THE MATCHING LAW APPLIES TO WAGTAILS' FORAGING IN THE WILD

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Field data concerning the time budgets and foraging success of pied wagtails (*Motacilla alba yarrelli*, Gould) are reanalyzed. It is found that the data are well described by the generalized matching law, with a marked bias towards spending time on the territory. In this case matching is not the result of maximizing reward rate, but it remains possible that it results from an allocation of time that maximizes survival.

Key words: matching, maximizing, time allocation, feeding rates, natural setting, foraging, wagtails

The simplest form of the matching law (Herrnstein, 1961, 1970) states that the relative frequency of responses made to an alternative is equal to the relative frequency of reinforcement produced on that alternative. It was shown by Baum and Rachlin (1969) that relative time allocation can also match the relative frequency of reinforcement. Considering time rather than responses, the generalized matching law (Baum, 1974b) for two alternatives can be stated as

$$\frac{T_1}{T_2} = b \left(\frac{R_1}{R_2}\right)^s, \qquad (1)$$

where T_1 and T_2 = total time allocated to the two alternatives, R_1 and R_2 = total reinforcements produced on the two alternatives, and bias, b, and sensitivity, s, are constants for given conditions. Bias measures preference that is not accounted for by reinforcers obtained, and sensitivity measures the differential sensitivity of the behavior ratio to the reinforcement ratio (Baum, 1974b).

The matching law has had considerable success in describing choice in the laboratory (Baum, 1979; de Villiers, 1977). Baum (1974a) showed matching in free-ranging pigeons, but his study involved the standard operant schedules rather than an environmentally determined pattern of food availability. In this paper I reanalyze data concerning the foraging of pied wagtails (*Motacilla alba yarrelli*, Gould) under natural conditions, and show that matching occurs.

The pied wagtail is an insectivorous bird with a body mass of about 23 g. It is resident in Britain throughout the year. The data that are analyzed in this paper were collected on Port Meadow, near Oxford, England, during the winters of 1973–74 to 1978–79. Port Meadow is an area of open grassland about two miles long and half a mile wide and is bounded on the west by the river Thames. During the winter some birds defend territories along the river. These territories consist of both banks, with a total length of about 600 m (see Houston, McCleery, & Davies, 1985). Other birds feed in a flock on the meadow (for details, see Davies, 1976; Davies & Houston, 1981, 1983). Birds in the flock and birds on territories experience different patterns of food availability. The river washes food items (insects and spiders) onto its banks, so that food accumulates along a territory (Davies & Houston, 1981). As a result, the longer the time since a stretch of territory has been visited, the higher the resulting feeding rate, as is illustrated in Figure 1. Owners tend to walk a regular circuit round their territory (Davies & Houston, 1981), which should result in a constant time since a stretch of territory was visited. Yet as Figure 1 shows, there is considerable variation in return time within the day, and hence a variation in feeding rate. This variation can arise because the previous visit to the stretch was made by an intruder
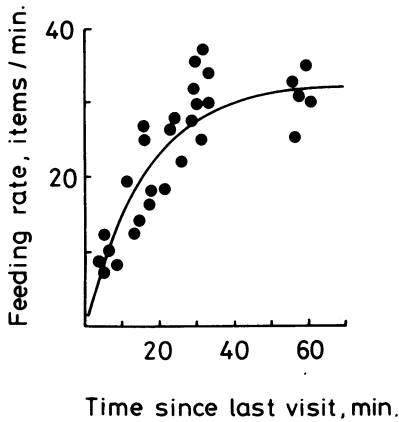
Fig. 1. Example from one day: the feeding rate along a stretch of a territory as a function of the time since the stretch was last visited (and hence depleted). The data points were obtained by measuring the feeding rate of the territory owner along a 10-m stretch of the river bank in relation to the time since that stretch was last visited by a wagtail. The curve is a fitted exponential, fitted by least-squares regression. Insect abundance, and therefore the curve of resource renewal, varied from day to day.

rather than by the owner. It can also arise because the owner chases an intruder and hence loses its place in its circuit (Davies & Houston, 1981). In the situation studied here, the feeding rate in the flock was fairly constant on any given day, and birds in the flock fed without bringing about any apparent depletion (Davies, personal communication). On days when the feeding rate was very low on a territory, the owner left for part of the day and fed in the flock. The flight to the flock took about 30 s. The items consumed in the flock and on the territory were similar (Davies & Houston, 1981).

By watching individual birds for the whole day, Davies determined their allocation of time to the territory and the flock, and the resulting numbers of food items obtained (see Davies, 1976; Davies & Houston, 1983, for the detailed data). The natural variations in food availability on territories and in the flock, and the resulting time allocation of territory owners, give a wide range of feeding rates and times spent on territory and in the flock. These data are given in Table 1. The total number of journeys between the territory and the flock was not recorded, so I have not included journey time in the analysis. As each journey was less than a minute in duration and each visit

to flock or territory lasted on the order of many minutes (Davies & Houston, 1983), the effect on time proportions of ignoring these journey times is small. To analyze the data in terms of matching, the standard procedure of taking the log (base 10) of the relevant variables was used. The resulting distribution of points is shown in Figure 2. Linear regression is not the best way to establish the functional relationship between these two variables, because they are both subject to error (Kendall & Stuart, 1973). Instead, the technique described by Bartlett (1949) is used. This indicates that the slope (s in Equation 1) is close to one but significantly different from it, and that there is a marked bias (b in Equation 1) in favor of spending time on the territory. The statistical analysis is as follows: (a) by Bartlett's (1949) technique:

$$\log_{10}\left[\frac{T_F}{T_T}\right] = 0.78 \log_{10}\left[\frac{R_F}{R_T}\right] - 0.26,$$

where T_F and T_T = time spent in flock and on territory, and R_F and R_T = reinforcers obtained in flock and on territory. Matching equation parameters are $b = 0.55$ and $s = 0.78$. In tests of significance, for all t values, degrees of freedom = 24. There is no significant departure from straight line ($t_L = 1.26$). The slope is significantly different from zero ($t_0 = 10.22$) and from one ($t_1 = 4.45$). The 90% confidence interval on slope is from 0.30 to 1.32; the 90% confidence interval on intercept is from −0.2 to −0.32. (For the data from 1977–1979, the regression equation has a slope of 0.77 and an intercept of −0.27.) (b) By ordinary linear-regression analysis:

$$\log_{10}\left[\frac{T_F}{T_T}\right] = 0.79 \log_{10}\left[\frac{R_F}{R_T}\right] - 0.26.$$
$$r^2 = .94$$

The regressions are essentially unchanged if only the data from 1977–1979 are used. The sample size of the data from 1974 is too small to permit these years to be analyzed separately. In 1974 Davies was particularly concerned with behavior in the flock; therefore, observations were made on days during which territorial birds spent most of their time in the flock.

Table 1

Data on winter foraging by territorial pied wagtails. R_F = rewards from flock feeding (over a given day); R_T = rewards from territory (over a given day); T_F = time in flock (over a given day); and T_T = time on territory (over a given day).

Date	Bird	$\dfrac{R_F}{(R_T + R_F)}$	$\dfrac{T_F}{(T_F + T_T)}$	Territory rate Items/ min	Flock rate Items/ min
15 Jan 1974	I	.98	.92	3.8	28.7
15 Jan 1974	II	.89	.69	9.8	28.7
21 Jan 1974	I	.83	.76	6.2	25.4
23 Jan 1974	I	.74	.53	8.2	21.7
25 Jan 1974	I	.80	.68	11.2	21.7
31 Jan 1974	I	.79	.57	9.5	26.3
5 Feb 1974	I	.98	.89	5.4	28.8
5 Feb 1974	II	.91	.71	7.2	28.8
7 Feb 1974	I	.72	.65	7.4	28.8
16 Nov 1977	A	.55	.49	15.7	20.0
16 Dec 1977	C	.58	.52	13.8	15.0
22 Dec 1977	C	.25	.12	11.6	26.0
9 Jan 1978	C	.08	.05	12.8	18.0
17 Jan 1978	C	.04	.03	15.4	18.0
19 Jan 1978	C	.07	.07	18.8	18.0
20 Jan 1978	C	.10	.13	19.8	18.0
16 Feb 1978	D	.06	.07	19.8	16.0
21 Feb 1978	E	.19	.18	14.6	16.0
22 Feb 1978	E	.13	.07	8.9	16.0
24 Feb 1978	E	.30	.36	15.4	13.8
21 Nov 1978	G	.11	.17	17.1	12.5
8 Jan 1979	G	.43	.34	11.3	18.1
8 Jan 1979	H	.52	.39	11.8	18.1
9 Jan 1979	G	.16	.06	8.6	18.1
10 Jan 1979	H	.55	.30	7.8	21.8
10 Jan 1979	G	.76	.50	9.5	21.8
30 Jan 1979	G	.91	.80	6.3	16.0

Fig. 2. The relationship between $\log_{10}(T_F/T_T)$ and $\log_{10}(R_F/R_T)$, where T_F is time spent in flock, T_T is time on territory, R_F is rewards from foraging in flock, and R_T is rewards from foraging on territory. The line is the matching line. Unfilled circles are data from 1974; filled circles are data from 1977–1979.

DISCUSSION

The analysis summarized above suggests that wagtails match with a bias towards being on their territory as opposed to being in the flock. Given this demonstration of matching under field conditions, it is interesting to consider why the result holds and what relationship it may have to laboratory studies.

Because the data rely on natural variation in feeding availability, it is possible that matching is an artifact, generated by an environmental correlation. The wide range of feeding rates and time allocations, together with the lack of any positive correlation between feeding rate on territory and feeding rate in the flock, argues against this possibility.
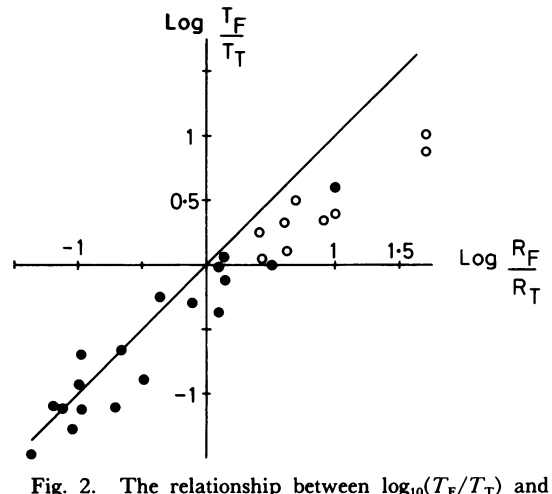
Is it possible to relate the feeding opportunities of the wagtails to conventional operant procedures? Because there is apparently no depletion of prey density, feeding in the flock resembles a ratio schedule, with the schedule parameter changing from day to day. The contingencies that operate on a territory are more complicated. The renewal illustrated in Figure 1 is somewhat similar to a variable-interval schedule, but it is operating over the whole territory with the renewal experienced by the owner being modified by the actions of other wagtails that feed on the territory. These intruders can be evicted by the owner, but this in turn disrupts the owner's pattern of movement and hence its feeding rate. The owner also has, at least in theory, the possibility of varying its walking speed and the range over which it responds to intruders (Houston et al., 1985). However, the concurrent variable-interval variable-ratio (concurrent VI VR) procedure can be considered an approximate description of the wagtails' feeding opportunities. The birds' behavior can then be compared with the behavior of pigeons reported by Herrnstein and Heyman (1979). The average time allocations of the 4 pigeons in their study showed a bias towards the interval schedule with a sensitivity close to one. Their regression equation is:

$$y = 1.036x + 0.111,$$
$$r^2 = .966$$

where $y = \log_{10}$(time on interval schedule/time on ratio schedule) and $x = \log_{10}$(reinforcements from interval schedule/reinforcements from ratio schedule). With the present notation, this means that $b = 1.29$ and $s = 1.036$. In terms of a bias towards the renewing schedule, the wagtail data have a b value of approximately 1.8. Although s in the wagtail data is significantly different from one, the 90% confidence interval includes one.

This comparison thus suggests that the matching behavior of the wagtails is qualitatively similar to that observed in the laboratory; however, it also raises another issue. Ziriax and Silberberg (1984) argue that the concurrent VI VR procedure is almost certain to produce matching over a wide range of choice ratios. This is not the place to attempt to evaluate that argument. It can be pointed out, however, that the matching shown in Figure 2 holds over a wide range of time allocations and that the contingencies that operate on a territory are more complex than those of a variable-interval schedule.

Davies and Houston (1983) showed that the wagtail's pattern of time allocation does not maximize its overall feeding rate. This failure of rate maximization is not surprising, for it can be argued that a small bird in winter should maximize its probability of surviving the winter, and this is not necessarily achieved by maximizing its rate of energetic gain (Houston & McNamara, 1985; McNamara & Houston, 1982). On some days the territories are the only possible feeding sites on the meadow. They are thus an important long-term asset for a wagtail, and the bias towards spending time on a territory may reflect this importance.

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