Territorial behaviour of Pied Wagtails in winter

N. B. Davies

These studies, previously published in detail in specialist journals, are so fascinating that they deserve a wide audience, hence this invited summary paper prepared especially for 'British Birds'.

For many small birds, winter is a critical time of the year. Days are short, food is scarce and many individuals starve to death. The main aim of my wagtail study was to discover how the behaviour they adopt in winter increases their feeding efficiency and hence chances of survival. My study site was Port Meadow on the outskirts of Oxford. Many of the Pied Wagtails Motacilla alba yarrellii which winter in the Thames valley are visitors which breed farther north (Davis 1966, Broom et al. 1976).

Some fed in flocks on flooded pools, while others defended feeding territories along the River Thames which flowed along one side of the meadow (fig. 1). The flock birds wandered widely; for example, in one winter, I colour-ringed 150 and yet saw only six of these regularly on the meadow. Some were seen on the nearby rubbish tip and others in gardens adjoining the meadow. Many of those along the river, on the other hand, defended the same territory throughout the winter. The boundaries were rather stable and each wagtail occupied a stretch of about 300m of river, defending both banks against intruders. There seemed to be considerable competition for the territories: whenever an owner disappeared, its place was quickly taken by another. Most owners were males, as in Zahavi’s (1971) study in Israel.

Winter time-budget

By sitting on the river bank, I was able to watch a territory owner continuously throughout the whole day without ever losing sight of it. In midwinter, with only 8½ hours of daylight, an owner spent 90% of the time feeding. From data on time-budgets, the daily energy expenditure was estimated to be 22.4 Kcal (table 1a). This estimate is undoubtedly crude, but it agrees well with other methods (Kendeigh et al. 1977; Davies 1981).
Since the wagtails picked up such small items, it was impossible to see exactly what they were eating, so I relied on the indirect method of analysing prey remains in their faeces. The main remains were the wings of small flies (especially chironomid midges), wing cases of small beetles and the mandibles and legs of spiders. I kept a wagtail in captivity and found that this kind of analysis gives a very good measure of prey eaten (Davies 1977). Prey items eaten in winter were, on average, worth 3.5 cal. The average feeding rate was 18 items per minute, and the daily energy intake was estimated to be 21.7 Kcal (table 1b), which approximately balances the energy expended.

The main conclusion from these very rough calculations is that, even with what seems to be a phenomenal feeding rate of one small insect every 3 or 4 seconds throughout the whole winter's day, a wagtail only just achieves energy balance. There seems little doubt that, like other small birds in winter (Gibb 1956, 1960), Pied Wagtails are hard pressed to find enough food, so we would expect any behaviour that improved their feeding efficiency to have strong selective advantage.

### Table 1(a)

<table>
<thead>
<tr>
<th>Activity</th>
<th>Hours per day</th>
<th>Daily cost (cal.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foraging</td>
<td>7.65</td>
<td>10,710</td>
</tr>
<tr>
<td>Resting</td>
<td>0.53</td>
<td>371</td>
</tr>
<tr>
<td>Defence</td>
<td>0.32</td>
<td>448</td>
</tr>
<tr>
<td>Sleeping</td>
<td>15.30</td>
<td>10,850</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td><strong>22,379</strong></td>
</tr>
</tbody>
</table>

### Table 1(b)

Calculation of midwinter daily energy intake by Pied Wagtails *Motacilla alba*

\[
\text{18 prey/min} \times 459 \text{ min.} = 8,262 \text{ prey} \times 3.5 \text{ cal. each} = 28,917 \text{ cal.} \times 75\% \text{ digestive efficiency} = 21,687 \text{ cal.}
\]
**Territory versus flock profitability**

Owners sometimes left their territories to feed with the flock, but they kept returning to the river at regular intervals to evict any intruders that had landed there while they were away (Davies 1976). The owners’ change in behaviour when they joined the flock was remarkably quick. I often saw two territorial neighbours vigorously chasing each other and displaying at a territory boundary and then, less than a minute later, both feeding peacefully side by side in the flock.

Faeces analysis showed that the same sized items were taken in both the territories and the flock, so feeding rate measurements give a good idea of their relative profitability. On some days, the feeding rates were highest in the flock, yet the owners still often spent most of their time on territory, forgoing the short-term gain that they would have enjoyed from joining the flock. It seems likely that the long-term advantage of a predictable food supply on the river outweighed the exploitation of the more ephemeral food supply elsewhere on the meadow, even when this was temporarily more profitable. The long-term advantage of the territories became clear on very cold days, when the meadow froze and the flock birds were forced to seek food elsewhere. At these times, there was a sudden increase in the recovery of dead wagtails from the national ringing scheme (Cawthorne & Marchant 1980). The territorial individuals, however, were still able to feed on their territories during these severe periods because the river continued to wash food up onto the banks.

**Defence of a renewing food supply**

The key to an understanding of the territorial behaviour of wagtails along the river was that they exploited a renewing food supply. Typically, an owner walked systematically around its territory, picking up insects from the river edge, a circuit which took 40 minutes to complete (fig. 2a). After it had visited a stretch of bank, the food was depleted temporarily, and time was needed for more insects to wash up. Ideally, we might suppose that the territory size would be such that, by the time the owner completed the circuit, enough insects had accumulated onto the river edge for it to feed at a profitable rate the next time round. Similar systematic cropping of a renewing food supply has been recorded in other birds (Bibby & Green 1980; Kamil 1978).

Once the importance of prey renewal has been recognised, the reason for territorial defence becomes obvious. If other wagtails were allowed to land, they would deplete the food, so that an owner would suffer a decreased feeding rate when it next visited the stretch. Some intruders did land on the territories undetected, and this resulted in a sudden decrease in the owner’s feeding rate when it came across the depleted stretch (fig. 3). It is hardly surprising, therefore, that owners evicted any intruders that they did detect.

They not only chased off other Pied Wagtails, but also Robins *Erithacus rubecula*, Grey Wagtails *M. cinerea* and Meadow Pipits *Anthus pratensis* which ate insects and so also depressed the owner’s feeding rate. One Meadow Pipit was chased so relentlessly that it fell into the river and floated off
Fig. 2. (a) Owner Pied Wagtails *Motacilla alba* exploit their territories systematically. The circuit of the river bank takes, on average, 40 minutes to complete. (b) When a territory is shared between two wagtails, each, on average, walks half a circuit behind the other and so crops only 20 minutes' worth of food renewal downstream. On the other hand, they tolerated the presence of seed-eaters, such as Linnets *Carduelis cannabina*, which did not deplete the insect food supply.

Territory defence, therefore, was the way the Pied Wagtail protected the prey-renewal times on its territory.

**Behaviour of intruders**

Intruders were very noisy and conspicuous whenever they flew over or landed on the territories, calling loudly 'chisick'. If an owner was present, it replied with a different call, 'cheewee', and the intruder then usually flew off. At first sight, the noisy call of the intruders is puzzling: why didn't they attempt to sneak on to a territory undetected?

Even if they did sneak on, however, they would often end up feeding in places recently depleted by the owner. The most profitable place for an intruder to land would be just ahead of the owner, where the renewal time of insects would be greatest, but here the intruder would be easily spotted. If, on the other hand, it landed some way off, it would be feeding over depleted stretches. Measurements showed that intruders which landed undetected fed at only 11 items per minute on average, which is less than the rate needed to achieve energy balance. It seems, therefore, that intruders benefit by calling, to 'knock on the door', and, if a reply indicates that an owner is in residence, they do better to leave, because occupancy is a sign of a depleted feeding area.
Only territory owners called ‘cheewee’. Two observations support the idea that it is an ownership signal. First, whenever an owner flew into another territory, it gave the ‘chisick’ call typical of an intruder. Secondly, on one occasion, an intruder landed on a territory when the owner was away in the flock. After 20 minutes’ trespassing, the owner still had not returned, and the newcomer appeared to build up confidence, because it began to give ‘cheewee’ calls to other wagtails overhead.

If ‘cheewee’ is an ownership signal, then we would predict that tape-recordings of ‘cheewee’ would elicit a strong aggressive response from the owner, because the broadcast would simulate the presence of an intruder who was announcing ownership. I did this playback experiment on seven territories, and on every occasion the owner immediately flew over to the loudspeaker and displayed in front of it. Some hovered persistently nearby for up to 3 minutes after the playback had ended. In contrast, when I broadcast ‘chisick’, the owners simply replied ‘cheewee’ and then carried on feeding. They did not approach the speaker and behaved as they normally did to an intruder’s call, as if expecting the intruder to retreat on perceiving the ownership signal (Davies 1981).

**Territory sharing**

Although an owner defended a territory of a fixed size throughout the winter, its defensive behaviour varied depending on the food supply. On days when food was very scarce, it spent much of the time in the flock, but returned periodically to defend its territory. If food was more abundant, the owner spent all day on its territory and occupied it alone. As food increased further, owners often shared their territories by tolerating the presence of another bird. These ‘satellites’ were usually dull-coloured first-winter birds from the flock, which landed on the territories and appeased the owners with special postures described in detail by Zahavi (1971). In Israel, Zahavi found that satellites tended to be females. I call these birds satellites
because their relationship with the owner is of a very temporary nature (a week, or sometimes just a day or two). It is possible that a satellite is sometimes the future mate of the territory owner, but this is often not the case, since a satellite may be seen appeasing several different territory owners during the course of a winter. Snow (1958) has described similar temporary associations by Blackbirds *Turdus merula* on winter territories.

What determines whether owners accept or evict satellites? The presence of a satellite brings a benefit to the owner because it helps to defend the territory against intruders and neighbours, in many cases doing half of the defence. It also, however, imposes a cost, because sharing the territory means that the owner has less food than it would if it remained alone. Owners and satellites usually shared the territory by each walking, on average, half a circuit behind the other, so that, instead of cropping the food at 40 minutes’ worth of renewal time, the owner got only 20 minutes’ worth (fig. 2b).

Whether it will pay the owner to accept a satellite depends critically on food abundance (fig. 4). When food is scarce, cutting the food-renewal time by half has a big effect on the owner’s feeding rate, so he does better to remain alone. As food abundance increases, however, the cost of sharing the territory decreases and, in addition, because intruder pressure increases, help with defence becomes very beneficial. A mathematical model was used to quantify exactly how these costs and benefits combined to influence the owner’s feeding rate. The results showed that, indeed, the owner tolerated a satellite only when the benefits of help with defence outweighed the costs of sharing the food (Davies & Houston 1981). In other words, the owner will share its territory only when it itself will enjoy a higher feeding rate by doing so. It seems likely that owners accept only females or young birds as satellites because they are easier to evict when food on the territory becomes scarce and the owner does better by remaining alone.

In the spring, there is usually a sudden increase in the food supply as small insects emerge with the first warm weather. Owners then stop evicting intruders and tolerate the presence of any wagtail that lands nearby. This makes good sense, because prey are so abundant that a wagtail does not suffer a decrease in feeding rate even if it walks directly in the footsteps of another bird.
Conclusion
It may seem surprising that the wagtail’s behaviour is so finely tuned to variations in its food supply, but, by accepting a satellite on days of high food abundance, an owner can increase its own feeding rate by up to 33%. Indeed, making the correct decision over territory sharing is probably an important determinant of whether the owner will get enough food to stay alive. I have no idea as to how the owners decide whether to share their territories or not. Obviously, they do not work out mathematical equations! Presumably, they use simple rules; for example, their tolerance of satellites may depend on their own hunger level or on external cues like the temperature, which is correlated with insect abundance.

By whatever means they achieve their behaviour, it is clear that wagtail territorial defence is beautifully designed to increase feeding efficiency in winter.

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References

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