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# FORAGING BEHAVIOURAL ECOLOGY OF THE SUPERB LYREBIRD

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Foraging was investigated in a Superb Lyrebird population in southern Victoria. Soil invertebrate food resources were moderately patchily distributed and the fact that foraging effort and success varied greatly spatially suggested that the birds located patches mainly by trial-and-error. The similarity of the nestling's diet, the soil invertebrate fauna and probably the adult's diet, plus the high mean capture rate of 14–18 prey per min foraging, indicated relatively unselective prey consumption by adult lyrebirds. Soil invertebrate abundance exhibited no highly consistent seasonal pattern; however, it showed some tendency to increase in summer and autumn when fledglings were being reared rather than in spring during the period of nestling care. Foraging was probably energetically expensive because >80% of foraging time was spent digging in soil at a mean rate of 78–84 foot movements per min; only 5–8% of foraging time was spent walking or running at a low speed between excavation sites which averaged < 2 m apart. Foraging lyrebirds followed both fairly straight and quite circuitous routes, the latter being more common in the non-breeding season and resulting in intensive exploitation of a localized area. The mean daytime defecation rate (approx. 3 per h) and faecal energy density (8.54–9.28 kJ per g dry mass) indicated that the species probably has a slow gut passage rate, but is highly efficient at assimilating energy from its diet. Lyrebirds' foraging ecology could make them particularly susceptible to habitat fragmentation and to disturbance that increases the cost of digging.

## INTRODUCTION

The Superb Lyrebird *Menura novaehollandiae* inhabits mainly wet sclerophyll forest and cool temperate rainforest below 1 500 m in the Great Dividing Range in mainland south-eastern Australia. The bird's diet is unusual in comprising mainly soil invertebrates, which it obtains by digging with powerful, clawed feet (Reilly 1988). How its concealed prey are distributed in time and space is poorly understood and whether it finds them by trial-and-error searching or by detecting cues indicating their presence is unknown. The bird's large mass (900–1 500 g) and high absolute energy requirements could mean that in the absence of useable cues about prey distribution, it could not afford to be very selective about the quality of prey it consumes, particularly in winter when substantial time investments in courtship and breeding are made (Lill 1986). The soil invertebrate fauna in lyrebird habitat includes many arthropods with hard exoskeletons (Robinson and Frith 1981). Insectivorous birds exploit a highly nutritious food resource, but they must break down their prey's hard exoskeleton to gain access to the nutrients. This is done partly with the beak, but mainly in the gizzard, and consequently they tend to combine a high energy assimilation efficiency with a slow gut passage rate (Castro *et al.* 1989). Therefore if lyrebirds are indeed relatively unselective in their feeding, their digestive strategy should tend to conform to this common insectivore pattern.

Superb Lyrebirds are fairly unusual among altricial land-birds in temperate Australia (Ford 1989) in commencing breeding in mid-winter, a time when their estimated energy requirements are already quite high and foraging conditions are presumably sub-optimal. Lyrebird development is very protracted (Reilly 1988) and Robinson and Frith (1981) have suggested that a winter start to breeding is adaptive because it results in temporal coincidence of the energetically demanding nestling stage and a spring peak in food resources. However, our knowledge of lyrebird foraging ecology is currently insufficient to permit an understanding of how it might affect and/or be affected by the timing of breeding.

Although not officially designated as threatened, the Superb Lyrebird has protected status throughout its range and exhibits several traits common in bird species vulnerable to extinction, namely a fairly narrow habitat tolerance, low reproductive rate, poor flying ability and a tendency to nest at or near ground level. Further substantial reduction and modification of its habitat seems likely and there are currently no effective broad-scale control methods for its exotic predators. Having a better understanding of its foraging behavioural ecology will be important in devising effective conservation strategies if the species' viability is further reduced.

This study documents foraging behaviour and food availability in a lyrebird population in southern Victoria. The main aims of the investigation were: (i) to increase our understanding of the strategies that lyrebirds use to find and exploit their unusual food resources, (ii) to elucidate the relationship between foraging conditions and the timing of breeding and (iii) to obtain basic information on foraging that may help in the conservation of the species.

## METHODS

*Study area*

The investigation was conducted in Sherbrooke Forest Park, approximately 35 km east-south-east of Melbourne (37°48'S, 145°00'E) from 1973 to 1981. The park comprises approximately 821 ha of mainly wet sclerophyll forest dominated by mountain ash *Eucalyptus regnans* (see Gullan and Robinson 1980 for a full description of the vegetation) and is 200–490 m above sea level. Meteorological data for the area were summarized by Lill (1979).

*Food abundance and dispersion*

The soil invertebrate fauna of an area in which much foraging behaviour was monitored was sampled by taking soil cores (approx. 322 $cm^3$) with an augur on three grids on the eastern side of a creek valley. Two rectangular grids (G1: 384.4 $m^2$ and G2: 403.6 $m^2$) about 200 m apart were each sampled twice, in winter (July 1974) and the following summer (January 1975). In July, both grids were sampled at 55 sites evenly spaced at 3.1 m intervals. In January, only 30 and 28 sites, respectively, were sampled on these grids; the G1 sites were arranged in three strips of ten and the G2 sites in four blocks in a chequer board design. Within the strips and blocks, a 3.1 m spacing of sites was retained. Grid 3 (G3) comprised two intersecting transects, 350 m and 315 m long, respectively. It had 18 sampling sites; inter-site spacing was 35 m on the shorter and 50 m on the longer transect. G3 sites were repeatedly sampled for invertebrates over a 26 month period commencing in 1979, initially at 3 month and later at 2 month intervals.

Invertebrates were extracted from soil samples in two ways: (a) for G1 and G2, by wet sieving and flotation: a minimal mesh size of 0.531 mm was employed, Calgon and kerosene were used as dispersal and flotation agents, respectively, and the animals were preserved in 70% alcohol (b) for G3, into absolute alcohol by a dynamic dry funnel method based on the Tullgren system (Kaczmanek 1993). The former technique may not be equally efficient for all taxa present (Wood 1965). Neither method was particularly effective for earthworms, which either fragmented during sieving or did not respond to the heat source; consequently they were excluded from analyses. The parameters measured were: invertebrate density (animals per kg soil); invertebrate biomass (g per 10 kg soil); invertebrate density at the taxonomic level of order (animals per kg soil) (G1 and G2 only); soil moisture content (%) (G3 only and restricted to the last 16 months of the sampling period i.e. 7 sampling times).

*Foraging behaviour*

Foraging behaviour of adults was recorded during the breeding (May–October) and non-breeding seasons. Some individuals were identified by colour bands or distinct morphology, but observations were also made on unidentified birds. Measurements were only taken during 'steady foraging' i.e. prolonged periods of foraging uninterrupted by other major activities (such as parental behaviour, territory defence or courtship) except maintenance behaviour. Behaviour was timed (± 1 sec) with a stopwatch. The parameters measured were:

(a) the percentages of foraging time spent digging for prey and walking (and occasionally running) between excavation sites; walking time was calculated indirectly by subtracting digging time from digging + walking time. Most observations lasted 60 min.

(b) Digging bout duration: the total time spent digging at any one excavation site.

(c) Digging rate: the number of foot movements per sec of digging; some measurements extended for the entire excavation bout, but many lasted only 1 min to maintain accuracy.

(d) Inter-site distance: the distance travelled between consecutively excavated sites, measured as the number of paces taken between sites multiplied by grand mean pace length. Mean pace length was determined independently by observing the exact placement of a bird's feet at the beginning and end of a short walking sequence (up to 5 paces), immediately measuring (± 1 cm) the distance and dividing the result by the number of paces taken.

(e) Walking velocity: the mean number of paces per sec of continuous walking multiplied by grand mean pace length; usually an entire movement between consecutive excavation sites was measured. Results are expressed in km per h.

(f) Prey capture rate: digging bout duration divided by the number of prey caught during the bout.

Routes taken by steadily foraging lyrebirds were sketched and their dimensions approximately measured (± 1 m) by pacing immediately post-observation. Measurements taken were: (a) the spread i.e. the linear distance between the two points on the route which were furthest apart (see Fig. 1) and (b) the linear start-to-finish distance. The hourly rates of Doubling-back (reversing direction without retracing the actual route; see Fig. 1c), Retracing (retracing part of the route; see Fig. 1a and c) and Crossing (crossing the route already taken; see Fig. 1a) were calculated.

*Faecal production and energy content*

Defecation intervals of adults were timed (± 30 sec) throughout the year during continuous observation sessions lasting up to 3.8 h. For females, recording excluded periods of nest attendance. Faeces collected immediately after defecation were desiccated and weighed (± 0.01 g) and the energy densities (kJ per g dry mass) of a representative subsample were determined in a Gallenkamp adiabatic bomb calorimeter.

*Data analysis*

Although the particular lyrebirds whose foraging behaviour I studied seemed largely unaffected by my presence, many individuals are fairly unapproachable and difficult to observe, even in Sherbrooke Forest. I sampled foraging behaviour to allow as far as possible for likely sources of variation (gender, season, time of day and individual) and mostly obtained adequate sample sizes, but the data still unavoidably comprised quite unequal numbers of repeated measures on a fairly limited sample of observable birds. Therefore they violate some of the assumptions of, and are not really amenable to, significance testing. Accordingly, I present mainly summary statistics and do not attempt seasonal, diurnal and individual comparisons; possible trends and gender differences are also interpreted conservatively. This is a drawback, but it is doubtful whether it could be avoided for any lyrebird study population. When reporting sample sizes, the number of observations and the number of individuals sampled are often both given.

Seasonal and spatial variation in soil parameters on G3 were examined by ANOVA (randomized block design) and *post hoc* pairwise comparisons of means by Tukey's HSD test. Seasonal variation in the soil fauna of G1 and G2 was also analysed by ANOVA. Because the amount and configuration of sampling differed seasonally on both these grids, analysis of spatial variation in their soil invertebrate faunas was restricted to testing the July density and biomass (G2 only) data for deviation from a uniform distribution with Kolmogorov Smirnov (KS) one-sample tests and calculating their variance/mean ratios. Data were log or arcsine transformed prior to analysis as appropriate.

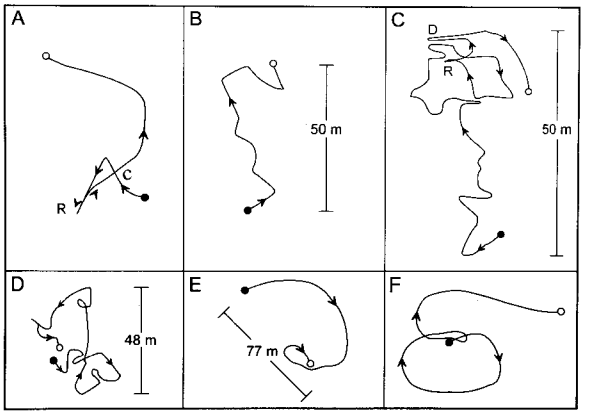


Figure 1. *Representative routes taken by steadily foraging females. The diagrams are not drawn to scale. Black and white circles show starting and finishing points, respectively.* **A.** *Female 1, afternoon, 4.5 h duration, breeding season (incubation stage). Route ended at nest. R indicates Retracing and C crossing (see Methods)* **B.** *Female 2, morning, 1.0 h, breeding season (not nesting). Route began at night roost; female accompanied by young from previous season. Spread is indicated.* **C.** *Female 1, morning, 3.7 h, breeding season (not nesting). Spread and examples of Doubling back (D) and Retracing (R) indicated.* D. *Female 4, afternoon, 1.83 h, breeding season (not nesting). Spread indicated.* **E.** *Female 2, morning, 1.25 h, non-breeding season. Spread indicated. Route started at night roost, female accompanied by young from previous season.* F. *Female 3, morning, 3.0 h, breeding season (incubation stage). Route started at female's nest.*

## RESULTS

### *Food abundance and dispersion*

Table 1 summarizes soil invertebrate density and biomass on G1 and G2 and the associated significance tests. Density, but not biomass, was significantly higher in January than in July on both grids. Thus the mean mass of individual invertebrates on these grids must have been greater in July. Neither mean density nor mean biomass differed significantly between the two grids. The density of soil invertebrates was not uniform on either grid in July. On G1, it

TABLE 1

Density and biomass of soil invertebrates on Grids 1 and 2 in July and January. Values are mean, range and (n). Matched samples were used for significance tests: matched samples were the entire samples in January.

| Month | | Density (animals/kg soil) | | Biomass (g/10 kg soil) | |
|---|---|---|---|---|---|
| | | Full sample | Matched sample | Full sample | Matched sample |
| July | G1: | 23<br>2–173<br>(54) | 25<br>2–173<br>(30) | 0.654<br>0.004–2.617<br>(29) | 0.76<br>0.122–2.617<br>(17) |
| | G2: | 26<br>5–120<br>(55) | 23<br>6–54<br>(27) | 1.515<br>0.09–9.631<br>(55) | 1.04<br>0.1–5.89<br>(27) |
| January | G1: | | 34<br>8–161<br>(30) | | 0.91<br>0.14–3.08<br>(17) |
| | G2: | | 68<br>11–815<br>(27) | | 1.9<br>0.03–8.39<br>(27) |

ANOVA results:

| | Log density (df = 1,110): | Log biomass (df = 1,84): |
|---|---|---|
| season effect | $F = 15.413$, $P < 0.001$ | $F = 1.576$, $P > 0.05$ |
| grid effect | $F = 3.879$, $P > 0.05$ | $F = 1.719$, $P > 0.05$ |
| s × g interaction | $F = 0.03$, $P > 0.05$ | $F = 0.324$, $P > 0.05$ |

varied among the sampling sites by a factor of 87 (N = 54, Max diff. = 0.89) and on G2 it varied by a factor of 24 (N = 55, Max diff. = 0.898) ($P < 0.001$ in both cases, KS test). The magnitude of the variance/mean ratios for density on the two grids (37 and 14, respectively) indicated a substantial degree of clumping of invertebrates at the 3 m scale (Southwood 1978). Invertebrate biomass was also non-uniformly distributed among sites on G2 in July, varying from 0.09–9.631 g per 10 kg soil (N = 55, Max diff. = 0.615, $P < 0.001$, KS test); however, its variance/mean ratio of 2.7 indicated a lesser degree of clumping than that observed for density.

There was significant temporal variation in invertebrate density, biomass and soil moisture content on G3 (Table 2). Density was significantly higher in January and April, 1980 than at any other time, but otherwise relatively constant. Excluding a few high outlier values for the peak months from this analysis did not affect the outcome. Biomass exhibited no consistent seasonal pattern over the sampling period, but was significantly higher in December, 1980 than at any other time. Soil moisture reached a statistically significant peak in October, 1980 (mean 29.1%) and a significant trough in February, 1981 (mean 16.3%). Invertebrate biomass and soil moisture content were significantly, if weakly, correlated ($r_{106} = 0.205$, $P < 0.05$), but invertebrate density and soil moisture content were not ($r_{124} = 0.064$, $P > 0.05$).

Soil invertebrate density and biomass also varied significantly spatially on G3, but soil moisture content did not. Mean invertebrate density ranged among sites from 22–60 animals per kg soil ($F_{(17,187)} = 1.864$, $P < 0.05$). However, based on comparisons of means by Tukey's HSD test, no site differed significantly from more than two (11.1%) other sites and only 2.6% of the possible pairwise combinations of sites exhibited significant differences. Mean invertebrate biomass varied among sites from 0.079–0.434 g per 10 kg soil ($F_{(17,170)} = 2.504$, $P < 0.01$), but no site differed significantly from more than one (5.6%) other site and only 2.6% of possible pairwise combinations of sites exhibited significant differences. Mean soil moisture content ranged among sites from 20.8–27.6% ($F_{(17,102)} = 1.591$, $P > 0.05$).

TABLE 2

Temporal variation in soil invertebrate abundance and moisture content on Grid 3. Density measured per kg soil, biomass per 10 kg of soil. n = 12 sites per sample. Values respectively are mean and range.

| Year | Month (Sample No.) | Density | Biomass | Moisture % |
|---|---|---|---|---|
| 1979 | July (1) | 33 | 0.298 | |
| | | 11–84 | 0.044–0.894 | |
| | October (2) | 39 | 0.644 | |
| | | 5–95 | 0.057–2.262 | |
| 1980 | January (3) | 63 | 0.279 | |
| | | 21–167 | 0.027–0.734 | |
| | April (4) | 74 | 0.447 | |
| | | 16–185 | 0.061–3.413 | |
| | June (5) | 39 | 0.218 | 25 |
| | | 11–120 | 0.006–0.736 | 18–31 |
| | August (6) | 20 | | 28 |
| | | 6–43 | | 21–38 |
| | October (7) | 30 | 0.52 | 29 |
| | | 6–55 | 0.027–3.079 | 12–54 |
| | December (8) | 33 | 0.359 | 22 |
| | | 9–77 | 0.067–1.187 | 15–32 |
| 1981 | February (9) | 18 | 0.088 | 16 |
| | | 6–41 | 0.005–0.276 | 13–22 |
| | April (10) | 29 | 0.457 | |
| | | 13–71 | 0.111–1.055 | |
| | June (11) | 21 | 0.469 | 24 |
| | | 2–78 | 0.047–2.884 | 11–32 |
| | September (12) | 18 | 0.274 | 26 |
| | | 8–31 | 0.014–2.332 | 21–32 |

ANOVA and Tukey's HSD results for Time Effect:

logdensity $F_{(11,187)} = 7.851$, $P < 0.001$: pairs of sample means differing significantly were 2 × 11; 3 × 1, 6,7,9,10,11,12; 4 × 6,7,9,11,12; 8 × 11

logbiomass $F_{(10,170)} = 4.625$, $P < 0.001$: pairs of sample means differing significantly were 8 × 1,2,3,4,6,7,9,10

arcsine moisture content $F_{(6,102)} = 15.676$, $P < 0.001$: pairs of sample means differing significantly were 7 × 9; 8 × 9,11; 10 × 6,7,8,9.

Table 3 summarizes soil invertebrate density at the taxonomic level of order for G1 and G2 combined in July and January. Twenty-one taxa (20 orders and the class Symphyla) were recorded and 20 were present in both months. Rank orders of taxa for July and January based on mean density values were strongly correlated ($r_s = 0.938$, $n = 21$, $P < 0.001$, Spearman rank test). The 7 numerically dominant invertebrate groups were ants (adult and larval), fly larvae, beetles (adult and larval), mites, centipedes, amphipods and millipedes. These groups comprised 38% of the invertebrate taxa recorded, but collectively they accounted for 84% of the total soil invertebrate abundance in July and 87% in January. Two to six-fold increases in the mean density of fly larvae, adult and larval ants, centipedes (Juliformia) and amphipods were particularly prominent in the overall increase in invertebrate density from July to January. The suite of numerically dominant soil invertebrate orders was fairly similar to that recorded by Robinson and Frith (1981) for Tidbinbilla, Australian Capital Territory.

The density of each of the numerically dominant taxa was spatially non-uniform on both grids in July. Maximum difference values in KS one-sample tests for G1 (listed first) and G2 were: Hymenoptera 0.906 and 0.942; Diptera 0.887 and 0.829; Coleoptera 0.919 and 0.87; Acari 0.964 and 0.906; Juliformia 0.976 and 0.96; Geophilomorpha 0.952 and 0.94; Amphipoda 0.98 and 0.968 and Lithobiomorpha 0.759 and 0.482 ($n = 55$ and $P < 0.001$ in KS tests in all cases). This

TABLE 3

Density of soil invertebrate orders on Grids 1 and 2 combined in mid-winter and mid-summer. All minimal values were 0. Taxa are listed in order of overall mean density.

| | Density (animals/kg soil) | | | |
|---|---|---|---|---|
| | July | | January | |
| Order | Mean | Maximum | Mean | Maximum |
| Hymenoptera | 7.781 | 159.832 | 22.641 | 802.823 |
| Diptera | 3.878 | 17.167 | 7.871 | 45.265 |
| Coleoptera | 3.639 | 40.085 | 3.316 | 10.006 |
| Acari | 1.665 | 12.144 | 2.564 | 21.441 |
| Juliformia | 0.682 | 4.023 | 3.098 | 16.693 |
| Geophilomorpha | 1.675 | 5.97 | 1.779 | 6.147 |
| Amphipoda | 0.366 | 3.217 | 2.274 | 17.757 |
| Lithobiomorpha | 1.138 | 7.92 | 1.387 | 9.352 |
| Hemiptera | 0.948 | 13.712 | 0.993 | 11.222 |
| Araneida | 0.863 | 5.808 | 0.787 | 3.786 |
| Lepidoptera | 0.254 | 2.169 | 0.478 | 12.016 |
| Unidentified | 0.208 | 5.814 | 0.474 | 3.741 |
| Isopoda | 0.074 | 1.584 | 0.326 | 3.741 |
| Pseudoscorpionida | 0.252 | 3.045 | 0.081 | 1.163 |
| Polydesmoidea | 0.113 | 1.173 | 0.221 | 3.741 |
| Opiliones | 0.167 | 2.515 | 0.189 | 1.299 |
| Scolopendromorpha | 0.056 | 1.006 | 0.15 | 1.891 |
| Collembola | 0.117 | 4.224 | 0.013 | 0.72 |
| Mecoptera | 0.016 | 0.503 | 0.034 | 1.564 |
| Orthoptera | 0.016 | 0.831 | 0.033 | 1.191 |
| Symphyla | 0.016 | 1.223 | 0.02 | 0.701 |
| Scorpionida | 0.012 | 0.528 | 0 | 0 |

non-uniformity is reflected in the density maxima (essentially ranges, because all minima were 0) listed for many of these taxa in Table 3. However, variance/mean ratios >2 were only recorded for colonial Hymenoptera (G1 66.3; G2 20.5), Diptera (G1 3.1; G2 3.8), Coleoptera (G2 6.8), Acari (G2 2.2) and Lithobiomorpha (G2 2.4).

*Foraging behaviour*

Foraging behaviour parameters are summarized in Table 4. Considering the entire data set, digging bout duration was extremely variable, the coefficients of variation (CV) being 209% and 188% for males and females, respectively. Prey capture rate and inter-site distance were also very variable; CVs for males and females, respectively, were 71% and 81% for the former and 61% and 76% for the latter parameter. Some of this variation was temporal, but a significant spatial component was indicated by the high variances also recorded within observation sessions. Thus the mean within-session CVs were: Males — Digging bout duration 178%, Prey capture rate 50% and Inter-site distance 55%; Females — Digging bout duration 141%, Prey capture rate 44%, and Inter-site distance 66%. Digging rate was less variable, the overall CVs for males and females being 23% and 21%, respectively.

During steady foraging, the mean time allocation of males was: 5% walking between excavation sites at a mean velocity of 1.691 km per h, 87% digging for (and consuming) prey at a mean rate of 78 digging movements per min and 8% in maintenance activities, such as brief feather ruffling and stretching. On average, a male travelled 1.85 m between consecutive excavation sites, dug for 1.63 min per site and captured 29 prey per site. Thus, on average, each prey item captured by a male during steady foraging effectively required the performance of 4.4 digging movements taking 3.4 sec and 0.4 paces taking 0.2 sec.

The mean time allocation of steadily foraging females was: 8% walking between excavation sites at a mean speed of 1.308 km per h, 80% digging for (and consuming) prey at a mean rate of 84 digging movements per min and 12% in maintenance behaviour. On average, females travelled 1.5 m between consecutive excavation sites, dug for 1.8 min per site and captured 25 prey per site. Therefore the effective mean cost of each prey item for a female was 6 digging movements taking 4.3 sec and 0.2 paces taking 0.1 sec. Time-activity budgets of steadily foraging males and females appeared to be quite similar.

Routes taken by steadily foraging females in the breeding and non-breeding seasons varied from fairly straight (Fig. 1b) to quite circuitous (Fig. 1c,d). The spread of 7 routes taken by 3 or more females over periods of 1–3.7 h was 32–192 m; the linear start-to-finish distances of six of these ranged from 18–82 m. Four or more females foraging steadily in the breeding and non-breeding seasons (20 observations totalling 47.58 h) had overall doubling back, retracing and crossing rates of 0.66 per h (range 0–4.02 per h per female), 0.12 per h (range 0–0.54 per h per female) and 0.3 per h (range 0–1.2 per h per female), respectively. One male foraging steadily in the non-breeding season (4 observations totalling 12.15 h) had overall doubling back, retracing and crossing rates of 0.82 per h, 0.0 per h and 0.41 per h, respectively. However, two males foraging

TABLE 4

Mean values of behavioural parameters for lyrebirds foraging steadily in Sherbrooke Forest. Total observation times for time digging and walking and time digging were 33.97 and 37.29 h, respectively. Walking sometimes included running. + signs indicate inclusion of observations on an unknown number of unidentified individuals. See Methods for definitions of parameters.

| | Mean (±SD) | Range | Sample size | |
|---|---|---|---|---|
| | | | Measurements | Birds |
| Time spent digging and walking (sec/min) | | | | |
| Males | 55 (4) | 44–60 | 17 | 5 |
| Females | 53 (8) | 33–60 | 23 | 6+ |
| Time spent digging (sec/min) | | | | |
| Males | 52 (6) | 36–59 | 17 | 3+ |
| Females | 48 (9) | 23–56 | 26 | 5+ |
| Digging rate (foot movements/sec) | | | | |
| Males | 1.3 (0.3) | 0.7–22 | 225 | 4 |
| Females | 1.4 (0.3) | 0.8–2.2 | 272 | 5 |
| Digging bout duration (min) | | | | |
| Males | 1.63 (3.42) | 0.017–27.783 | 440 | 6+ |
| Females | 1.8 (3.38) | 0.017–29.4 | 551 | 4+ |
| Prey capture rate (sec/capture while digging) | | | | |
| Males | 3.4 (2.4) | 0.1–15 | 374 | 8+ |
| Females | 4.3 (3.5) | 0.9–32 | 488 | 8+ |
| Inter-site distance (paces) | | | | |
| Males | 7.1 (4.3) | 1–25 | 173 | 7+ |
| Females | 6.6 (5) | 1–33 | 251 | 4 |
| Distance per pace (cm) | | | | |
| Males | 26.1 (3.2) | 19.6–33 | 30 | 3 |
| Females | 22.7 (2.6) | 17.8–27.2 | 30 | 3 |
| Walking velocity (paces/sec) | | | | |
| Males | 1.8 (0.4) | 1–3 | 63 | 4 |
| Females | 1.6 (0.3) | 0.9–2.2 | 146 | 4 |

in the breeding season (16 observations totalling 26.57 h) had overall mean rates as follows: doubling back 0.38 per h (range 0–2.88 per h), retracing 0.08 per h (range 0–0.22 per h) and crossing 0.15 per h (range 0–0.36 per h). In the breeding season, males often followed longer and less circuitous foraging routes (Fig. 2c,d) than at other times of year (Fig. 2e).

### *Faecal production and energy content*

Faecal production rates of adult lyrebirds are summarized in Table 5. At the observed defecation rates, during daytime an adult male would have excreted, on average, an estimated 3.18 g (dry mass) per h of faeces with a caloric content of 29.53 kJ and a female 3.61 g (dry mass) per h of faeces with a caloric content of 30.85 kJ. Given

TABLE 5

Faecal production of adult lyrebirds. N = measurements; individuals. Energy densities are expressed per g dry mass. Defecation intervals were determined from 34.20 h of observation on males and 41.02 h on females.

| | Mean (±SD) | Range | N |
|---|---|---|---|
| Defecation interval (min): | | | |
| Males | 19.9 (6.3) | 2–36 | 140;7 |
| Females | 18.3 (8.3) | 3–49 | 153;5 |
| Faecal dry mass (g): | | | |
| Males | 1.06 (0.43) | 0.59–2.19 | 42;10 |
| Females | 1.10 (0.51) | 0.22–2.40 | 35;7 |
| Faecal energy density (kJ/g): | | | |
| Males | 9.28 (1.59) | 6.01–11.78 | 18;8 |
| Females | 8.54 (2.18) | 3.36–12.18 | 18;6 |

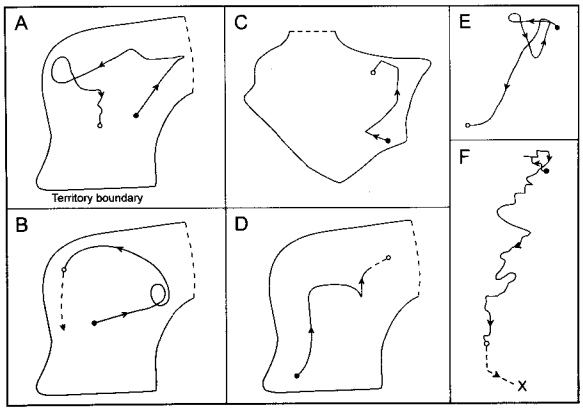


Figure 2. *Representative routes taken by steadily foraging males The diagrams are not drawn to scale. Foraging routes A–D were followed in the breeding season and E–F in the non-breeding season. Routes A–B were taken by one male and C–F by another neighbouring male. Routes A–D started in the males' main display areas. Black and white circles show starting and finishing points, respectively. Broken lines show parts of territory boundaries only approximately known. Each of the territories was several hundred metres in diameter.* **A.** *Mid-day, 3.25 h duration. Route ended in male's main display area.* **B.** *Mid-day, 3.07 h. Broken line at end of route shows approximate return path taken to main display area after rigorous observation ceased.* **C.** *Late afternoon, 1.23 h. Route incorporated 4 display mounds and ended at night roost site.* **D.** *Late afternoon, 0.72 h. Route ended at night roost site.* **E.** *Morning, 5.83 h.* **F.** *Evening, 1.77 h. Broken line at end of route shows flight path to night roost site (X).*

the annual variation in daylength, males would thus have excreted during daytime an estimated mean of 30–47 g (dry mass) of faeces containing 280–439 kJ daily and females 34–54 g (dry mass) containing 292–459 kJ. In view of the observed variances (see Table 5), it is doubtful whether the apparent mean sex differences in faecal parameters were significant, even though females average 20% lighter than males.

## DISCUSSION

### *Food dispersion and foraging technique*

Some bird species that hunt concealed, patchily distributed prey can exploit cues about the spatial distribution of their food in a manner that increases their foraging efficiency (Wenzel 1971), but many have to rely on trial-and-error searching (Feare 1984). The invertebrate food resource of Superb Lyrebirds is concealed, mostly in the soil. The density and biomass of this resource were spatially heterogeneous, particularly at the 3 m scale; this dispersion was strongly influenced by the patchy occurrence of the three dominant components, adult and larval ants and beetles and fly larvae. The marked spatial variation in foraging effort by lyrebirds suggested that they responded to this patchiness, but was this simply the result of trial-and-error sampling or did the birds exploit cues about food dispersion? 'Knowledgeable' individuals might be expected to target food-rich sites selectively and exploit them maximally. This should be reflected in relatively low variances in digging bout duration and prey capture rate; however, both parameters were extremely variable, both overall and within observation sessions.

On a time scale of a few hours, steadily foraging lyrebirds sometimes followed a circuitous route and consequently moved quite a short linear distance (Fig. 1c,d). Despite this, they doubled back and particularly retraced or crossed their route infrequently and very rarely reused an excavation site exploited earlier in the observation session. The result, a fairly intensive, but non-repetitive exploitation of a localized area before moving on, was somewhat reminiscent of area-restricted searching in some other species using similar food resources (Smith 1974; Zach and Falls 1976). For birds exploiting a spatially patchy, concealed food resource by trial-and-error sampling, there must be a strong premium on optimal use of each rich patch found. However, circuitous foraging routes were far from universal and were less evident during breeding, when males in particular followed straighter, longer routes. At this time, males foraged mainly in non-display periods at midday and late afternoon; midday movements combined foraging and a surveillance circuit of much of the territory (Fig. 2a,b) and late afternoon movements combined foraging and travelling to a specific roosting site (Fig. 2c,d). This was presumably an effective way for lyrebirds to budget their time, although it may have reduced foraging efficiency. Females also tended to follow somewhat less circuitous foraging routes whilst nesting, although circling back to the nest site whilst foraging during a recess, possibly for predator surveillance, was observed several times (Fig. 1f).

If lyrebirds had limited access to cues about spatial variation in food abundance, it seems unlikely, given their large mass and expensive foraging technique, that they could have afforded to be very selective about which prey they consumed. Perhaps the most compelling support for this prediction was the high mean prey capture and consumption rate recorded for adults, namely one prey about every 3–4 sec of digging.

The adult Superb Lyrebird's diet has not been quantified, but that fed to the nestling has (Robinson and Frith 1981; Lill 1986) and provides a second, if less conclusive, type of evidence for a relative lack of selectivity in taking prey. Nineteen (86%) of the 22 invertebrate taxa recorded from soil samples in this study also featured in the nestling's diet in Sherbrooke Forest (and the Maroondah Catchment, approximately 30 km distant) during the course of this study (Lill 1986); moreover, the absent taxa were rare in the soil anyway, with mean densities of only 0.016–0.189 animals per kg. Conversely, approximately 80% of the taxa recorded by Lill (1986) in the nestling's diet occurred in the soil samples taken in the present study; the absent taxa comprised, on average, only 2.4 to 3.9% of items in nestling meals. Thus on a presence/absence basis at the level of order there was a strong correspondence between the soil invertebrate fauna and the nestling's diet. However, this correspondence went further, because rank orders of invertebrate taxa based on their mean densities in the nestling's diet and soil were significantly correlated ($r_s = 0.465$, $N = 15$, $P < 0.05$, Spearman Rank test, one tailed). Thus the diet fed to the nestling did not appear to be a highly selected subset of the total soil fauna, at least when considered at the taxonomic level of order.

Given that during the breeding season the mean prey capture and consumption rates of females with ($22 \pm 9$ prey per min, $n = 118$; 3 females) and without nestlings ($20 \pm 11$ prey per min, $n = 198$; 8 or more females) were similar and not dramatically greater than those of males ($17 \pm 8$ prey per min, $n = 214$; 3 or more males), the similarity in the composition of the soil fauna and the nestling's diet probably also extends to the adult's own diet. However, a full quantitative documentation of the latter is required to resolve this question unequivocally.

Direct observation also indicated that foraging lyrebirds unselectively removed most of the available invertebrates from a profitable excavation site, as Smith (1988) has also suggested. Their digging disturbed the soil sufficiently to mean that renewal of the site's invertebrate fauna was probably slow. Sustainable foraging by territorial individuals could thus only occur if their return times to foraging sites were appropriately tuned to invertebrate replenishment rates and competitors were excluded or competitive interference by them minimized. The degree of physical restoration of a site could be a guide to its faunal replenishment status and would be straightforward to monitor visually. Lyrebird territoriality may well also be partly concerned with excluding feeding competitors; however, the ratio of adult male:female body mass is about 1.2, but males defend territories that are typically much more than 20% larger than those of females (Lill 1979; Reilly 1988). Therefore male territory size at least is probably influenced by additional factors and maximizing mating opportunities could be one of them.

The lyrebird's foraging technique must be costly, because digging in soil is a very energetically expensive activity (Vleck 1979). Lyrebirds spent 80–90% of their foraging time digging and each prey item captured required, on average, 4–6 digging actions with the feet. Admittedly walking or running between foraging sites is relatively inexpensive compared with flying (Lill 1986), but on average lyrebirds travelled less than 2 m at a velocity of less than 2 km per h between excavation sites and spent only 5–8% of steady foraging time in locomotion.

### *Defecation regime and digestive strategy*

Avian defecation regimes vary with diet (Sibly 1981). Frugivores and grazing herbivores exploiting a nutrient-poor or nutrient-inaccessible diet commonly have low utilization efficiencies, rapid gut passage rates and defecation rates and high faecal energy densities (Marriott and Forbes 1970; Herrera 1984; Karasov and Levey 1990). Granivores, with a greater and/or more readily accessible dietary nutrient content, have high utilization efficiencies and low faecal energy densities (Kendeigh *et al.* 1977; Castro *et al.* 1989). Insectivores consume highly nutritious food, but many must spend much time and energy fragmenting their prey's hard exoskeleton, mainly

in the gizzard, to gain access to the nutrients; consequently they typically have a fairly high energy assimilation efficiency and a low faecal energy density, but also a relatively slow gut passage rate and defecation rate (Feare 1984; Castro *et al.* 1989; Levey and Karasov 1989).

Sherbrooke Forest lyrebirds consumed many arthropods with hard exoskeletons and did little pre-processing with the beak. Their mean diurnal defecation rate (approx. 3 defecations per h) was low relative to those of many frugivores and grazing herbivores (e.g. the Cedar waxwing *Bombycilla cedorum*, 24 defecations per h, Holthuizen and Adkisson 1984; the White-fronted goose *Anser a. albifrons*, 17 defecations per h, Owen 1972). Their mean faecal energy density (approx. 8.5–9 kJ per g dry mass) was much lower than those of some browsing herbivores (e.g. ptarmigan *Lagopus* spp., 19–30 kJ per g dry mass, Moss 1973), but closer to those of some small granivores (e.g. the zebra finch *Poephila guttata*, 12.82 kJ per g dry mass, El-Wailly 1966). Given the body mass disparities involved, these comparisons are obviously rough; however, they do suggest that lyrebirds probably exhibit the combination of a slow gut passage rate and a high efficiency in assimilating energy from the diet that characterizes many insectivorous birds, although experimental verification is obviously necessary. It should be noted, however, that the reported energy content of lyrebird faeces probably overestimates unassimilated energy levels by up to 5%, because of the default inclusion of urinary energy (Drodz 1967). Unfortunately it is difficult to extrapolate from the present estimate of daytime faecal energy loss to a 24 h figure due to a lack of comparative data on nocturnal defecation parameters in invertebrate-consuming birds.

### *Seasonal food availability and the timing of breeding*

In many altricial birds, the nestling phase is very energetically demanding for breeding adults (Bryant and Westerterp 1980; Ricklefs and Williams 1984) and consequently it has been argued that breeding should be timed to facilitate exploitation of a seasonal peak in food availability for the nestlings (Lack 1968). There is persuasive evidence of this for some species (Perrins 1979; Newton 1979). Robinson and Frith (1981) suggested that lyrebirds in the Australian Capital Territory commenced breeding in winter because this resulted in temporal coincidence of the nestling phase and one of the seasonal peaks in abundance of the nestling's invertebrate diet.

However, in the present investigation soil invertebrate abundance did not increase significantly in the August–October period when nestlings were being raised. Indeed surprisingly there was no really consistent seasonal pattern of soil invertebrate abundance, but if anything it tended to be greater in mid-summer than in spring. Robinson and Frith (1981) documented a second peak in soil invertebrate abundance in autumn and this also occurred on G3 in 1980. Fledglings are still accompanied by and partly dependent on their mother throughout summer and autumn. Therefore maximizing food availability for the dependent fledgling rather than for the nestling may be a more critical influence on the timing of breeding and dictate a winter start. However, the estimated mean daily parental energy expenditure on feeding the fledgling is clearly less than that on feeding the nestling (Lill 1986). It is also conceivable that food availability for the developing young is simply not the major ultimate determinant of the timing of breeding, as suggested for some other temperate zone Australian passerines (Bell 1986). Given that annual variation in climatic conditions and food availability can be quite marked in Australia (Ford 1989), it is also possible that the length of the sampling period in the present study was inadequate to detect an average increase in soil invertebrate abundance in spring.

### *Conservation*

Lyrebirds occupy large territories (Reilly 1988), presumably partly because they require a large area for efficient foraging, given that their food resource is spatially fairly patchy and slow to renew and that the individual prey items are relatively small. This facet of their foraging ecology could make them particularly susceptible to habitat fragmentation that results in a small habitat patch size. Because their foraging technique is energetically costly, they could also be negatively affected by any habitat disturbance that further increases the cost of digging, such as a decrease in soil moisture retention caused by a reduction in the vegetation cover.

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