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The influence of time of day and environmental conditions on the foraging behaviours of willie wagtails, *Rhipidura leucophrys*

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Abstract

The insectivorous willie wagtail, *Rhipidura leucophrys*, exhibits a range of discrete, easily identified foraging behaviours that include wagging the tail and flashing the wing. We investigated whether wagtails adjust these, and other foraging behaviours, according to the time of day and environmental conditions. The rates of tail-wagging and wing-flashing were influenced by the time of day and light intensity. Tail-wagging was more frequent at the start and end of the day, while wing flashing was more frequent during the middle of the day. The rate of aerial prey captures was also highest during the middle of the day and lower in the early morning and late afternoon. These daily patterns of foraging behaviours correspond with the patterns of insect activity, which was greater in the middle of the day than in the early morning or late afternoon. The field data, together with experiments using a model wagtail tail, support the view that tail-wagging and wing-flashing are used to flush insect prey.

Introduction

The foraging decisions of small animals are thought to depend on their current energy reserves and the time of day (McNamara and Houston 1986, 1990, 1992; see also Caraco *et al.* 1990). Diurnal changes in foraging investment, in which birds forage most intensely in the morning and in the late afternoon, have been widely reported (Aschoff 1966; Wolf and Hainsworth 1977; Wyndham 1980; Powers 1991; Bednekoff and Houston 1994). These studies of foraging decisions have usually focussed on how an animal allocates its time between foraging behaviour and other activities. However, the foraging activities of birds that feed on flying insects may be restricted to certain periods each day, when the light and temperature conditions are favourable for capturing their prey (e.g. Lewis and Taylor 1964).

Some insectivorous birds may display even more subtle variations in their foraging behaviour. For example, many birds wing-flash and tail-wag, apparently in order to startle insects on the ground into movement, and thereby facilitate their capture (Goodwin 1967; Harrison 1976; Pizzey 1980; Cameron 1985; Slater *et al.* 1986; Jackson and Elgar 1993; Jablonski 1996). If tail-wagging and wing-flashing assist in foraging behaviours, the rate at which they occur may depend upon current energy reserves, time of day and the relative abundance and taxonomic composition of the available prey.

The willie wagtail, *Rhipidura leucophrys*, is an insectivorous pursuit predator that actively forages on open ground, searching for insects in a series of hops and runs accompanied by tail-wags and wing-flashes. Tail-wagging and wing-flashing are distinct behaviours: in the former, the tail is partly fanned and wagged from side to side, while the bird wing-flashes by abruptly raising its wings. Prey items are gleaned from the ground or captured in the air, sometimes after short pursuit flights. A wide variety of arthropod taxa have been recorded in the diet of the willie wagtail, but it is dominated by flying taxa (Cameron 1985; Barker and Vestjens 1990).

Here, we investigate the daily variation in the foraging behaviours of the willie wagtail, and identify the factors responsible for any consistent patterns. In particular, we examine the role of

tail-wagging and wing-flashing in foraging, and attempt to confirm experimentally that tail-wagging can function in disturbing insects into flight.

Methods

Field sampling

Wagtails were observed in three large urban parks in Melbourne from May to September 1994. Sampling was conducted during five daily time intervals, each of which lasted approximately 80 min. The first and last 30 min of this sampling period were devoted to behavioural observations, and the middle 20 min to insect collection. The first sampling interval began 10 min after civil twilight commenced; this was the earliest time at which birds could be observed easily with binoculars on a cloudy day. The second sampling interval took place in the mid-morning. The third interval commenced 40 min before the sun reached transit altitude. The fourth interval took place in the mid-afternoon, and the last sampling interval finished 10 min before civil twilight ended. The Sunrise, Sunset and Civil Twilight chart for Melbourne 1994 (Bureau of Meteorology, Victoria) was used to calculate the start and finish time of each sampling interval.

The parks were sampled alternately, ensuring that no park was sampled during successive time intervals. The samples were replicated under a range of light regimes, in order to maximise the range of light intensity. This sampling program yielded 58 sampling periods, with 3–5 replicates of each time interval at each location.

Behavioural observations

As many birds as possible were observed during each sampling interval, but on some occasions only one or two birds were found. Although every effort was made to select a different bird for each observation, it was inevitable that the same bird was sampled more than once. The birds were not individually marked, so they could not be distinguished individually.

Wagtails were observed from a distance of 5–20 m, and their behaviour was recorded verbally onto a continuously running tape recorder. Each bird was selected arbitrarily and its behaviour recorded for about 5 min or until it was no longer visible. A different bird was then selected.

The following behaviours were recorded. 'Tail-wags', in which the tail moves horizontally from side to side; one tail-wag is a movement of the tail from the centre to one side and back again. 'Wing-flashes', in which the wings are abruptly raised while the bird remains stationary on the ground. 'Flights' are to or from a perch, or from one patch of ground to another. Flights in which a prey item is clearly being pursued and/or captured are called 'flutters'. Other prey-capture behaviours include 'pecks' in which a prey item is pecked from the substrate and 'snaps' in which a flying prey item is captured while the bird remains on the ground. It was difficult to determine whether or not a successful capture had occurred, but flutters, pecks and snaps more realistically represent prey-capture attempts. Perching and behaviours on the perch were also recorded. We recorded the duration of three non-foraging behaviours: 'singing', 'preening' and 'social' behaviour that involves interactions with other birds, including the presumed mate.

The data recorded on the audio tapes were later transferred to computer file using a personalised event recording program. Each foraging sequence (of up to 5 min) was used to generate a rate of foraging behaviour per minute. Air temperature in the shade and light intensity were measured at the beginning and end of each sampling interval.

Insect sampling

The number of available flying insects was estimated during the middle 20 min of each sampling interval by sweep-netting with a 36-cm-diameter sweep-net of 1-mm mesh. Five samples were collected during each sampling interval from an area of the park where wagtails had been observed foraging. Each sample consisted of ten sweeps made close to the ground to capture invertebrates on and above the grass. All samples were collected from the same general area but no place was swept over twice during the same sampling interval. The contents of the net were placed in separate containers and later identified in the laboratory.

The role of tail wagging: experimental tests

The role of tail-wagging in flushing insects was examined experimentally using a model willie wagtail tail. The tail was constructed from thin, black cardboard strips to the same dimensions as those of museum specimens from the Museum of Victoria. The tail was attached to a lever and placed in a transparent perspex

box measuring $33 \times 19 \times 17$ cm high. A piece of turf from one of the study sites was placed at the base of the box as a substrate. A clear perspex lid was designed so that it could be placed in one of two positions in the box, either below or above the tail. The general procedure for each experiment was as follows. Laboratory-reared bushflies, *Lucilia cuprina*, were anaesthetised with carbon dioxide and 10–20 were transferred into the container. A table lamp with a 100-W bulb was placed over the box, and light directed down into it so that the tail cast a shadow over the substrate. After the flies had recovered from the effects of the carbon dioxide (usually within 3 min) the tail was wagged twice. The proportion of flies that flew from the substrate in the next 5 s was then estimated.

The influence of tail-wagging, light and air movements in disturbing the flies was examined by incorporating three treatments: with and without tail-wagging; under red and white light; and with and without air movement. Most insects are unable to detect red light and hence are not expected to be disturbed by the movement of the tail under these conditions. Air movement was prevented by placing the perspex lid under the tail. Each experimental treatment was replicated 10 times and new flies were used in each replicate.

Data analysis

Statistical analyses were carried out using Systat 5.2 for the Apple Macintosh (Wilkinson 1992). The distribution of data was assessed visually and transformed appropriately when it was not normal. The number of birds in this study was unlikely to be more than 14, and although our sampling procedure artificially inflates the sample size, it is unlikely that any systematic bias between individuals is responsible for the observed variation. Nonetheless, we attempt to reduce Type I errors by rejecting the null hypothesis at the 0.001 level for analyses that use each foraging sequence (of up to 5 min) as an independent value. The conventional 0.05 level was used for other analyses that use sampling periods or days as independent values.

Results

Insect activity and time of day

The majority of insects collected during the sweep-net sampling were flies (order Diptera), which were dominated by ephydriids, and some small sciarids and chironomids. Other insect groups included pteromalid wasps, aphids and a few psocopterans, coleopterans, thysanopterans, and lepidopterans. Availability of prey varied with the time of day ($F_{4,516} = 35.72$, $P < 0.0001$). Total adult insect activity was lowest in the early morning, at only 2.5 insects per sample, and increased during the day to over 16 per sample in the mid afternoon. Activity levels decreased in the late afternoon to only about 6 insects per sample (Fig. 1).

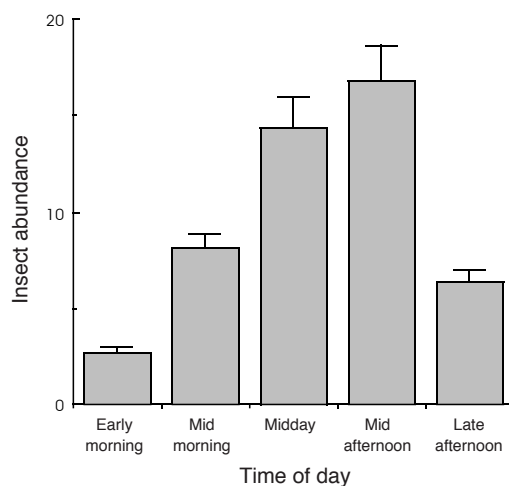


Fig. 1. Relative insect abundance (insects per 10-sweep sample) at five time intervals during the day. Values are means with bars as standard errors.

Foraging behaviour and time of day

The rate of both tail-wagging and wing-flashing were influenced by the time of day (Table 1). The rate of tail-wagging was higher in the early morning and late afternoon compared with the middle of the day (Fig. 2a), whereas wing-flashing occurred infrequently in the early morning and was more than ten times higher from mid morning to mid afternoon (Fig. 2b). The mean rate of tail-wagging over each sampling interval was significantly negatively correlated with that of wing-flashing ($r = -0.329$, $n = 58$, $P = 0.012$). This suggests that the birds may not have altered the combined rate of tail-wagging and wing-flashing across different times of the day, which was the case ($F_{4,516} = 1.41$, n.s.).

Snapping was a relatively infrequent foraging behaviour, but followed a trend similar to that of wing-flashing. Birds snapped most frequently from mid morning to mid afternoon, and less frequently in the early morning and late afternoon (Table 1). Birds also fluttered less frequently in the early morning, but the rate increased during the morning and fluctuated slightly for the rest of the day (Table 1). Wagtails generally pecked at about the same rate throughout the day, but the rate was lower during the middle of the day (Table 1). Foraging effort, defined as the combined rate of tail-wags, wing-flashes, flutters, pecks and snaps, did not vary significantly with the time of day ($F_{4,516} = 2.13$, n.s.).

Table 1. The mean (\pm s.e.) rates of wagtail foraging behaviours (per min) at five time intervals during the day

n , the number of foraging sequences; *, $P < 0.001$

Behaviour	Time of day					$F_{4,516}^1$
	Early morning $n = 97$	Mid morning $n = 118$	Midday $n = 97$	Mid afternoon $n = 102$	Late afternoon $n = 107$	
Tail-wags	16.4 \pm 1.2	10.1 \pm 0.9	10.4 \pm 0.9	9.0 \pm 0.8	16.0 \pm 1.1	10.92*
Wing-flashes	0.5 \pm 0.2	5.5 \pm 0.6	5.3 \pm 0.6	5.8 \pm 0.6	1.9 \pm 0.4	37.07*
Pecks	12.5 \pm 0.9	12.5 \pm 1.2	9.2 \pm 0.9	13.0 \pm 1.3	12.8 \pm 1.1	2.79
Snaps	0.1 \pm 0.1	1.0 \pm 0.1	1.2 \pm 0.2	1.2 \pm 0.1	0.5 \pm 0.1	22.83*
Flutters	0.5 \pm 0.1	2.5 \pm 0.3	2.1 \pm 0.2	2.5 \pm 0.2	2.1 \pm 0.2	23.12*

¹ ANOVA of log-transformed data

Foraging location, environmental conditions and behaviour

Pecking, fluttering, snapping and wing-flashing were observed infrequently or not at all when the birds were on a perch, and tail-wagging occurred at a higher rate on the ground than on the perch (Table 2). The birds also spent a higher proportion of time interacting with other birds on the ground than they did on the perch. There was no difference between the ground and the perch in the proportion of time spent singing and preening. Wagtails made short flights from the perch at a higher rate than they did from the ground.

There were no significant differences in the tail-wagging rate, or the wing-flashing rate between observations that contained social behaviour compared with those that did not. The rate of tail-wagging in a sampling interval did not differ between observations with singing (mean = 13.3, s.e. = 1.2, $n = 86$) compared with those without (mean = 12.2, s.e. = 0.5, $n = 435$; $t = 1.28$, n.s.), but wing-flashing occurred at a lower rate in observations with singing (mean = 2.6, s.e. = 0.5, $n = 86$) than in those without (mean = 4.1, s.e. = 0.3, $n = 435$; $t = 2.20$, n.s.). The latter pattern is most likely because wagtails wing-flashed infrequently in the early morning, the period in which most singing occurred.

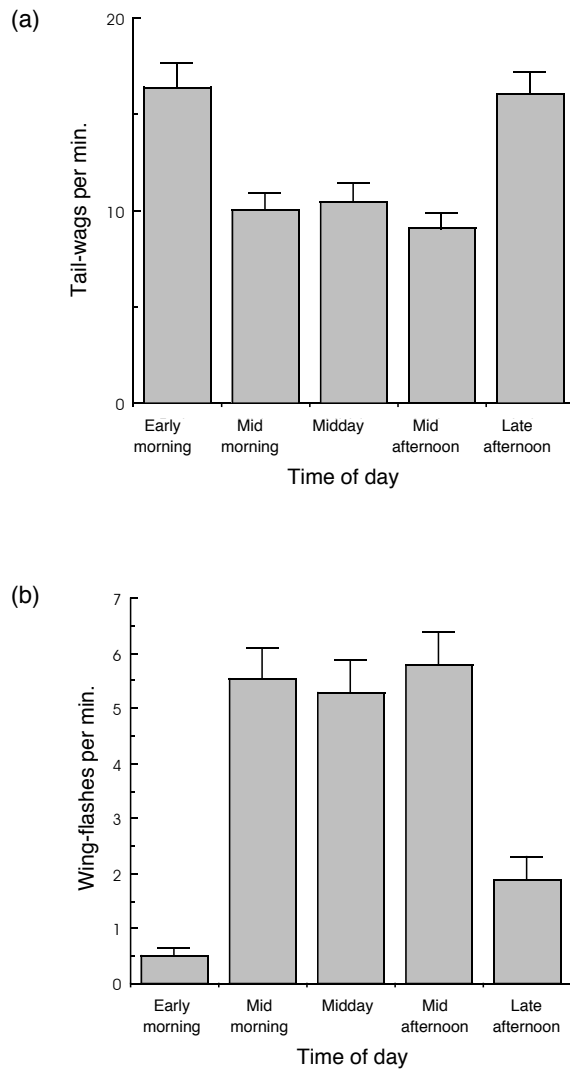


Fig 2. The mean rate of (a) tail-wagging and (b) wing-flashing of willie wagtails at five time intervals during the day. Values are means with bars as standard errors.

Table 2. Comparison of tail-wagging rate, flight rate (both per min) and proportion of time spent in three non-foraging behaviours by wagtails on the perch and on the ground
*, $P < 0.001$ (Wilcoxon Signed-ranks Test)

Behaviour	Ground				Perch				Z
	mean	s.e.	median	n	mean	s.e.	median	n	
Tail-wags	11.849	0.831	10.451	58	4.760	1.356	1.295	47	4.53*
Flights	1.201	0.097	1.031	58	13.995	3.272	5.928	47	5.66*
Singing	0.009	0.004	0.001	58	0.009	0.004	0.002	58	0.30
Preening	0.030	0.016	0.005	58	0.013	0.004	0.000	58	1.45
Territorial	0.027	0.007	0.012	58	0.002	0.001	0.000	58	4.41*

Wagtails tail-wagged more frequently under low light conditions ($r = -0.35$, $n = 58$, $P < 0.01$), but the rate was not correlated with temperature ($r = -0.23$, $n = 58$, n.s.). In contrast, the rates of wing-flashing and snapping were positively correlated with light intensity ($r = 0.50$, $n = 58$, $P < 0.001$, and $r = 0.46$, $n = 58$, $P < 0.001$, respectively) and air temperature ($r = 0.44$, $n = 58$, $P < 0.001$, and $r = 0.56$, $n = 58$, $P < 0.001$, respectively). The flutter rate was positively correlated only with air temperature ($r = 0.46$, $n = 58$, $P < 0.001$). Finally, pecking rate was not correlated with either light intensity ($r = -0.09$, $n = 58$, n.s.) or air temperature ($r = -0.18$, $n = 58$, n.s.).

The results of the experiments showed that tail-wagging startled some flies into flight, and that this was precipitated by a change in light intensity, but not air movement. A 3-way analysis of variance revealed a significant tail-wag and light regime interaction ($F_{1,72} = 8.37$, $P < 0.006$), and significant tail-wag ($F_{1,72} = 9.30$, $P < 0.004$) and light regime ($F_{1,72} = 21.78$, $P < 0.001$) main effects; all other main effects and interactions were not significant. Essentially, more flies took flight under white light when the tail was wagged (proportion = 0.172, s.e. = 0.039) than when the tail was not wagged (proportion = 0.045, s.e. = 0.014). However, tail-wagging had no effect on the flies in red light (proportion = 0.011, s.e. = 0.006).

Discussion

Bednekoff and Houston (1994) suggest that the frequently reported bimodal distribution of foraging effort by small birds (e.g. Aschoff 1966; Wolf and Hainsworth 1977; Wyndham 1980; Powers 1991) is related to the uncertainty of food supply. Birds should forage intensely in the morning in order to replenish their energy reserves and to allow plenty of time to recover from unsuccessful foraging bouts or interruptions to foraging (McNamara and Houston 1992). Foraging effort should also increase in the late afternoon to enhance overnight survival (McNamara and Houston 1992). An insectivorous pursuit predator, such as the wagtail, would seem to be especially susceptible to both uncertainty in food supply and foraging interruptions, as the availability of prey is highly variable. It is surprising that the distribution in the combined rate of foraging behaviour for wagtails was not consistent with this prediction.

There are striking changes in the frequency of several foraging behaviours of wagtails over the course of the day, consistent with previous studies of other birds (Davies 1977a, 1977b; Collins and Morellini 1979; Collins and Briffa 1982). In particular, the frequency of behaviours that are associated with the capture of flying prey increase from low levels in the early morning to a high in the middle of the day, then decrease again in the late afternoon. These changes in behaviour are matched by changes in the abundance of available insect prey, a pattern that has been noted in other species. For example, the spotted flycatcher, *Muscicapa striata*, switches between actively searching for prey in the canopy to scanning for flying prey from a perch (Davies and Green 1976; Davies 1977b), depending upon the abundance of large dipteran prey. American redstarts, *Setophaga ruticilla* (Holmes *et al.* 1978) and Australian scarlet robins, *Petroica multicolor* (Ford *et al.* 1990) engage in more aerial foraging when flying insects become abundant in the middle of the day. In contrast with behaviours associated with capturing aerial insects, wagtails peck at a relatively constant rate throughout the day. Pecking probably involves the capture of flightless arthropods, whose availability may not change with temperature, or who are unmoved by tail-wagging or wing-flashing.

All members of the genus *Rhipidura* and a number of other insectivorous bird taxa incorporate fanning and/or wagging of the tail and jerky movements of the wings into their foraging behaviour (Selander and Hunter 1960; Goodwin 1967; Harrison 1976; Cameron 1985; Simpson and Day 1986; McLean 1989; Jackson and Elgar 1993). Wing-flashing and tail-wagging appear to be complementary activities for wagtails. The function of these behaviours is not clear, although it is widely thought that such movements flush insects from the ground, facilitating their capture (Goodwin 1967; Jackson and Elgar 1993; Jablonski 1996). While these behaviours may aid in balance or perform an inter- or intra-specific signalling function (Jablonski 1996), several lines of evidence from this study suggest that, for wagtails,

they are primarily associated with foraging. First, the rate of tail-wagging was negatively correlated with light intensity and may reflect differences in the startle and flight response of insects under different contrasts of light (see also Jackson and Elgar 1993). Insects may be less easily startled by the shadow of a bird under low light intensities, so wagtails should wag their tails more frequently to maintain a constant rate of food intake. Second, the experiment with a model wagtail tail confirmed that tail-wagging has the potential to flush flies from the ground, and that light intensity affects the efficiency of tail-wagging. Air currents did not flush flies from the ground, contradicting the suggestion by McLean (1989) that air movement caused by the flushing behaviours of grey fantails, *R. fuliginosa*, disturbs their insect prey.

Wagtails appear to devote a constant effort to disturbing prey throughout the day, but do so using different methods that may have different associated costs and benefits. Wing-flashing is a more vigorous behaviour that may be more energetically costly than tail-wagging. One possible advantage of wing-flashing over tail-wagging is that the wings are closer to the bird's head, and a wing-flash may startle insects around the bird, including those in front of it. The head is held high during this behaviour, possibly to prepare for the quick pursuit of a flying insect. In contrast, the tail is at the opposite end to the head, and it may be difficult to capture quickly prey flying up from behind the bird. In the morning and late afternoon, however, insects are less active, and may only move rather than take flight when disturbed by a flushing behaviour. This movement could alert the wagtail to the insect's position on the ground, allowing it plenty of time for capture. The head is held low during tail-wagging, consistent with the idea that wagtails are searching for prey on the ground. Thus, wing-flashing may be favoured when flying insects are most abundant, and the presumably less energetically costly tail-wags are used mostly in the early morning and the late afternoon, when insects are generally less active.

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