OWNERS AND SATELLITES: THE ECONOMICS OF TERRITORY DEFENCE IN THE PIED WAGTAIL, *MOTACILLA ALBA*

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SUMMARY

(1) Pied wagtails defended winter feeding territories along a river. They fed on insects that were washed up onto the river banks. These formed a renewing food supply: after a stretch had been depleted, time was needed for prey abundance to return to a profitable level. The wagtail’s feeding rate therefore depended on the time that had elapsed since the stretch was last depleted (the return time).

(2) Territory owners increased their return time, and hence feeding rate, by systematic search around the territory and by evicting intruding conspecifics and other species that depressed their food supply.

(3) Sometimes intruders landed on a territory undetected. This often decreased the owner’s feeding rate because it visited stretches soon after they had been depleted by the undetected intruder. Juvenile intruders were more likely to land on a territory undetected, probably because they had duller plumage than the adults.

(4) A territory was more profitable to an owner than to an intruder because the owner achieved greater return times. Intruders did worse because they did not know where the recently depleted stretches of the territory were. Even if intruders landed undetected, they often fed over areas that had recently been depleted by the owner.

(5) Owners defended a territory of a fixed length, but their defence behaviour varied. Often the owner defended the territory alone but sometimes it associated with a sub-ordinate (a satellite). Owners showed rapid changes in behaviour towards satellites; sometimes they chased them off and sometimes they allowed them to reside on the territory unmolested.

(6) Satellites imposed a cost on the owner because they depleted the food supply on the territory. However, they also brought a benefit in the form of help with territory defence against intruders.

(7) We develop a model which quantifies these costs and benefits, and show that owners vary their tolerance of satellites so as to maximize their own daily feeding rate. On days of high food abundance, when intruder pressure is greatest, owners tolerate satellites. We show that owners increase their feeding rate by this association, because the benefits gained through help with defence outweigh the costs incurred through sharing the food supply with another bird. On days of low food abundance, when an owner would have a higher feeding rate by being alone, it evicts the satellite from the territory.

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0021-8790/81/0200-0157$02.00 © 1981 Blackwell Scientific Publications
INTRODUCTION

The pied wagtail, *Motacilla alba*, is a widely distributed passerine bird that defends feeding territories in winter. Observations in Egypt (Hartley 1946; Goodwin 1950), Israel (Zahavi 1971), Britain (Davies 1976) and Japan (Watanabe & Maruyama 1977) have all shown that a territory is often defended by one bird alone, but sometimes a subordinate associates with the owner for a period varying from one day to several weeks. These subordinate birds, which we shall call ‘satellites’, land on territories and attempt to appease the owner with special postures, described in detail by Zahavi (1971).

Owners, who are usually males, show rapid changes in behaviour towards satellites; sometimes they chase them off and sometimes they allow them to reside on the territory unmolested. Although the satellites are females (Zahavi 1971) or birds in juvenile plumage (this study) they are not simply offspring or mates of the owners, since the association is of a temporary and rapidly changing nature, and satellites are seen appeasing several different territory owners during the course of a winter (Zahavi 1971; Watanabe & Maruyama 1977). Apparent pairing in winter, unrelated to breeding, has also been described in other species (Snow 1958).

In this paper we attempt to explain why owners sometimes tolerate satellites and sometimes evict them. We assume that, through natural selection, wagtails adopt territorial behaviour that maximizes their fitness. Because the territories are concerned solely with feeding and are abandoned at the end of the winter (Zahavi 1971; Davies 1976), we assume that fitness depends on feeding efficiency. Pied wagtail territory owners feed for 90% of the daylight hours in winter and have to collect one prey item (small insects) every 4 s in order to achieve energy balance (Davies 1976, 1980). There must be a strong selective advantage for any behaviour that improves feeding efficiency and thus enables the wagtail to increase its food intake or spend more time resting or looking out for predators. It seems reasonable, therefore, to quantify the costs and benefits associated with territory defence, and the economics of sharing a territory with a satellite, in terms of the way this affects the owner’s feeding efficiency.

We first describe field observations and measurements on the feeding behaviour of territory owners to explain why there are benefits arising from the eviction of intruders. Then we look at the interactions between owners and satellites. A satellite imposes a cost on the owner because it depletes the food supply on the territory. However, it also brings a benefit in the form of help with territory defence against intruders. We develop a model to analyse how these costs and benefits affect the feeding efficiency of the owner and examine the circumstances under which the owner may enjoy a net benefit from the association.

STUDY AREA AND WAGTAIL SOCIAL ORGANIZATION

Observations were made during two winters, 1977–78, and 1978–79, on Port Meadow, near Oxford, England, where the social behaviour of pied wagtails had been studied previously (Davies 1976, 1977). There were up to 300 wagtails present on the meadow during winter. Some fed together in a flock around shallow pools in the centre of the meadow. Others defended territories along the River Thames which flowed along one side of the meadow. Territories were set up in October and abandoned in early March when the weather became warmer and there was a spring emergence of insect prey, especially chironomids.
Each territory owner occupied a stretch of the river and defended both banks against intruders. Owners fed by walking along the water’s edge and picking up small insects that were washed up by the river onto the muddy banks. Individuals were colour ringed for identification and a few could also be recognized by their plumage pattern, which is very variable in this species. In 1978–79, the three territories studied were defended throughout the winter and their boundaries remained stable. In 1977–78, due to heavy rain, the river frequently burst its banks and flooded the meadow. During these periods owners abandoned their territories. When the floods receded, new birds often occupied territories along the river and the boundaries changed. The six territory owners studied in this winter were therefore followed for only a month or two each (Table 1). Despite these changes in boundaries and ownership after flooding, the length of river bank defended was about the same in each territory (Table 1).

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Nine territories were studied in detail. All of the owners were adult males except for territory 3 which was defended by a bird in juvenile plumage. Adult males have a striking plumage of black and grey feathers on the back with white faces and underparts. In their first winter, juveniles are duller in colour and have olive-grey backs, dull underparts and, often, yellow markings on the face. Territory 7 was occupied by an adult male owner and a juvenile satellite from mid-October until the end of December. Then there was a cold spell, the owner disappeared and the satellite defended the territory alone for 3 weeks in January until it too disappeared.

On seven out of the nine territories studied, satellites were seen with the owners for part of the winter (Table 1). All satellites were birds in juvenile plumage whose sex was not determined. In Zahavi’s (1971) study, territory owners were usually males and satellites females (determined by dissection), though females were sometimes observed to defend territories. Therefore it seems that territory owners are usually adult males but adult females or juveniles also sometimes defend territories.

Although territory size remained constant during the winter, the defensive behaviour of owners varied dramatically. When food on the territory was very scarce, the owners left to feed elsewhere though they came back to the territory at regular intervals to defend
it (Davies 1976). When food was very abundant the owners gave up defending their territories altogether and ignored intruding wagtails. This happened on some days in early spring, but if the food supply decreased again, normal territorial behaviour was quickly resumed. In between these two extremes were days on which the owner spent all or most of the day on its territory either alone or with a satellite, and it is these two types of territory defence with which we are concerned in this paper.

Table 1 shows the number of days that each owner was observed alone or with a satellite. Satellites were more likely to be tolerated in early winter, but their presence was not simply a seasonal effect. For example, Fig. 1 shows changes in territorial behaviour

![Variations in territorial defence during the winter in two pied wagtails](image)

**Fig. 1.** Variations in territorial defence during the winter in two pied wagtails. Four levels of defence are indicated. The upper NT refers to days of high food abundance when owners allowed all other wagtails to feed on their territories. O + S refers to days on which owners associated with a satellite but evicted all other wagtails. O refers to days that the owner was alone and chased off all other wagtails, including satellites. The lower NT refers to days of low food abundance (often days of heavy frost or snow) where owners abandoned their territories and fed elsewhere.

of two owners during the winter. On territory 4 a satellite was present in mid-winter while on territory 9 one was present at the start of the winter. Owners often showed rapid changes in behaviour towards satellites; on one day an owner and satellite may be feeding together peacefully on the territory while on the next day the owner might evict the satellite whenever it attempted to land. A few days later both birds may once again be together on the territory. Sometimes one territory owner tolerated a satellite bird while the next door neighbour did not. Our aim is to explain why owners show these changes in behaviour towards satellites. First of all, however, we must understand why pied wagtails that feed along the river can benefit from defending a territory.

**DEFENCE OF A RENEWING FOOD SUPPLY**

*Resource renewal*

The territorial wagtails were insectivorous during the whole winter; analysis of prey remains in the birds’ faeces showed that they fed mainly on small Diptera, spiders and beetles (Davies 1976). Owners foraged almost exclusively by picking up prey at the
edge of the river, where aerial insects that had fallen onto the water were washed up onto the banks. On some days it was easy to see dead and dying insects floating on the river and being deposited on the mud at the water’s edge.

A terylene net, 10 m long, was pegged out at the edge of the river and the number of insects washed up onto the net was counted over a period of 3 h. The number increased at first and then seemed to level off (Fig. 2). One explanation of this is that after a time insects at the water’s edge tend to be washed away again by the river. In fact we often saw this happening both to prey on the mud and on the net. If there is both an input and an output of prey at the river edge then it can be shown that insects will build up and then level off in the form of an exponential curve (see Appendix).

![Graph](image)

**Fig. 2.** Counts of the number of insects washed onto a terylene net stretched out along the river bank in a pied wagtail territory. The number of insects appears to increase at first and then level off. Three days data: on days 1 and 2 the owner was alone on its territory; on day 3 it had abandoned the territory.

The main point is that the insects form a renewing food supply. After they have been depleted from a stretch of the river edge, it will take time for further prey to wash up onto the bank. To see how this pattern of resource renewal influenced the feeding rate of the pied wagtail, territories were marked out with numbered stakes at 10-m intervals along the river edge. Birds were observed through binoculars and their feeding rate, measured by pecking rate, was recorded on a cassette tape recorder. Because the birds were feeding on immobile prey and made distinct pecks, we think it is reasonable to assume that one peck represents one prey item. By observing a length of the territory for several hours and recording all the visits to each 10 m stretch, it was possible to see how a bird’s feeding rate varied with the time since the stretch was last visited by a wagtail. We attempted to get measurements of feeding rate for as wide a range as possible of times since a previous wagtail visit.

Figure 3 shows the results from 3 days on one territory. Although the patterns are different on the three days it is clear that a wagtail’s feeding rate is low if the stretch has recently been visited (and depleted). Feeding rate increases with time since depletion and exponential curves give a reasonably good fit to the data. We observed the feeding rates of territory owners, their satellites and intruding wagtails that landed on the territories undetected. On any one day, all birds followed the same relationship of feeding rate with time since depletion (Figs 3 & 4). Therefore a territory offers the same potential profitability to an owner, a satellite or an intruder. All that influences a wagtail’s feeding
rate is the time since the stretch was last depleted. If we just consider the owner’s feeding rate, then Fig. 4 shows that this is influenced by the time since depletion in exactly the same way, irrespective of whether a satellite, an intruder or the owner itself was the last visitor to the stretch.

Fig. 4. (a) All birds, whether owners (●), satellites (○) or intruders (▲), follow the same relationship of feeding rate v. time since the patch was last depleted. Therefore, for a given return time the territory is equally profitable to owners, satellites and intruders. (b) The feeding rate of the owner follows the same relationship with time since depletion, irrespective of whether the patch was last depleted by itself (●), its satellite (○) or an intruder (▲). Therefore all birds deplete patches to the same extent. The data for these two figures are from 9 days on which owners associated with satellites; data from four territories.
Fig. 5. Two examples from one territory of how the feeding rate of an owner is reduced when it visits a stretch soon after depletion by an undetected intruder. In both cases the sudden drop in the owner's feeding rate corresponds to the exact stretch that was recently visited by the intruder (indicated by lines above graphs). The territory was marked with pegs every 10 m along the river bank and the x axis represents a section of the territory.

Eviction of intruders

Given this pattern of resource renewal, it makes sense that wagtails feeding along the river defend territories. If other wagtails were allowed to land on the territory then the owner's feeding efficiency would be reduced because it would be visiting stretches soon after they had been depleted by other individuals. By evicting intruders, owners are able to increase the time allowed for resource renewal between successive visits to the same stretch (see also Charnov, Orians & Hyatt 1976; Baker 1978).

Whenever intruding conspecifics were detected they were always evicted. Owners sometimes pursued an intruder far out of the territory, for up to 500 m across the meadow, before returning to the river bank. Intruders that flew along the river were chased by several owners in turn as they passed from one territory to the next. Sometimes intruders landed undetected and this could have a severe effect on the owner's feeding performance. Figure 5 shows two examples where an owner's feeding rate suddenly decreased over a stretch recently depleted by an undetected intruder. It is little wonder that owners evict so vigorously any intruder that they do detect!

Juvenile intruders had a much greater chance of landing on a territory undetected (46.0% occasions) than adult intruders (23.4%). This was not simply because juveniles were more persistent at attempting to land on a territory; there were approximately

| Table 2: Number of intrusions onto territories by adults and juveniles when the owner is present or absent |
|-------------------------------------------------|-----------------|-----------------|
| No. intrusions                                   | Adult intruder  | Juvenile intruder |
| Owner present                                   |                 |                  |
| spotted immediately                             | 59              | 54               |
| land undetected                                 | 18              | 46               |
| Owner absent                                    |                 |                  |
| land on territory                               | 29              | 26               |
equal numbers of intrusions by adults and juveniles when the owner was absent (Table 2). Intruders that landed further away from an owner were less likely to be detected immediately, and for all distances except those very close to the owner, juveniles were more likely to escape detection than adults (Fig. 6).

![Graph](image)

**Fig. 6.** (a) The probability that a territory owner will spot an intruder immediately it lands on the territory decreases with distance. (b) If adult and juvenile intruders are plotted separately, it can be seen that juveniles (□——□) are less readily spotted by owners than adults (■——■). This is probably because they have dull coloured plumage compared with the striking black and white plumage of the adults (see text).

It could be argued that this difference is one of reaction rather than detection. Perhaps juvenile intruders inflict a smaller depletion cost than adults? However, as we saw earlier (Figs 3 & 4) all wagtails follow the same curve of feeding rate with time since depletion and satellites (juveniles), intruders and the owners themselves all deplete stretches to the same extent. The most likely explanation is that juveniles really are more difficult to detect, perhaps because of their duller plumage. Dull colouring in other birds (Rohwer 1978; Ewald & Rohwer 1980) and in fish (Fernald & Hirata 1977) also aids sneaky trespassing onto territories.
TABLE 3. Interspecific territoriality. The number of occasions that various species were chased out of the territory or allowed to land unmolested in relation to their diet overlap with the pied wagtail

<table>
<thead>
<tr>
<th>Species</th>
<th>No. occasions</th>
<th>Diet overlap with pied wagtail</th>
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<tbody>
<tr>
<td>Grey wagtail, <em>Motacilla cinerea</em></td>
<td>25 Chased, 7 Not chased</td>
<td>Yes</td>
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<tr>
<td>Meadow pipit, <em>Anthus pratensis</em></td>
<td>11 Chased, 2 Not chased</td>
<td>Yes</td>
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<tr>
<td>Robin, <em>Erithacus rubecula</em></td>
<td>6 Chased, 0 Not chased</td>
<td>Yes</td>
</tr>
<tr>
<td>Skylark, <em>Alauda arvensis</em></td>
<td>2 Chased, 1 Not chased</td>
<td>Some</td>
</tr>
<tr>
<td>Starling, <em>Sturnus vulgaris</em></td>
<td>– Not chased</td>
<td>No</td>
</tr>
<tr>
<td>House sparrow, <em>Passer domesticus</em></td>
<td>1 Chased, * No Not chased</td>
<td>No</td>
</tr>
<tr>
<td>Linnet, <em>Acanthis cannabina</em></td>
<td>1 Chased, 15 Not chased</td>
<td>No</td>
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<tr>
<td>Mistle thrush, <em>Turdus viscivorus</em></td>
<td>– Not chased</td>
<td>No</td>
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<tr>
<td>Black-headed gull, <em>Larus ridibundus</em></td>
<td>– Not chased</td>
<td>No</td>
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<tr>
<td>Dunlin, <em>Calidris alpina</em></td>
<td>– Not chased</td>
<td>No</td>
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* Numerous occasions.

Although conspecifics present the gravest threat of food depletion, the pied wagtail's winter diet overlaps with that of other species as well. Table 3 shows, in a qualitative way, that diet overlap is a good predictor of interspecific territoriality in the pied wagtail. Owners were just as vigorous in their eviction of grey wagtails and meadow pipits as they were with conspecifics. On one occasion a meadow pipit was chased so relentlessly over the river that it fell into the water and floated downstream for several seconds before it managed to take off and escape!

It was possible to quantify in a more rigorous way the effect of other species by seeing whether the owner's feeding rate was depressed if an individual of another species was

![Fig. 7](image)

**Fig. 7.** The influence of recent visits to stretches of the territory by (a) grey wagtails and (b) linnets on the feeding rate of the pied wagtail territory owner. The owner's feeding rate is influenced by visits to the territory by grey wagtails (a), Spearman rank correlation coefficient, $r_s = 0.706, P < 0.01$, but not by linnets (b), $r_s = -0.079$, NS. As predicted, owners chase out grey wagtails from their territories, but not linnets (see Table 3).
a recent visitor to a stretch of the territory. We did this for two species that also frequented the river bank. Grey wagtails are insectivorous, have a depressive effect on the pied wagtail’s feeding rate and therefore, as expected, they are evicted. Linnets, on the other hand, eat seeds, have no depressive effect, and are tolerated (Fig. 7).

![Graph showing movements of territory owners](image)

**Fig. 8.** An example of an all-day watch on the movements of one owner round its territory. The territory is represented as one long stretch at the top of the figure: in reality it consists of two banks on either side of the river. The entire territory was marked by pegs at 10 m intervals and the position of the owner was recorded throughout the day except for a short gap at lunch time. Solid lines represent feeding and dashed lines, flights round the territory.

**Systematic search**

A second way of increasing feeding efficiency was that, like other species that exploit a renewing food supply (Gill & Wolf 1977; Kamil 1978; Bibby & Green 1980), pied wagtail owners fed round their territories systematically. Typically, an owner would spend most of the day circuiting regularly around its territory. Sometimes, if there were no interruptions from intruders, an owner would walk up one bank of the river to its territory boundary, fly across the river and then proceed back down the other side again, thus
completing a perfect circuit of about 600 m. Usually, however, there were interruptions by intruders or an owner would break its circuit to fly over to feed on the other bank. Figure 8 gives an example of an all-day continuous watch of a territory owner. Although there are a few rapid revisits to the same part of the territory, in general it is clear that there is systematic foraging. By feeding in this regular way, owners increase the time allowed for resource renewal to occur between successive visits to the same stretch.

Obeying boundaries with neighbours

Neighbouring owners displayed to each other at their territory boundaries. These boundaries were strictly obeyed and even if the neighbour was not in the vicinity, an owner would rarely cross over to feed in the next door territory, (Fig. 9). The pattern

![Image](image_url)

**Fig. 9.** Neighbouring territory owners obey their territory boundaries and rarely trespass next door. Examples from two pairs of neighbours showing the number of visits made by each bird to a stretch of the river bank on either side of its territory boundary.

of systematic search and the eviction of intruders meant that owners could exploit their own territories more efficiently than that of a neighbour. On its own territory, a wagtail enjoyed a good feeding rate because it allowed long times for resource renewal between successive visits to a patch. However, whenever it trespassed next door, even if not detected, it had a lower feeding rate by virtue of the fact that it often visited stretches that had recently been depleted by the neighbour.

Table 4 shows observations on two neighbouring territories. Both the owners did better on their own territories than when they trespassed next door. The strict obedience of boundaries occurs because it is not profitable to trespass onto an occupied stretch, where the time since the last visit is unknown.

The profitability of territories to intruders

By the same argument, intruders onto territories have a lower feeding rate than owners because, even if they do land undetected, they often feed over stretches that, unknown
TABLE 4. The return times (time since the stretch was last depleted) and feeding rates of two neighbouring pied Wagtails on their own territories and when trespassing on that of the other owner. Means and standard errors, with sample sizes in brackets. Significance levels for Mann Whitney U-test, 2-tailed

<table>
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<th>Return time (min)</th>
<th>Feeding rates (items per min)</th>
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<tr>
<td></td>
<td>Territory A</td>
<td>Territory B</td>
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<tr>
<td>Owner A</td>
<td>22.6 ± 2.2 (33)</td>
<td>10.2 ± 2.5 (15)</td>
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<tr>
<td>Owner B</td>
<td>19.0 ± 5.3 (4)</td>
<td>44.6 ± 7.7 (10)</td>
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<tr>
<td>Owner A</td>
<td>17.7 ± 1.0 (39)</td>
<td>9.7 ± 1.4 (17)</td>
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<tr>
<td>Owner B</td>
<td>12.2 ± 0.8 (3)</td>
<td>22.8 ± 1.9 (30)</td>
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This data is from one day, when owner A and owner B were each observed both on their own territories and trespassing on the other’s territory. Owner A had a satellite while owner B was alone.

to them, have recently been depleted by the owner (Table 5). As emphasized earlier (Fig. 4), the feeding rate of an intruder follows the same curve with time since depletion as that of the owner. Therefore intruders are not doing worse because they are less efficient at foraging, or spending time looking out for the owner, etc. They do worse simply because they do not know where the recently depleted stretches are on the territory.

Therefore by exploiting its territory systematically, an owner can make it unprofitable for intruders to land. The most profitable place is just in front of the owner, where the time since the last depletion is greatest. However, any intruder that lands just in front of the owner is easily spotted and evicted (Fig. 6). If an intruder lands far away from an owner it can avoid detection but will be feeding over a less profitable stretch. This may explain why intruders often call loudly ‘chis-ick’ when flying over or landing on a territory. In effect, they may be asking whether the territory is occupied. If it is, the owner will always reply with a territorial call ‘chee-wee’ (Davies 1981). The sign that a territory is occupied signals that it is unprofitable. We call this type of defence, where an owner deters intruders by making it unprofitable for them to trespass, ‘defence by depletion’. In Fig. 10 we have analysed all occasions where an intruder landed on a territory and then left of its own accord. Intruders only persist in their trespass if they can attain a good feeding rate. If they experience a low rate, for example because they are feeding over depleted stretches, then they may leave of their own accord after a few minutes.

This system of defence by depletion suggests a different explanation for the decrease of ‘detection’ of an intruder with increasing distance from the owner (Fig. 6). Perhaps

TABLE 5. Comparison of the feeding rates and return times (time since the stretch was last depleted) of territory owners and intruders. Data from eight territories. Means and standard errors. Significance level for a 2-tailed Wilcoxon matched pairs test for 21 days data when owners were alone on their territories

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<th>Feeding rate (items per min)</th>
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<tr>
<td>Owner</td>
<td>40.4 ± 2.9</td>
<td>18.0 ± 2.7</td>
</tr>
<tr>
<td>Intruder</td>
<td>20.2 ± 4.0</td>
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<td>(P &lt; 0.01)</td>
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</tbody>
</table>
the owner is able to detect intruders wherever they land on the territory, but does not bother to evict intruders that land at a distance because these are feeding over depleted stretches and will leave of their own accord anyway! This is a possible explanation, but it cannot explain the difference between the reaction to adult and juvenile intruders with distance (Fig. 6). In addition, the profitability of trespassing at different distances from the owner varies depending on the direction in which the owner is walking. A stretch just in front of the owner is profitable, but one the same distance behind is unprofitable because it has just been depleted. The fact that owners always chase intruders who land nearby suggests that the best explanation of Fig. 6 is still the difficulty of detection at long distances. Even if intruders land in recently depleted patches, and find it unprofitable to persist in their trespass, they may still deplete the stretch even further and thus reduce the owner’s feeding rate.

THE COSTS AND BENEFITS OF SATELLITES

We are now in a position to describe the costs and benefits to an owner of allowing a satellite to settle on its territory. We will quantify the costs and benefits and then use a model to analyse how these combine to influence the owner’s feeding rate.

Observations were made for a total of 42 days (data from eight territories); on sixteen of the days an owner allowed a satellite to stay on its territory while on the other 26 days it remained alone and evicted any bird that landed. For each day the relationship between feeding rate and return time was plotted, using the observed natural variation in return times (see Fig. 3 for examples). The owner’s feeding rate, $F$, at a given spot can be represented as an exponential function of the time since the patch was last depleted (the return time, $R$). If there are no intruders then $R$ will be the time since the owner itself last visited the patch. Thus

$$F = k(1 - e^{-br})$$

(1)
where $k$ and $b$ are fitted parameters for each day that characterize the food abundance on the territory and how rapidly it renews after depletion (see Fig. 3). This equation will be approximately true if items renew exponentially (see Appendix) and handling time is negligible. The asymptotic feeding rate ($k$) in our constructed curves for each day is well below the upper limit imposed by handling time. The maximum rate observed when food was abundant in the spring, and territorial boundaries had broken down, was 100 items per min, over twice the maximum $k$ value we observed when the birds were territorial. This suggests that handling time may be as small as 0.01 min per item.

**The costs of a satellite**

We assume a ‘steady state’ in which $R$ is the same for every point on the circuit. When the owner was alone on its territory $R$ was $40.4 \pm 2.9$ min ($n = 89$). When the territory was shared with a satellite, $R$ for the owner was $23.2 \pm 2.3$ min ($n = 47$) and for the satellite, $19.7 \pm 1.8$ min ($n = 44$). Therefore sharing the territory resulted in halving the return time (Fig. 11). On 4 days the owner and satellite spent most of their time in different halves of the territory, while on 12 days they both circuited round the whole territory, in effect one being half a circuit behind the other. As we would predict from the fact that the owner and satellite achieved the same return time when the territory was shared, their feeding rates were also the same (owner $19.8 \pm 1.4$, satellite $18.7 \pm 1.6$ items per min, Wilcoxon matched pairs test, 2-tailed, for 16 days, NS).

---

**Fig. 11.** The frequency distribution of return times for owners that are alone on their territories (a), owners when they share the territory with a satellite (b) and satellites (c). Sharing the territory results in halving of the return time.
The benefits of a satellite

Although satellites imposed the cost of a halving of the owner’s return time, they also brought a benefit because they helped defend the territory against intruders (Table 6). On three of the territories the satellites did about half of the defence while on four territories they did about a third of the defence. Satellites appeared to be just as vigorous in their eviction of intruders as were the owners. On one occasion while the owner was displaying to a neighbour, an intruder landed and the satellite flew over, evicted it, and then joined the owner in displaying to the neighbour.

Table 7 presents the data for those territories where the satellite did only about a third of the defence. It shows that intruders tended to land equidistant from the owner and the satellite. When they did so, or when they landed nearer to the owner, then the owner chased them off. When intruders landed nearer the satellite, the satellite usually evicted them.

When both owner and satellite were defending, an intruder was less likely to land on the territory undetected (Table 8). However, if it did manage to land on the territory, then

<table>
<thead>
<tr>
<th>Territory</th>
<th>No. defences by Owner</th>
<th>Satellite</th>
<th>Percent defences by satellite</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>13</td>
<td>5</td>
<td>27.8</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>1</td>
<td>33.3</td>
</tr>
<tr>
<td>4</td>
<td>8</td>
<td>2</td>
<td>20.0</td>
</tr>
<tr>
<td>5</td>
<td>6</td>
<td>6</td>
<td>50.0</td>
</tr>
<tr>
<td>7</td>
<td>44</td>
<td>22</td>
<td>33.3</td>
</tr>
<tr>
<td>8</td>
<td>8</td>
<td>7</td>
<td>46.7</td>
</tr>
<tr>
<td>9</td>
<td>13</td>
<td>15</td>
<td>53.6</td>
</tr>
<tr>
<td>Total</td>
<td>94</td>
<td>58</td>
<td>38.1</td>
</tr>
</tbody>
</table>

Table 7. The influence of where the intruder lands on the territory on whether it is evicted by the owner or the satellite. Data from territories 1, 2, 4 and 7 where the satellite did less than half of the defence

<table>
<thead>
<tr>
<th>Intruder lands</th>
<th>No. occasions intruder chased by</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Owner</td>
<td>Satellite</td>
</tr>
<tr>
<td>Equi-distant from owner and satellite</td>
<td>12</td>
<td>–</td>
</tr>
<tr>
<td>Nearer owner</td>
<td>3</td>
<td>–</td>
</tr>
<tr>
<td>Nearer satellite</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td>16</td>
<td>6</td>
</tr>
</tbody>
</table>

Table 8. Intrusions onto territories on days that the owner is defending alone compared with days that both the owner and a satellite are defending. Data from seven territories

<table>
<thead>
<tr>
<th>No. occasions:</th>
<th>Owner defending alone</th>
<th>Owner with a satellite</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intruder spotted immediately</td>
<td>97</td>
<td>39</td>
</tr>
<tr>
<td>Intruder lands on territory undetected</td>
<td>66</td>
<td>7</td>
</tr>
<tr>
<td>Prob. intruder spotted immediately</td>
<td>0.595</td>
<td>0.848</td>
</tr>
<tr>
<td>Time (min) undetected intruders trespass before evicted</td>
<td>7.3 ± 1.2</td>
<td>6.7 ± 1.1</td>
</tr>
<tr>
<td>(mean ± standard error)</td>
<td>(17)</td>
<td>(16)</td>
</tr>
</tbody>
</table>
it trespassed for the same length of time on the days that the owner had a satellite as when the owner was alone (Table 8).

The owner's dilemma

The owner's dilemma is whether to allow a satellite onto the territory. If it does so, it will enjoy the benefits of help with territory defence but suffer the cost of having to visit stretches after a renewal time of only half that which it would achieve if it was alone.

As we indicated earlier, there were great day to day variations in the amount of food available on the territory. There were corresponding variations in intruder pressure. The rate of intrusions onto the territory increased with the food abundance and was a straight line function of $k$, the asymptotic feeding rate (Fig. 12). Qualitatively, it can be seen that the owner will probably benefit most from the presence of a satellite when food is abundant on its territory. Under these conditions there are a lot of intruders and help with defence may be beneficial while, because food is abundant, the costs of a halving of the return time may not be too great. On the other hand the owner might do better alone on days when food is scarce because halving the return time may drastically reduce its feeding rate whereas, because intruder pressure is low, help with territory defence may not be of much benefit.

To quantify the situation we need to calculate how the cost of reducing $R$ by a half, and the benefit of reducing the defence costs, affect the owner's feeding rate on days of various levels of food abundance. The costs of a satellite can simply be represented as a halving of $R$ in eqn (1). To calculate the benefits of help with defence we first have to quantify intruder costs.

**Quantification of intruder damage**

We will represent intruder costs as time spent that cannot be devoted to feeding. Each intrusion inflicts a time cost and thus reduces the owner's feeding rate. There were three sources of time cost from intrusions.
(a) The time taken to chase each intruder away was about 1 min (mean time per intrusion from 31 days data = 0·9 ± 0·2 min).

(b) Intruders were often pursued for several hundred metres away from the territory. On returning to the river edge to resume feeding, after each intrusion, the owner was displaced 55·6 ± 8·4 m \((n = 50)\). We assume that on half of these occasions the owner was displaced forwards on its circuit round the territory and suffered no reduction in feeding rate. On the other half of the occasions the result of the displacement was that the owner retraced its steps over a stretch that it had just depleted before the chase. Assuming that no items were taken, the time to walk over this depleted stretch can be included as a cost of defence. With a mean walking rate of 14 m per min, this time cost is \(\frac{1}{2}(56 \div 14) = 2\) min.

(c) Not all intruders were spotted immediately; some landed unnoticed and depleted stretches of the territory. The mean time these intruders trespassed before being evicted was 6·9 ± 0·8 min \((n = 33)\). This time was the same whether the owner was alone or had a satellite (Table 8). The presence of undetected intruders often resulted in the owner visiting patches soon after they had been depleted (e.g. Fig. 5). We estimate the time cost of a depletion as follows.

An undisturbed owner feeds at a rate, \(F = k(1 - e^{-br})\) (eqn 1). When an undetected intruder feeds on the territory, the owner will spend a time, \(D\), going over a stretch which has been depleted. For simplicity assume that the renewal time is a constant, \(r\), over this stretch. Then the owner's feeding rate across it is given by, \(F_d = k(1 - e^{-br})\). We now convert \(F_d\) to a time \(x\) spent feeding at rate \(F\) and a time \(z = D - x\) not feeding. This time, \(z\), is thus the time cost of the depletion. The number of items taken during \(D\) is \(F_dD = kD(1 - e^{-br})\). Imagine all these items to be consumed in a time \(x\), so that \(D - x\) is wasted time due to the depletion. We require that the feeding rate during \(x\) equals \(F\), which means that

\[
\frac{kD(1 - e^{-br})}{x} = k(1 - e^{-br}).
\]

Therefore,

\[
x = \frac{D(1 - e^{-br})}{(1 - e^{-br})}
\]

and,

\[
D - x = z = D \left[1 - \frac{(1 - e^{-br})}{(1 - e^{-br})}\right]. \quad (2)
\]

A similar argument for the case where the territory is shared with a satellite leads to,

\[
z_s = D \left[1 - \frac{(1 - e^{-br})}{(1 - e^{-br/2})}\right]. \quad (3)
\]

The return time by the owner and satellite to stretches depleted by undetected intruders, \(r\), was 10·1 ± 2·6 min \((n = 22)\). We assume that \(D\) is 7 min, i.e. it takes the owner the same time to walk over the stretch as that taken by the undetected intruder.

Having quantified the three sources of time cost from intrusions, we can now work out the average cost per intrusion. When the owner is alone on the territory, 59·5%
of the intruders are spotted immediately they land (Table 8). These intruders are evicted before they do any depletion damage and therefore only cost \( (a) + (b) = (1 + 2) = 3 \) min. The remaining 40·5% also inflict a depletion time cost before they are spotted and evicted and thus cost a total of \( (a) + (b) + (c) = (1 + 2) + z \) min, where \( z \) is given by eqn (2). The mean cost per intrusion when the owner is alone is therefore given by,

\[
T_o = (0.595 \times 3) + 0.405 (3 + z) \text{ min.} \tag{4}
\]

When a satellite is present on the territory, the cost per intrusion is less because a greater proportion of the intruders are spotted before they do any depletion damage. Of the intruders 84·8% are spotted immediately they land (Table 8) and cost \( (a) + (b) = 3 \) min, while the remaining 15·2% also inflict a depletion cost, and cost a total of \( (a) + (b) + (c) = 3 + z_s \) min, where \( z_s \) is given by eqn (3). On days when an owner shares its territory with a satellite, the mean time cost per intrusion is therefore given by,

\[
T_s = (0.848 \times 3) + 0.152 (3 + z_s) \text{ min.} \tag{5}
\]

A model for the owner’s dilemma

Equation (1) gives the number of items obtained by the owner in 1 min of uninterrupted foraging. Because of the defence costs described above, however, the whole minute cannot be devoted to foraging and the feeding rate will therefore be less than this. The time cost per min is the number of intrusions per min, \( N(k) \) (see Fig. 12), multiplied by the time per intrusion, \( T \). When the owner is alone its feeding rate is,

\[
F_o = [1 - T_o \cdot N(k)] \cdot k(1 - e^{-br}). \tag{6}
\]

When the owner associates with a satellite the return time, \( R \), is halved, but defence costs are also reduced. The simplest case to model is when the satellite does half of the defence, where the owner’s feeding rate will be

\[
F_s = [1 - \frac{1}{2} \cdot T_s \cdot N(k)] \cdot k(1 - e^{-br/2}). \tag{7}
\]

If the satellite only does a third of the defence, then the owner must do two-thirds, so we subtract two thirds of the defence time from the left hand part of the expression in eqn (7). However \( T_s \) will also change. If the owner does two thirds of the defence then it will incur two thirds of the chase costs (cost a) and two thirds of the ‘interrupt circuit’ costs (cost b), but it will still only suffer a half of the depletion costs (cost c). This is because if intruders land equidistant from the owner and the satellite (Table 7), half of the depletions will affect the owner and half will affect the satellite. In other words, on half of the occasions the owner will be the next bird to walk over the depleted stretch and on half it will be the satellite. If we make these assumptions it is then easy to recalculate \( T_s \) for when the owner does two-thirds of the defence and predict the owner’s feeding rate from eqn (7), using the value of two-thirds the time costs instead of a half.

Testing the model

For each of the 42 days’ data we used eqns (6) and (7) to predict the feeding rates that the owner would achieve either by being alone or by allowing a satellite to reside on the territory. The values of the parameters used in the model were: \( R = 40, N(k) = 0.00325k - 0.0221 \) (from the regression equation in Fig. 12), \( T_o \) and \( T_s \) calculated from eqns (4) and (5), and \( b \) and \( k \) were the fitted values for the curves of feeding rate \( v \). return time on each day (see Fig. 3 for examples).
On some days the model predicted that owners would achieve a higher feeding rate by being alone. On other days it predicted that they would do better with a satellite. In Fig. 13 we have plotted two curves. These curves are drawn through the values of \( b \) and \( k \) at which owners should switch their behaviour to maximize their own feeding rate. One curve is the predicted switch if the satellite does half of the defence and the other is the predicted switch if it only does one third of the defence.

In Fig. 13 we have also plotted the values of \( b \) and \( k \) from our 42 days’ data and indicated whether the owner was alone or associated with a satellite. If the model assumes that the satellite does half of the defence, as was the case on three territories (Table 4), then the owner’s behaviour was as predicted on 23 out of 25 days that it was alone and 11 out of 15 days that it was with a satellite, with two points falling on the switching line. Thus a total of 34 days was correctly predicted.

When the model assumes that the satellite only does a third of the defence, as was the case on four territories (Table 4), the predicted switching line moves up and to the right. With the satellite helping less, it pays the owner to remain alone for a greater range of food abundance (Fig. 13). Now, 24 out of 26 days that the owner was alone are correctly predicted but only 9 out of the 15 days that the owner had a satellite, with one point falling on the switching line.

The feeding rates predicted by eqns (6) and (7) (assuming the satellite does half of the defence) differed by a factor of up to 1.33. Therefore by showing switches in behaviour from defending the territory alone to associating with a satellite, owners increased their own feeding rate by up to 33%.
Figure 13 just gives a crude measure of the owner’s behaviour in terms of whether it did or did not have a satellite. A more sensitive measure of the association is to score the amount of aggression shown by the owner towards a satellite and the exact percentage of the day that the satellite spent on the territory. Figure 14(a) shows that aggression towards the satellite was greatest when the model predicted that the owner would have a higher feeding rate by remaining alone. The result of frequent chases by the owner was that the satellite left the territory (Fig. 14(b)). Aggression decreased to a very low level under the conditions that the model predicted owners would do better by tolerating a satellite.

![Graphs showing aggression towards satellites](image)

**Fig. 14.** Owners show greater aggression towards satellites on days when their predicted feeding rate alone (eqn (6)) is greater than that predicted if they associate with the satellite (eqn (7)). On days when they would do better with the satellite present, they show little aggression (a). The result of increased aggression toward a satellite is that it leaves the territory (b).

**DISCUSSION**

*The weakness of the model*

We recognize that our model makes some great simplifications. It seems likely that there are also long-term costs and benefits involved in the owner-satellite association. For example, on one territory the owner disappeared after a cold spell of weather and the satellite then took over the whole territory for the rest of the winter. Therefore one of the benefits of being a satellite is the possibility of becoming the territory owner one day (see also Woolfenden & Fitzpatrick 1978; Wells 1977; Fellers 1979). Conversely, from the owner's point of view, one of the costs of accepting a satellite may be the risk of having the territory taken over by another bird. Perhaps this is why owners only accept females and juveniles as satellites. Females are smaller than males (Zahavi 1971; M. Hollands in prep.) and they, and juveniles which are presumably less efficient competitors, may be easier to evict if the owner decides to occupy the territory alone.

Feeding efficiency may not be the only short-term factor involved in the decision of whether to accept a satellite. The only occasion that a wagtail was seen to be attacked by a predator was when a territory owner was calling loudly while evicting an intruder: a sparrowhawk (*Accipiter nisus*), perhaps attracted by the display and calling, got within a metre of the wagtail which just managed to escape after some erratic manoeuvres.
over the river. If territory defence increases predation risk, then perhaps acceptance of a satellite is advantageous when intruder pressure is high in order to decrease this risk for the owner. Numerous other possible costs and benefits of associating with a satellite could be suggested.

The weakness in our approach is that we have not been able to quantify how these other factors, such as long-term costs and predator risk, will influence the position of the switching line in Fig. 13. It is likely that many factors, including food abundance and predator pressure, will influence social behaviour (Caraco, Martin & Pulliam 1980). This presents us with the difficult problem of how to combine these various selective pressures into some common currency so that we can predict the optimal behaviour assuming both feeding efficiency and predator avoidance, for example, determine the wagtail’s behaviour.

In our model, which just considers feeding efficiency, we have assumed that the common currency for the wagtail’s activities is time. We have treated time spent feeding over a depleted stretch and time spent chasing an intruder as equivalent time costs. If chasing was much more costly, for example in energetic terms, then using time as the common currency would lead to errors. More sophisticated models would take into account these different costs of different activities. Because the wagtail uses similar movements, namely running and flying, for both feeding and defence we think that time will be a reasonable measure of costs.

Conclusions from the model

Despite these problems, the fact that our model is reasonably successful in predicting changes in the wagtail’s behaviour suggests to us that it at least captures the essence of the territory owner’s dilemma. We have assumed that natural selection has resulted in efficient wagtails and, based upon this assumption, we have developed a model that predicts the optimal behaviour for one particular currency, namely daily feeding rate. If the model works, then our conclusion is that we have got the currency right. Optimality models have also been useful in studying decision making in other contexts (Krebs & Parker 1978; Pyke 1979).

We conclude that territory owning wagtails vary their tolerance of satellites so as to maximize their own daily feeding rate. Under the conditions that an owner tolerates a satellite, the owner enjoys an increased feeding rate because the benefits gained through help with defence outweigh the costs incurred through having to share the food supply with another bird. When the owner would have a higher feeding rate by being alone then it evicts the satellite from the territory.

We do not know how the wagtails achieve the predicted switch in behaviour. We are not suggesting that they actually assess all the factors that we have included in the model (e.g. intruder costs, rate of resource renewal, etc.) and then work out from eqns (6) and (7) whether they would have a higher feeding rate alone or with a satellite! It seems more likely that they use some simple rule that results in the optimal solution. For example insect abundance is probably correlated with temperature and the rate of resource renewal onto the banks may be predicted from the flow of the river or wind, and so on.

However the wagtails achieve the switch, we should not be surprised at their ability to adjust their behaviour so finely in relation to feeding efficiency. By varying their tolerance of satellites, owners can improve their own feeding rate by up to 33%. Because the wagtail must find one insect every 3 or 4 s throughout the winter’s day in order to achieve energy balance (Davies 1976, 1980) there must be strong selection pressure for
efficient behaviour. Making the correct decision may be an important determinant of whether the owner finds enough food to stay alive.

The satellite's options and group territoriality

We have approached the owner-satellite problem solely from the owner's point of view. This is because it was difficult to quantify the benefits of feeding away from the territory. Whether the satellite wants to come onto a territory must depend on how well it would do if it went elsewhere. Under certain conditions it seems likely that there will be a conflict between the owner and the satellite. Depending on feeding profitability elsewhere, there may be occasions when the owner would do better with a satellite but the satellite would do better away from the territory, and vice-versa. Therefore, because of this conflict, we would not necessarily expect all the observed behaviour of the owner to fall on the predicted sides of the switching line in Fig. 13.

This simple case where a territory is shared between two animals may help us to understand the conditions under which group territoriality has evolved (Brown 1978; Emlen 1978). It is always easy to handwave about costs and benefits, but our measurements show quantitatively that there are conditions under which it will pay an individual to share its territory. As food abundance increases further, then sharing with several other individuals may become profitable. The point at which it will benefit a territory owner to accept another individual will depend on the amount of help with defence that the other will contribute. Gaston (1978) put forward the idea of the payment principle, suggesting that subordinates may make it profitable for owners to accept them onto a territory by paying for permission to stay. Reducing the amount of defence done by the satellite wagtail shifts the position of the switching line (Fig. 13) but our data are not good enough to distinguish which line gives the best fit. The interesting possibility emerges that a satellite may adjust the amount of help it gives with defence to make it just profitable for the owner to accept it onto the territory.

Wagtail territoriality

Studies of other birds have shown that territory owners vary their territory size in relation to resource abundance (e.g. Gill & Wolf 1975). The pied wagtail, on the other hand, maintains a fixed territory size and adapts to changes in the food supply by varying its defensive behaviour. In this paper we have looked at just one of the changes in behaviour, namely whether to defend alone or with a satellite. We must emphasize that this is only one small aspect of the territorial strategy of the pied wagtail. Although the goal of short term maximization of feeding rate predicts the changes in behaviour of owners towards satellites, it is certain that long term factors must be important in determining other aspects of territoriality, such as the optimal territory size.

ACKNOWLEDGMENTS

We thank Anthony Arak, Tim Birkhead, Alan Grafen, John Krebs, John McNamara, Graham Pyke and Michael Taborsky for their comments on one earlier draft of the manuscript, and Chris Perrins and David McFarland for the facilities of the Edward Grey Institute and Animal Behaviour Research Group at Oxford.
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(Received 18 December 1979)

APPENDIX

Let $N(t)$ be the number of items at a point on the river bank as a function of the time since the last visit to the point.
Assume that items arrive at a constant rate, \( i \), and a proportion, \( w \), of the items present are washed away per unit of time.

\[
\therefore \frac{dN}{dt} = i - wN \quad (A)
\]

\[
\therefore \frac{dN}{i - wN} = dt
\]

which can be integrated to give

\[
\ln(i - wN) = \text{const.} - wt.
\]

From the initial condition \( N(0) = 0 \), \( \text{const.} = \ln i \)

\[
\therefore \ln(i - wN) = \ln i - wt
\]

\[
\therefore \frac{i - wN}{i} = e^{-wt}
\]

\[
\therefore N = \frac{i}{w} (1 - e^{-wt}). \quad (B)
\]

Equation (B) is an exponential function with initial slope \( i \) (this can be seen from eqn (A); \( dN/dt \approx i \), when \( N \) is small) and asymptote \( i/w \).