04. Rifleman: *peck rate*, t range = 0.10–0.93, median = 0.67; *movement rate*, t range = 0.10–0.32, median = 0.21; *height*, t range = -0.18–0.75, median = 0.16. In contrast to the result in Figure 3 for warblers, warbler height in the bootstrap procedure showed the least difference of the three variables.

Results from the boot-strapping analyses support a conclusion of reasonable independence in the 5-sample series. However, the test was structured to deliver positive t-test values if variance in the data for one individual was smaller than variance in the data selected randomly. If the two sets of variances were truly similar, then the ratio of positive:negative t values would be close to 1:1. They were not: just two of the 120 test results were negative, indicating slightly reduced variance for the within-individual data relative to the randomly selected data.

Taken together, the results from both analyses indicate few trends in the data, and that the variance was slightly lower for data taken from one individual relative to randomised data from all individuals. The conclusion that data taken in a 5-sample sequence were reasonably independent is supported.
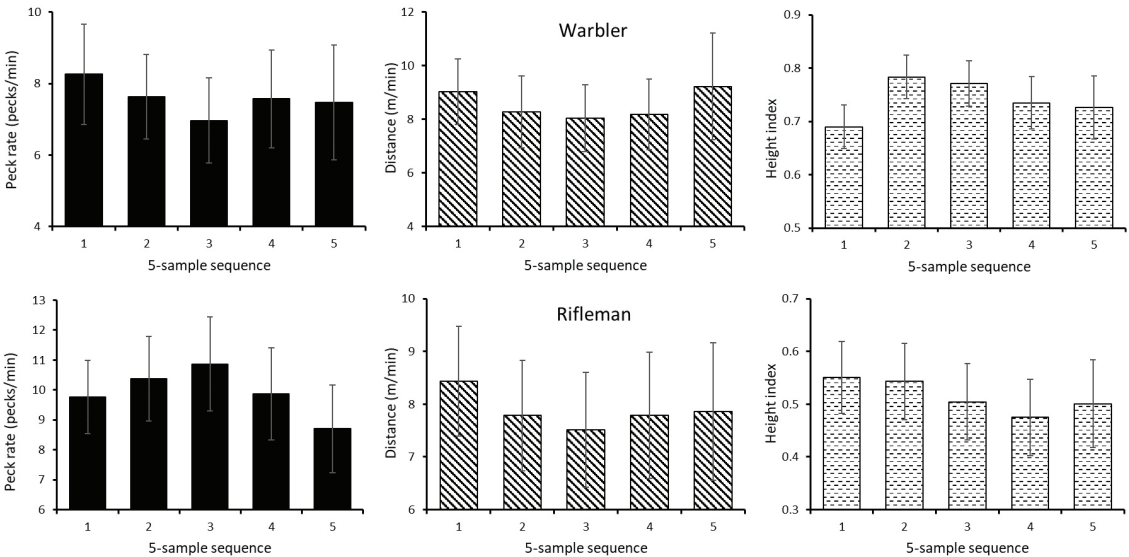

Figure 8. Patterns in the 5-sample sequence for continuous foraging behaviours for female riflemen (IN) and male warblers (FN). Bars are mean + 95% CI, N = 14 sample sequences.

DISCUSSION

Even when working intensively with individually identifiable small birds, it is difficult to detect the variation in behaviour amongst individuals that is documented here. Whelan (2001) referred to the distinctive foraging behaviour of individual birds as foraging microhabitats, but I believe that the principle of a "foraging personality" might be better applied to these birds. In a conceptually similar approach, Snijders *et al*. (2014) referred to exploration behaviour as a known personality trait in great tits (*Parus major*). Certainly, rifleman pairs showed unique foraging personalities as an emergent property of distinct individual patterns of behaviour within the pair. Such differences could reflect microhabitat variation in a complex environment, for example due to variation in soil quality or local-scale differences in invertebrate prey availability. However, the forest was homogeneous and even-aged, ground vegetation was heavily browsed and occasionally flooded, and the spatial scale was small (about 1 km^2). Both bird species lived in the study area at similar densities, yet riflemen demonstrated considerably more within-pair behavioural variability than warblers. The behavioural differences appear to reflect individual preferences, foraging specialisation, or learned differences in patterns of behaviour, rather than micro-scale, environmentally-driven behavioural variation.

The notion of a group-based (in this case, a pair) personality has considerable traction in the biological literature. Although not referring specifically to groups, Wolf & Weissing (2012) argued that personality differences should be treated as a key dimension of intraspecific variation in order to better understand ecological-evolutionary links. Aplin *et al*. (2014), Farine & Sheldon (2015), and Herbert-Reid (2017) discussed the principle of emergent group behaviour (= "group personality") based on the personalities of the individuals making up a group, and concluded that this is a real phenomenon needing further research. Further resolution is also needed of the links between learned outcomes, phenotypic consistency, and behavioural flexibility (a discussion of these relationships is in Lea *et al*. 2020).

In this study, although pairs exhibited distinct foraging personalities, individual birds also exhibited flexibility by adjusting their foraging behaviour to the differing demands of each breeding stage. Although almost every rifleman pair had a unique pattern of behavioural difference, the whole-season summary in Figure 2b suggests that behavioural difference decreased after the BL stage (when males and females contribute more equally to parental care). However, that result is not so evident in the more detailed analysis in Figure 1. There is an additional possibility, not addressed here, that each member of a pair adjusts its behaviour in relation to the foraging preferences (or personality) of its mate. Clearly, the relationships are complex and dynamic, and are not yet clearly understood.

The variation documented through the breeding stages shown for both species presumably reflects the changing demands of parental care requirements, along with variation in prey type and availability through time as temperatures warmed through the spring. Incubating female warblers in particular switched to relatively high-energy lunging and hover gleaning as their main feeding methods. They moved fast and pecked at very high rates, likely reflecting urgency to return to the nest and the energy costs of incubation. Despite the energetic costs of nest building and manufacturing eggs, during the BL period females moved at a more similar pace to the post-incubation period when males shared parental care and demands on the female were more similar to those of males. Even without taking data, an observer can easily identify incubating female warblers because of the urgency with which they move, and sample sizes for females were low in part because they were difficult to follow. It seems likely that the IN period is the most energetically demanding for them. In contrast, for rifleman, peck and movement rates of females and males were not distinctive during IN relative to the other breeding stages, likely because both sexes incubate. There were differences: incubating female and male riflemen used different feeding sites and substrates, with males foraging higher than females. However, the differences were no stronger than were found during other breeding stages. Part of the explanation for those differences may lie in the female/male size difference for rifleman (Lill 1991).

Distinctive behaviour in relation to breeding was also noticeable in riflemen, although during the BL stage and for a different reason. Female riflemen became noticeably sluggish when they were due to lay, due presumably to the weight of the large egg. Although obvious to an observer, that change cannot be seen in the data because it occurred for just a few hours each second day during the laying of 4–5 eggs. Female warblers also carry a large egg and lay every second day (Table 1), but do not become noticeably sluggish. The likely key difference is provisioning of female riflemen by males (Sherley 1989). Female riflemen can sit quietly while waiting to be fed, whereas female warblers cannot.

Although this analysis identifies considerable variability in the foraging behaviour of individual birds/pairs, the broader analysis of foraging behaviour also indicates considerable flexibility in response by each species to the demands of different stages of the breeding season. Overall, it is clear that

these birds respond to the current demands of the breeding cycle, presumably with further adjustment in relation to environmental conditions (Recher *et al.* 1996; Cueto & Lopez de Casenave 2002). Thus, it seems that all three aspects: individual preferences, flexibility in response to current environmental conditions, and the demands of each breeding stage, will act in concert to influence behavioural outcomes at any moment. Snapshots (samples) of foraging behaviour designed to explore ecological outcomes should attempt to take account of that variability if they are to genuinely capture the factors influencing bird foraging.

ACKNOWLEDGEMENTS

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Appendix 1. Dendrogram of all foraging behaviour variables for riflemen and warblers. Names are identified in the sequence: feeding behaviour, gender (F=female, M=male), breeding stage (BL, IN, FN, FF), species (GW = warbler, RM = rifleman). Travrate = movement rate. Feeding behaviour codes defined in Methods.