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SENSITIVITY TO RELATIVE REINFORCER RATE IN CONCURRENT SCHEDULES: INDEPENDENCE FROM RELATIVE AND ABSOLUTE REINFORCER DURATION

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Twelve pigeons responded on two keys under concurrent variable-interval (VI) schedules. Over several series of conditions, relative and absolute magnitudes of reinforcement were varied. Within each series, relative rate of reinforcement was varied and sensitivity of behavior ratios to reinforcer-rate ratios was assessed. When responding at both alternatives was maintained by equal-sized small reinforcers, sensitivity to variation in reinforcer-rate ratios was the same as when large reinforcers were used. This result was observed when the overall rate of reinforcement was constant over conditions, and also in another series of concurrent schedules in which one schedule was kept constant at VI 120 s. Similarly, reinforcer magnitude did not affect the rate at which response allocation approached asymptote within a condition. When reinforcer magnitudes differed between the two responses and reinforcer-rate ratios were varied, sensitivity of behavior allocation was unaffected although response bias favored the schedule that arranged the larger reinforcers. Analysis of absolute response rates on the two keys showed that this invariance of response-ratio sensitivity to reinforcement occurred despite changes in reinforcement interaction that were observed in absolute response rates on the constant VI 120-s schedule. Response rate on the constant VI 120-s schedule was inversely related to reinforcer rate on the varied key, and the strength of this relation depended on the relative magnitude of reinforcers arranged on the varied key. Independence of sensitivity to reinforcer-rate ratios from relative and absolute reinforcer magnitude is consistent with the relativity and independence assumptions of the matching law.

Key words: concurrent schedules, matching law, sensitivity to reinforcement, response bias, key peck, pigeons

In concurrent schedules of reinforcement, two response alternatives are available simultaneously and each response is maintained by its own schedule of reinforcement. Research has shown that steady-state performance in these schedules, attained after many sessions of training in a condition, is well characterized by a power function (Baum, 1974, 1979) called the generalized matching relation. This equation relates the subject's distribution of responses between schedules to relative reinforcement obtained from the two schedules. In logarithmic form,

$$\log\left(\frac{B_1}{B_2}\right) = a \log\left(\frac{R_1}{R_2}\right) + \log c.$$
 (1)

In Equation 1, *B* represents rate of responses and the subscripts 1 and 2 identify the schedules on which they occur. R represents reinforcement obtained for a response, and may be quantified in terms of reinforcer rate, reinforcer magnitude (often manipulated by varying the duration of access to food), or reinforcer immediacy (i.e., the reciprocal of the delay between a response and any reinforcer it produces). The constants a (sensitivity to reinforcement) and $\log c$ (bias favoring one response over the other) are estimated empirically from the data and may vary depending on the particular dimension of the reinforcing event that is manipulated. In the most common arrangement, the relative rate of reinforcement is varied using concurrent variable-interval (VI) schedules and equalsized immediate reinforcers of about 3-s duration. Typically, sensitivity to relative reinforcer rate has been found to fall in the range of 0.8 to 1.1 (see Baum, 1979; Davison & Mc-Carthy, 1988). Different values for *a* express the different sensitivity of behavior ratios when relative magnitude (M_1/M_2) or immediacy (I_1/I_2) of reinforcement is manipulat-

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ed. The existing data suggest that sensitivity is lower when relative magnitude is the independent variable (e.g., Schneider, 1973; Todorov, 1973; Todorov, Hanna, & Bittencourt de Sa, 1984). It is more difficult to generalize about variation of relative immediacy, although *a* is rarely lower and is often higher than when relative rate of reinforcement is varied (see Davison & McCarthy, 1988; Omino & Ito, 1993; Williams & Fantino, 1978).

In the present study, we ask whether sensitivity to reinforcer-rate ratios depends on the absolute or relative size of the reinforcers presented. We varied rates of reinforcement for two responses in several series of conditions. In each series, different magnitudes of reinforcement were used: In some series the reinforcers were both of small magnitude; in others, both were large; and in yet other series, reinforcers were large for one response and small for the other.

It is not clear how these variations in reinforcer size might affect performance. On the one hand, a commonly written extension of the matching law (Equation 2 below; Baum & Rachlin, 1969; Rachlin & Green, 1972) assumes that response ratios are affected only by *ratios* of reinforcer parameters (i.e., absolute values of reinforcer rate, magnitude, and delay are irrelevant), and that ratios of different parameters exert *independent* effects on relative responding:

$$\log\left(\frac{B_1}{B_2}\right) = a_r \log\left(\frac{R_1}{R_2}\right) + a_m \log\left(\frac{M_1}{M_2}\right) + a_i \log\left(\frac{I_1}{I_2}\right) + \log c.$$
(2)

In Equation 2, the effects of varying (say) reinforcer-magnitude ratios are captured by the parameter a_m and should not modulate the effects of other reinforcer ratios (independence). Further, only relative values of any reinforcement parameter are represented (relativity). Therefore, Equation 2 predicts no effect of our variations in absolute or relative reinforcer magnitude on sensitivity to reinforcer-rate ratios, a_r

In contrast, a number of studies have shown failures of both relativity and independence. Research on human preference suggests that when choice outcomes are similar on one dimension, sensitivity of preference to

outcome differences on another dimension is enhanced (Mellers & Biagini, 1994), suggesting nonindependence. In the terms of the matching law, several researchers have reported that sensitivity to reinforcement ratios measured on one dimension depends upon absolute values on the same reinforcement dimension (a failure of the relativity assumption), upon relative values on another dimension, or upon absolute values on other reinforcer dimensions (failures of both relativity and independence). Alsop and Elliffe (1988) and Logue and Chavarro (1987) varied absolute and relative reinforcer rate and found diverse changes in sensitivity to reinforcer ratios, depending on how the absolute values of reinforcers at the two alternatives were varied: Sensitivity to rate increased when overall absolute rate of reinforcement was increased but decreased when absolute magnitude or immediacy of reinforcement was increased. Davison (1988) varied the absolute rates of reinforcement for two concurrent operants, keeping them equal for the two alternatives while varying their relative magnitudes. Sensitivity to relative magnitude of reinforcement decreased as reinforcer rates increased (in Equation 2, a_m depended on absolute reinforcer rates R_1 and R_2). Sensitivity to relative immediacy of reinforcement also shows dependence on rate of reinforcement, but the changes are in the opposite direction, increasing with the rate of reinforcement (e.g., Fantino, 1969; Fantino & Davison, 1983; Grace, 1994).

These changes in sensitivity challenge the generalized matching relation, and the diverse directions of change suggest that a whole new characterization of performance in choice situations may be needed. As Davison (1988) suggested and Davison and Nevin (1999) reiterated, future theoretical developments may not be forthcoming until a more complete catalogue of interactions among various parameters of reinforcement is available. In particular, Davison noted that no information exists about the effects of overall reinforcer size on sensitivity to relative reinforcer rate, and Davison and Nevin noted that data concerning the effects of relative reinforcer magnitude on sensitivity to relative reinforcer rate are sparse. The present study continues the investigation of interaction among reinforcement parameters by asking

whether sensitivity to ratios of reinforcer rates is dependent on the absolute and relative magnitudes of reinforcers.

METHOD

Subjects

Twelve homing pigeons, with varied experimental histories, were maintained at 80% to 85% of their free-feeding body weights. Water and grit were always available in their living cages, where supplementary feed of mixed grain was given roughly 3 hr after experimental sessions to maintain prescribed weights.

Apparatus

Four similar experimental chambers, measuring approximately 32 cm by 34 cm by 34 cm, each contained an interface panel on which were mounted three keys and a hopper containing wheat. Keys were 21 cm from the grid floor and 9 cm apart, and the hopper was centered in the panel and 6 cm from the floor. Only the side keys were used in the experiment. Pecks on either of the keys that exceeded about 0.15 N produced a 0.05-s blink of the green lamp behind the key and a relay click. During reinforcement, the hopper was raised and illuminated white. An exhaust fan in the chamber helped to mask extraneous sounds. All experimental events were scheduled and recorded by on-line computers located in another room. In Part 1, a PDP-11® computer was used with custom interfacing and software. In Parts 2 and 3, an IBM-compatible computer with MED Associates interfacing and software was used.

Procedure

Birds were always trained in the chamber assigned to them at the beginning of experimentation, and experimental sessions lasted 40 to 45 min throughout. Responses on the two side keys were reinforced according to independent variable-interval (VI) schedules formed from 12 randomized intervals taken from the Fleshler and Hoffman (1962) progression. Intervals were sampled from the schedule without replacement and in an irregular order. Any response that directly followed a peck on the other key (i.e., a changeover) was not reinforced and started a changeover delay of 2.5 s in Part 1 and 3 s in Parts 2 and 3, during which no responses were reinforced, and which was reset if another changeover occurred.

Table 1 gives the schedule combinations used in the experiment and the orders in which they were conducted for each subject. There were three parts to the experiment, each using 4 subjects. In Part 1, Birds B1 through B4 were trained in two series of conditions: one in which reinforcers were 1.5-s access to wheat and another in which they were 5-s access. These reinforcer magnitudes were always equal for the two response alternatives. Over conditions within each series, ratios of reinforcer rates on the two alternatives were varied, keeping the overall rate of reinforcement approximately constant. The range of VI schedules used was the same for each series.

In Part 2, Birds A1 through A4 were trained in three series of concurrent VI VI schedules. Within each series, the VI schedule in effect on the left key was varied over conditions while that on the right key was always VI 120 s. In one series, reinforcers from both keys were 2 s long, in another the varied schedule arranged 2-s reinforcers while the constant schedule arranged 6-s ones, and in the remaining series both schedules arranged 6-s reinforcers. Again, the range of VI schedules used over conditions was the same in all three series. An error by the experimenters during Part 2 resulted in Bird A2 not being trained in Condition 2 and being trained twice in Condition 1. This error could not be remedied because it was not detected until after Bird A2 had died.

In Part 3, Birds A11 through A14 were trained in three series of concurrent VI VI schedules. Within each series, the VI schedule in effect on the left key was varied over conditions while that on the right key remained constant at VI 120 s, as in Part 2. In one series, reinforcers from the left (varied) key were 2 s long and those from the right (constant) key were 6 s long, in another series both schedules arranged 4-s reinforcers, and in the third series the varied schedule arranged 6-s reinforcers while the constant schedule arranged 2-s ones. Again, the range of VI schedules used over conditions was the same in all three series.

Initially, training continued in each condition for at least 20 sessions and until a stabil-

Table 1

Schedule combinations used in the experiment. Schedule values and reinforcer durations are given in seconds. At the bottom of the table, condition numbers are listed for each bird in the order in which they were conducted. The numbers in parentheses next to condition numbers are the training sessions given to the subject to that condition, and asterisks indicate conditions that were abandoned because responding could not be maintained.

	VI sch	nedules	Reinforcer durations		
Condition	Left	Right	Left	Right	
Part 1 (Birds B1–F	34)				
1	30	150	1.5	1.5	
2	40	80	1.5	1.5	
3	80	40	1.5	1.5	
4	150	30	1.5	1.5	
5	30	150	5	5	
6	40	80	5	5	
7	80	40	5	5	
8	150	30	5	5	
Part 2 (Birds A1–A Series 1	A4)				
1	40	120	9	9	
9	60	120	- 9		
3	240	120	- 9		
4	480	120	2	2	
Series 2					
5	40	120	6	6	
6	60	120	6	ő	
7	240	120	6	ő	
8	480	120	6	6	
Series 3					
0	40	190	9	6	
9 10	40	120	2	6	
10	940	120	2	0	
11	480	120	2 9	6	
14 Dout 9 (Dinda A11	414)	120	4	0	
Series 1	-A14)				
1	40	120	2	6	
2	60	120	2	6	
3	120	120	2	6	
4	240	120	2	6	
5	480	120	2	6	
Series 2					
6	40	120	4	4	
7	60	120	4	4	
8	120	120	4	4	
9	240	120	4	4	
10	480	120	4	4	
Series 3					
11	40	120	6	2	
12	60	120	6	2	
13	120	120	ő	$\overline{2}$	
14	240	120	ő	$\overline{2}$	
15	480	120	ő	9	

Condition numbers in order of exposure for each subject and training sessions given in each. Part 1

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Part 2
A1 8 (35), 5 (35), 12 (35), 11 (22), 6 (29), 7 (20), 10 (20), 9 (30), 4 (35), 1 (35), 3 (25), 2 (25)
A2 12 (22), 9 (25), 8 (28), 5 (35), 10 (35), 7 (26), 6 (22), 11 (35), 8 (35), 9 (35), 4 (33), 1 (20), 3 (35), 1 (35)
A3 9 (35), 8 (31), 5 (35), 12 (21), 11 (35), 6 (24), 7 (35), 10 (22), 4 (35), 2 (23), 3 (35), 1 (23), 3 (35)
A4 12 (22), 5 (35), 8 (35), 9 (20), 10 (24), 7 (32), 6 (23), 11 (32), 1 (26), 3 (35), 4 (28), 2 (31), 11 (25), 12 (21)
Part 3
A11 3 (30), 1 (48), 5 (30), 11 (43), 15 (35), 2 (30), 14 (42), 12 (33), 4 (31), 13 (57), 8 (34), 6 (30), 9 (33), 7 (32),
10 (30)
A12 3 (30), 5 (41), 1 (31), 15 (31), 11 (44), 4 (30), 12 (35), 14 (39), 2 (31), 13 (68), 8 (34), 9 (32), 6 (32), 10
(30), 7 (30)
A13 3 (30), 11 (34), 15 (61), 1 (30), 5 (30), 12 (47), 14 (48), 2 (30), 4 (46), 13 (76), 8 (35), 7 (30), 10 (41), 6
(41), 9 (31)
A14 3 (30), 15 (50), 11 (34), 5 (30), 1 (30), 14 (58), 12 (34), 4 (30), 2 (46), 13 (57), 8 (34), 10 (41), 7 (31), 10
(41), 6 (30), 9 (30)

ity criterion, which required minimal sessionto-session variability, was met. The criterion was that for five consecutive sessions, the proportion of responses that occurred on the left key did not deviate from the mean proportion over those five sessions by more than .025. However, this proved to be too stringent; for example, after 50 sessions in Part 1 Bird B1 had not attained stability in its first condition, and we decided to use data from the last 10 of 35 training sessions in any condition in which the criterion was not satisfied. This was adopted from that point on except that in two cases training was interrupted by a 2.5-month break, and we adopted the further requirement that at least 20 sessions were conducted after the break. In conditions in which the stability criterion was met, data for the condition were taken from the five sessions in which it was satisfied. In cases in which the criterion was not met, the performances in the last 10 sessions (of the 35) were used, to minimize the effects of sessionto-session variability in responding while at the same time representing the level of performance attained after extended training. In Part 3, we used data from Sessions 21 through 30 to characterize performance in each condition. The possible impact of these data-selection methods on our results was assessed through post hoc analyses described below.

RESULTS

Response and reinforcer rates in each of the last five or ten sessions in each condition (depending on whether or not our stability criterion was met) were calculated by dividing the number of events by a time base (session duration less time occupied by reinforcement). These rates were averaged over sessions for each bird to give steady-state performances in the condition. These mean response rates and reinforcer rates, with their standard deviations, are given in the Appendix. We were unable to obtain data for Birds B1 and B2 in one small-reinforcer condition (Condition 2 of Part 1) because it was impossible to maintain responding, although they responded steadily with the same reinforcer magnitude in other conditions. After two attempts in each case, this condition was abandoned. Bird B4 also failed to complete the same condition on the first attempt, but did complete it on a second attempt. Part 2 was conducted to provide data from more subjects, and used slightly larger reinforcers than Part 1 to ensure that entire series of conditions could be completed with all subjects.

Reinforcer-Ratio Sensitivity

Figure 1 shows log response ratios plotted as a function of log reinforcer ratios for all conditions in Parts 1 and 2. In Part 1, slopes of the regression lines were steeper for conditions with small reinforcers for 3 birds, but the reverse was true for the 4th (Bird B2). In Part 2, the data points vary around the regression lines more than in Part 1, but similar disagreement occurred across birds: The regression-line slope was steeper with smaller reinforcers for Bird A3, the reverse was true for Bird A2, and the slopes were nearly the same for the remaining 2 birds. Thus, overall,



Fig. 1. Log response ratios plotted as a function of log reinforcer-rate ratios in conditions with equal-sized reinforcers on the two keys in Parts 1 (upper row) and 2 (middle row), and in conditions with unequal-sized reinforcers on the two keys in Part 2 (bottom row). The solid lines are least squares regression lines, and their slopes and intercepts (with their standard errors in parentheses) are given in the panels. In the upper two rows the open symbols give the data obtained using small reinforcers, for which regression parameters are given in the upper left of the panel, and filled symbols give the data obtained using large reinforcers and the related regression parameters are at the bottom of the panel. The origin is marked by a cross.

results from Parts 1 and 2 indicate that sensitivity to ratios of reinforcer rates did not vary systematically with changes in reinforcer magnitude. The lowest row in Figure 1 gives data from conditions in Part 2 in which unequal-sized reinforcers were used on the two keys and the rate of small (2-s) reinforcers was varied over conditions. The data were variable for Birds A2 and A4. Sensitivities were lower than those obtained with equal small reinforcers for all 4 subjects (although the difference was modest for Bird A3). They were also lower than those observed with equal 6-s reinforcers for 3 of the 4 subjects (the exception was Bird A3). Overall, the results suggested a possible effect of relative reinforcer magnitude on sensitivity to relative reinforcer rate, but variability was such that no strong conclusion could be reached.

Part 3 was conducted to investigate more

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fully whether sensitivity to relative reinforcer rate depends on relative reinforcer magnitude and, in particular, to assess again whether equal-sized reinforcers promote higher sensitivity than unequal-sized reinforcers, as suggested by Part 2. Figure 2 gives log ratios of response rates plotted as a function of log ratios of reinforcer rates from Part 3. The results from conditions with equal-sized reinforcers on the two schedules were not different from those in either of the unequal-sized reinforcer series. That is, sensitivity estimates shown in the center column did not differ systematically from those in the left or right columns. Similarly, varying the frequency of small reinforcers on one schedule, with a constant rate of large reinforcers on the other, produced sensitivity estimates that were not consistently different from those found when the frequency of large reinforcers with small reinforcers on the constant schedule was varied (left vs. right columns). Greater sensitivity was found for Birds A11, A12, and A14 when the varied key arranged large reinforcers, but the reverse was true for Bird A13. Overall, the data do not support the conclusion that reinforcer magnitude affects sensitivity of response ratios to reinforcer-rate ratios.

Asymptotic and Transitional Performances

Because our stability criterion proved to be too stringent and we used slightly different rules for determining asymptotic performance in each part of the experiment, we conducted several additional analyses to assess whether our findings concerning sensitivity to relative reinforcement rate were robust. For Part 1, Figure 3 shows the relative response rates obtained in all sessions in each condition. This confirms that relative response rate generally reached an asymptote in these conditions. When our stability criterion was not met (training continued for 35 sessions, and the 35th session is indicated by a filled triangle), the average of the last 10 sessions generally provides a reasonable estimate of the asymptotic performances observed. In questionable cases (B1 in Condition 1 and B3 in Condition 3) prolonged training might have produced more extreme response ratios, and slightly steeper matching lines in the small-reinforcer series. Our conclusion that sensitivity was not systematically related to absolute reinforcer magnitude

would remain, however, because both subjects already showed steeper matching lines with small reinforcers than with large ones.

Figure 3 also provides the opportunity to examine the rate at which relative response rate changes when the reinforcer-rate ratio is reversed, separately for conditions with equal (small or large) reinforcers for each schedule. The first four conditions conducted in Part 1 involved repeated transitions between concurrent VI 30-s VI 150-s and concurrent VI 150-s VI 30-s schedules (or vice versa), one with large reinforcers for both alternatives (Conditions 5 and 8) and the other with small reinforcers for both (Conditions 1 and 4), with order counterbalanced across subjects. Again, however, the size of the reinforcer had no systematic effect. Progress toward the asymptotic response allocation over the first few sessions in small-reinforcer conditions was noticeably slower than that in largereinforcer conditions for Birds B1 and B4, but not for Birds B2 and B3. A more detailed analysis, not shown here, quantified progress in each condition session by session. The difference between relative response rate in a session and the asymptotic relative response rate in the previous condition was divided by the difference between asymptote in the previous condition and the asymptote eventually reached in the current condition. This analysis showed that for Birds B2 and B3, progress in the first few sessions was actually faster in the small-reinforcer conditions than in the large-reinforcer conditions, the reverse of what is apparent for Birds B1 and B4 (Figure 3).

For Parts 2 and 3, the orders in which conditions were presented and the systematic changes in overall reinforcer rates do not support analysis of choice in transition. With regard to asymptotic performances in conditions, there were sufficient training sessions for all birds in each condition for a post hoc application of the criterion used by Davison and colleagues (e.g., Alsop & Davison, 1986). The criterion is that five times in a condition, not necessarily consecutive, the median relative response rate of five sessions must be within 0.05 of the median of the immediately preceding five sessions. When all subjects have met this criterion, conditions are changed for all subjects and data from the last five training sessions are used. Unlike



Fig. 2. Log response ratios plotted as a function of log reinforcer ratios for each series in Part 3. The origin is marked by a cross in each panel. The left column gives data from conditions with 2-s reinforcers on the varied (V) schedule and 6-s reinforcers on the constant (C) schedule, the center column gives results from conditions with 4-s reinforcers on both schedules, and the right column gives results from conditions with 6-s reinforcers on the varied schedule and 2-s reinforcers on the constant schedule. Least squares regression lines are drawn, and their slopes and intercepts (with their standard errors in parentheses) are given in each panel.

Davison's usual procedure, we exposed our subjects to conditions in different orders. Nevertheless, we were able to apply this criterion to conditions in Parts 2 and 3 of the present work, and repeat our regression analyses with data selected according to this criterion.

With very few exceptions, Davison's stability criterion confirmed that our performances were stable. To select data from a condi-

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Fig. 3. Relative response rate in each session of each condition in Part 1. The squares show the averages of the five stable sessions or the last 10 sessions, used for the analysis in Figure 1. When the stability criterion was not met, a triangle on the horizontal axis indicates the 35th session, and the squares indicate the average of Sessions 26 through 35 (except that training for Bird B4 in Condition 8 was affected by a break in experimentation; see text).

Table 2

		Davison's criterion		Last 10 sessions		
Bird	Conditions	Slope (S)	Intercept	Slope (S)	Intercept	
B1	1-4			0.96 (0.05)	-0.06	
	5-8			0.80 (0.05)	-0.02	
B2	1-4			0.78 (0.14)	0.00	
	5-8			0.86 (0.08)	-0.03	
B3	1-4			1.05(0.1)	-0.02	
	5-8			0.89 (0.05)	0.11	
B4	1-4			1.0 (0.15)	-0.04	
	5-8			1.0 (0.08)	-0.01	
A1	1-4	0.51 (0.04)	0.03	0.62 (0.05)	0.03	
	5-8	0.52(0.15)	-0.00	0.64 (0.18)	-0.04	
	9-12	0.16(0.05)	-0.40	0.11 (0.09)	-0.42	
A2	1-4	0.71 (0.08)	0.08	0.82 (0.03)	0.03	
	5-8	0.93(0.15)	-0.01	1.02(0.1)	-0.05	
	9-12	0.57(0.26)	-0.51	0.68 (0.18)	-0.51	
A3	1-4	0.67(0.07)	0.10	0.71 (0.06)	0.05	
	5-8	0.30 (0.11)	-0.22	0.49 (0.11)	-0.13	
	9-12	0.75(0.04)	-0.45	0.68 (0.09)	-0.47	
A4	1-4	0.59(0.25)	0.06	0.6 (0.18)	0.04	
	5-8	0.77(0.15)	-0.19	0.66 (0.19)	-0.16	
	9-12	0.49 (0.13)	-0.44	0.47(0.17)	-0.41	
A11	1-5	0.62(0.15)	-0.44	0.49 (0.14)	-0.48	
	6-10	0.8 (0.05)	0.08	0.91 (0.02)	0.03	
	11-15	0.7 (0.17)	0.41	0.76(0.1)	0.38	
A12	1-5	0.46(0.24)	-0.44	0.56 (0.16)	-0.43	
	6-10	0.54(0.22)	-0.02	0.6 (0.13)	-0.03	
	11-15	1.36(0.12)	0.38	1.03 (0.09)	0.32	
A13	1-5	0.72(0.09)	-0.46	0.81(0.1)	-0.47	
	6-10	0.66(0.06)	-0.05	0.73 (0.01)	-0.06	
	11-15	0.35(0.04)	0.52	0.40 (0.05)	0.5	
A14	1-5	0.71 (0.13)	-0.32	0.67 (0.13)	-0.36	
	6-10	0.72 (0.08)	0.09	0.71 (0.09)	0.08	
	11-15	0.86 (0.08)	0.38	0.63 (0.06)	0.38	

Regression analysis results for data selected using Davison's criterion of stability and using the last 10 sessions conducted. Davison's criterion could not be used in Part 1 because several conditions were changed before it was met.

tion for the regression analyses, we used the number of sessions required by the subject who was slowest to reach the criterion in that condition (on average, 22 sessions), and selected data from the last five. In Part 2, we found that all subjects had met this criterion by the time we stopped training in each condition, with the exception of Bird A2 in Condition 12. Bird A2 met our stability criterion after 20 sessions, but did not meet Davison's. For this condition, we used the last five sessions conducted for each bird. For two conditions, there were insufficient sessions conducted for 1 subject to use the session numbers dictated by the slowest bird, but one of these was met by a replication (Bird A2 in Condition 1), and the other (Bird A1 in Condition 7) fell short only one session. Table 2

gives the slopes and their standard errors and the intercepts of regression lines fitted to these data. In addition, because training often continued for many more sessions, we repeated the analyses again using data from the last 10 sessions conducted in every condition. These results are also given in Table 2. For Part 3, Bird A12 had not met Davison's stability criterion in Condition 15 after 30 sessions, when conditions were changed. In all other cases, we were able to select data according to this criterion. For Condition 15, we used the last five sessions actually conducted for all subjects. Again, Table 2 gives the resulting regression-line parameters for data selected this way, using the last 10 sessions conducted per condition.

The regression-line parameters in Table 2

show no systematic deviations from the values shown in Figures 1 and 2, confirming our main result. Using data from the last 10 sessions, we found slopes that were within ± 0.05 of the estimates shown in Figures 1 and 2 in 28 of 32 comparisons. Using Davison's criterion, the deviations from our slopes were a little greater. The average difference over 24 comparisons was almost 0.1, and pairs were within ± 0.05 of one another in only eight of these. Probably these deviations were greater because the Davison criterion was satisfied after fewer sessions than our own criterion, and performance may have been influenced more by previous conditions earlier in training. The direction of differences was not consistent, probably because of the joint variation of magnitude and rate of reinforcement. But regardless of which method is used to assess asymptotic performances, no reliable effects of relative or absolute reinforcer magnitude on sensitivity to relative reinforcement are apparent. Although there is some variation in sensitivity among conditions for some subjects, we conclude that it is not systematically related to relative or absolute reinforcer magnitude.

Absolute Response Rate

Finally, we analyzed the effects of varying the frequency of reinforcers of various sizes (in Parts 2 and 3) on absolute response rate on the two keys. Normalized response rates were calculated for each condition (response rate on each key in a condition divided by the average response rate for that key across conditions of the series) and were plotted as a function of reinforcers per hour on the varied key in logarithmic coordinates. This treatment yields roughly linear absolute responserate functions, the slopes of which quantify the contributions of response-rate changes on each key to relative reinforcement sensitivity. Least squares regression lines were fitted, and their slopes are plotted for each bird in each series in Figure 4. For response rate on the varied schedule, data from Part 2 and Part 3 show no systematic differences over the series of conditions. Thus, the function relating absolute response rate on the varied schedule to reinforcer rate on that schedule was not systematically affected by relative or absolute reinforcer magnitude.

For the constant schedule, negative slopes

in Figure 4 quantify the effect of reinforcement on one schedule over responding on the other, or reinforcement interaction (Catania, 1963). In Part 2, interaction was weak when the varied schedule arranged relatively small reinforcers and the constant schedule arranged large ones (points above 2,6 on the horizontal axis). When large reinforcers were used on both schedules (points above 6,6), interaction was stronger, as indicated by more negative slope values. There were no consistent differences in interaction between the series of conditions with equal-sized reinforcers on the two keys (cf. points above 2,2 and those above 6,6). In the lower row of Figure 4 (Part 3) the horizontal axis may be construed as a series in which the magnitude of the reinforcer on the varied schedule increased and that on the constant schedule decreased. These performances show reasonably steady increases in reinforcement interaction as the size of the reinforcer on the varied schedule was increased while the overall magnitude was kept constant. Thus, the only clear effect of reinforcer magnitude on the absolute response-rate functions was that in both Part 2 and Part 3, reinforcement interaction effects were stronger when the varied schedule arranged larger reinforcers.

DISCUSSION

The main result in the present work was that, notwithstanding some variability in estimates of sensitivity to relative reinforcer rate between series of conditions, sensitivity was independent of whether equal-sized small reinforcers or equal-sized large reinforcers were used. This result was obtained in conditions in which a constant overall rate of reinforcement was used (Part 1) and also when the overall reinforcement rate varied over conditions because one schedule was kept constant while the other was varied (Part 2). In addition, sensitivity was unaffected by unequal reinforcer magnitudes at the two concurrent alternatives. Whereas other related work has reported interactions among reinforcement parameters, our result supports the concatenated form of the generalized matching relation (Equation 2) in that it is consistent with assumptions of relativity and independence.

Although reinforcer-ratio sensitivity was un-



Fig. 4. Slopes of least squares regression lines relating log normalized response rate on each key to log reinforcer rate on the varied key in Parts 2 and 3. Filled symbols give slopes for data from the varied key, open circles give slopes for the constant key, and each point gives the slope from a different series, identified by the reinforcer durations on the horizontal axis. Error bars give the standard errors of slopes. The upper row gives results from Part 2, and the lower row gives results from Part 3.

affected, the large and small reinforcers were not equally effective in maintaining responding in Part 1. Responding could not be maintained reliably with reinforcers of 1.5-s duration on concurrent VI 40-s VI 80-s schedules. In addition, responding was also unreliable on concurrent VI 80-s VI 40-s schedules for Bird B1, although it recovered from complete cessation after a 10-day break in training, and we suspected that the bird had a chipped beak. The usual pattern within these failed attempts at Conditions 2 and 3 was that relative response rate failed to reverse from that in the previous condition, and overall response rate remained high for 10 to 20 sessions and then declined to near-zero levels over three to five sessions. Except for Bird B1 in Condition 3, breaks from training did not produce sustained recovery of responding. An exception was that Bird B4 in Condition 2 came to respond exclusively on the VI 40-s

schedule, yielding data that could not be analyzed as log ratios.

In contrast to this difficulty in Conditions 2 and 3, the 1.5-s reinforcer duration maintained responding at high levels for all subjects in Conditions 1 and 4, in which one of the schedules was richer than either schedule in Conditions 2 and 3 (i.e., VI 30 s) and performance always reversed to favor this component of the schedule (Conditions 4 and 5). Thus, the smaller reinforcers in Part 1 were sufficient to maintain responding reliably across components and across subjects only when they were obtained at high rates. Thus, our matching data indicated that sensitivity to relative rate of reinforcement remained about the same as reinforcer magnitude decreased, until the obtained combination of rate and magnitude of reinforcement became insufficient to maintain responding reliably.

The inability to maintain responding with

1.5-s reinforcers in Part 1 established a minimum usable reinforcer magnitude of 2 s, but it may be asked whether we varied magnitude up to a sufficiently large magnitude to make general claims about the effect on sensitivity to reinforcer-rate ratios. With our largest magnitude of reinforcement, occasional days without training were necessary to maintain prescribed body weights for some birds in some conditions. Greater magnitudes would have required us to adopt shorter experimental sessions, and we were concerned about possible distortion of our results by withinsession changes in performance (but see McSweeney, Swindell, & Weatherly, 1999). It remains possible that effects on sensitivity might be found with shorter sessions and a greater range of reinforcer magnitudes, but no effect was apparent over the range that could be used in these experiments.

Data from Part 2 suggested that, although overall magnitudes of reinforcement did not affect sensitivity to reinforcer rate, sensitivity was possibly affected by relative magnitude of reinforcement. That is, lower sensitivity was usually observed when unequal reinforcer magnitudes were used on the two keys and the smaller reinforcer varied in frequency than when small equal-sized reinforcers were used. Such a result, if robust, would contradict the independence assumption of Equation 2 because magnitude ratios should not affect sensitivity to reinforcer-rate ratios (a_r) . However this did not hold for all subjects in the comparison between conditions with equal-sized large reinforcers versus unequalsized reinforcers in Part 2. Moreover, the data were sometimes variable in Part 2. Overall, a total of 10 replications of conditions were conducted in Parts 1 and 2, of which eight produced good or reasonably good replication of results. Two exceptions, both in the series with unequal reinforcers, occurred with Birds A3 and A4. In Part 3, when we explicitly compared variation of the frequency of small, medium, and large reinforcers, keeping one schedule constant, the fits were generally good and the mean sensitivities for conditions with equal- and unequal-sized reinforcers were identical (0.69).

Parts 2 and 3 differed in the orders in which conditions were conducted, and the suggestion of an effect of relative magnitude in Part 2 may have been the result of order effects. In Part 2, successive conditions with unequal-sized reinforcers often had similar reinforcer rates, whereas in Part 3, we more often conducted successive conditions with a given magnitude ratio that had extremely different reinforcer rates, and the conditions with equal reinforcer magnitudes were conducted together in a block at the end. Rodriguez and Logue (1986) also jointly varied two reinforcer parameters (magnitude and delay), and reported effects of condition order on concurrent discrimination in their data. We used substantially more training sessions in each condition than Rodriguez and Logue did (who often used as few as 10 per condition), and would expect order effects to be thereby minimized, but we are unable to explain otherwise the variation in sensitivity estimates over conditions in our experiments.

Might the present failure to find an effect of reinforcer magnitude on sensitivity be due to either insufficient variation in magnitude of reinforcement or to insensitivity of our subjects' behavior to the particular magnitude differences used here? This seems unlikely. First, we varied reinforcer magnitude ratios substantially, over approximately one log unit in Part 3, a range that was similar to our variation in reinforcer-rate ratios. Second, the subjects' behavior was strongly affected by the different reinforcer magnitudes. In the three series of conditions in which unequal-sized reinforcers maintained responding on the two keys (Parts 2 and 3), the regression-line intercepts in Figures 1 and 2 indicated strong response biases favoring the schedule that arranged the larger reinforcers. In contrast, bias was close to zero when reinforcer magnitudes were equal on the two keys. These intercept values may be used to estimate log response ratios that would be obtained given exactly equal rates of reinforcement in each of these conditions, which may then be analyzed in relation to log reinforcer-magnitude ratios over series. Using this method to estimate sensitivity to relative reinforcer magnitude $(a_m \text{ in Equation } 2)$, we obtained values of 0.88, 1.04, 0.89 and 0.77 for Birds A1 through A4 in Part 2 and 0.9, 0.8, 1.01, and 0.73 for Birds A11 through A14 in Part 3. That is, the changes in regressionline intercepts produced by various reinforcer-magnitude ratios reveal high sensitivity to the magnitude ratios used, at least as high as

our sensitivity estimates for reinforcer-rate ratios (a_r in Equation 2). The reinforcer magnitudes used here therefore were different enough to exert substantial differential effects on responding, and we conclude that the effects of relative reinforcer rate are independent of both absolute and relative reinforcer magnitude.

Our support for the matching law is even more impressive when absolute rates of responding on the two keys are considered over conditions in which relative magnitude of reinforcement was varied. When the varied schedule arranged small reinforcers and the constant schedule arranged large ones, Figure 4 shows that changes in response rate on the constant schedule were weak. As the size of the varied-schedule reinforcer was increased (or that arranged by the constant one was reduced), reinforcement interaction became stronger. Despite these changes in the extent of reinforcement interaction observed on the constant key, the slopes of matching lines relating response ratios to reinforcer ratios did not vary systematically.

This study joins several others in investigating dependencies among the various parameters of reinforcement in determining choice. Similar to our results, Davison (1983) found that sensitivity to relative entries to the terminal link (i.e., to relative reinforcer rate) in concurrent chains was the same whether terminal-link delays to reinforcement were 0 s for both alternatives (i.e., standard concurrent VI VI) or 5 s for both. That is, in Davison's study, sensitivity to relative rate of reinforcement was independent of absolute delay. However, this independence from absolute reinforcer magnitude or delay is in sharp contrast to other results reported by Davison (1988). When Davison studied sensitivity to relative reinforcer magnitude at various overall reinforcer rates, he found interaction. Sensitivity to magnitude ratios decreased as the rate of reinforcers increased. Similarly, several authors using the concurrent-chains procedure have reported increases in sensitivity to immediacy ratios as overall absolute rates of entry to terminal links increase (e.g., Fantino, 1969; Fantino & Davison, 1983). These results are not consistent with Equation 2, which assumes independence, because there are clearly some circumstances in which interaction is found.

Recent attempts to formulate alternative models for reinforcement control of choice sometimes propose that the extent of control reflects the discriminability of the various discriminative stimuli and responses used by the experimenter (Davison & Jenkins, 1985; Davison & Nevin, 1999). According to this "confusion" theory, the subject assigns or allocates reinforcers to one or another of the stimulusresponse pairs arranged by the experimenter, with greater or lesser accuracy depending on the discriminability of stimulus-behavior and behavior-reinforcer relations $(d_{sb} \text{ and } d_{br}, \text{ re-}$ spectively, in Davison & Nevin, 1999). In a regular concurrent schedule, the same stimulus is presented continuously, and the critical discriminability is that of behavior-reinforcer relations. Misassignment or confusion as to what reinforcers go with what responses (low values for d_{br}) results in "perceived" reinforcer-rate ratios that are closer to indifference than the ratios observed by the experimenter, and these perceived ratios control behavior allocation according to a strict matching relation. Thus, undermatching in Equations 1 and 2 is interpreted as discrimination failure in confusion theory.

Although the confusion model is successful with data from some complex conditional discrimination procedures, incorporating reinforcer magnitudes into the model for simple concurrent schedules proves difficult (Davison & Nevin, 1999), and we believe that our own results pose additional challenges. The discriminability of behavior-reinforcer relations is claimed to depend on several features of the environment: It increases with differences in the outcomes of the two responses, with the discriminability of the stimuli that define the two responses, and with a changeover delay. It decreases with delay between the response and the reinforcer. Our relative and absolute reinforcer-magnitude manipulations should bear on the discriminability of response-reinforcer relations in confusion theory, but predictions concerning sensitivity to relative reinforcer rate are not borne out by our data.

First, although Davison and Nevin (1999) do not offer explicit predictions concerning the effects of varying absolute reinforcer magnitudes while keeping them equal, a plausible prediction from the dynamic process in confusion theory might be that long reinforcers reduce d_{br} in much the same manner as delay of reinforcement. Because the confusion process involves reevaluation of average reinforcement for different responses with each occurrence of a reinforcing event, and because the eventual duration of a reinforcer is not apparent until it ends, this reevaluation could take account of reinforcer duration only if it occurred at the end of, or perhaps continuously throughout (see Killeen & Smith, 1984), the reinforcer. Thus, long reinforcers should delay reevaluation, increasing confusion as to which of the two responses preceded the reinforcer, spreading response strength increasingly indiscriminately between them as the reinforcer persists and thereby reduce matching law sensitivity. We did not find this with the range of absolute reinforcer magnitudes used. Modeling of reinforcer magnitude effects within confusion theory will need to be handled in a way that avoids making d_{hr} dependent on absolute reinforcer magnitude and yet still accounts for the effects of relative magnitude.

With regard to relative reinforcer magnitude, a prediction from confusion theory is more straightforward. Unequal-sized reinforcers at the two alternatives should increase d_{br} , thereby increasing the slopes of the matching functions by comparison with those for conditions with equal-sized reinforcers. Our fitted slopes were shallow enough that ceiling effects on d_{br} are avoided, but greater sensitivity was not apparent (if anything, Part 2 suggested lower sensitivity). The absence of an effect would be expected if our different magnitudes of reinforcement were not strongly associated with different responses, but that is contradicted by our estimates of a_m given above, which were on average at least as great as sensitivity to relative rate of reinforcement, a_r . Modeling the effects of reinforcer magnitude in a way that does not have such implications for d_{br} would avoid the prediction of greater sensitivity with unequal magnitudes but would create difficulties with conditional discrimination procedures (especially the differential outcomes effect).

To conclude, sensitivity of response ratios to changes in ratios of reinforcer rates in concurrent schedules was independent of the magnitudes of reinforcers used at the two alternatives, provided that magnitudes were sufficient to maintain responding. Thus, our data support the matching relation to the extent that the independence assumption implicit in that relation holds when relative rate of reinforcement was varied over series with different relative and absolute magnitudes of reinforcement on the two alternatives. The dependencies among effects of various reinforcer parameters on choice, reported in other studies, do not occur with all dimensions on which reinforcers vary. Together with these, the present results and other findings of independence yield a complex picture that seems to require a new theoretical approach. Davison and Nevin's (1999) confusion theory handles some of these dependencies and is able to predict many results from conditional discrimination procedures, but neither it nor the matching law can account for all of the observed relations.

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APPENDIX

Asymptotic responses per minute on left and right keys (B_L and B_R), reinforcers per hour on left and right keys (R_L and R_R), and magnitudes of reinforcement (in seconds) for left and right keys (M_L and M_R). Data are given for all conditions in the experiment, listed in the order in which subjects were exposed to them. Standard deviations of response and reinforcer rates, calculated over sessions, are given in parentheses. In Parts 2 and 3, reinforcer rates were varied on the left key only.

Bird	$B_{\rm L}$	$B_{\rm R}$	$R_{\rm L}$	R _R	$M_{ m L}$	$M_{\rm R}$
Part 1						
B1	2.44 (1.55)	36.71 (18.16)	5.12 (3.07)	80.58 (23.62)	1.50	1.50
	66.00 (21.87)	14.90 (6.11)	85.78 (26.01)	16.73 (4.66)	1.50	1.50
	9.21 (2.14)	49.16 (9.12)	15.52 (1.68)	100.51 (4.51)	5.00	5.00
	66.46 (3.51)	18.54 (1.34)	113.67 (1.54)	21.22 (2.73)	5.00	5.00
	11.26 (3.60)	39.93 (3.68)	26.83 (3.50)	75.06 (2.31)	1.50	1.50
	16.41 (2.55)	26.85 (4.86)	37.46 (0.78)	78.34 (4.61)	5.00	5.00
	24.69 (10.91)	12.67 (5.76)	71.32 (27.39)	31.40 (9.98)	5.00	5.00
B2	7.46 (1.61)	51.02 (4.62)	17.10 (1.86)	117.45 (4.86)	5.00	5.00
	44.28 (3.63)	11.30 (1.55)	111.22 (3.10)	19.38 (1.70)	5.00	5.00
	8.21 (4.09)	26.57 (7.81)	14.60 (4.26)	85.49 (13.13)	1.50	1.50
	38.71 (1.82)	10.15 (0.66)	95.21 (3.48)	17.59 (0.79)	1.50	1.50
	23.28 (1.09)	40.03 (1.87)	38.86 (3.17)	80.20 (4.16)	5.00	5.00
	39.56 (1.03)	22.16 (1.72)	81.01 (2.60)	36.95 (3.62)	5.00	5.00
	18.86 (2.74)	45.27 (3.22)	34.27 (2.24)	73.42 (2.90)	1.50	1.50
	23.39 (1.72)	41.82 (1.06)	35.97 (1.54)	73.33 (2.97)	5.00	5.00
B3	48.98 (4.06)	7.89 (0.96)	105.62 (2.21)	15.69 (2.71)	1.50	1.50
	4.51 (2.51)	37.08 (13.77)	9.85 (3.93)	87.05 (24.82)	1.50	1.50
	19.96 (11.17)	0.96(0.9)	66.71 (15.39)	3.69 (2.81)	5.00	5.00
	9.81 (2.89)	40.65 (4.61)	16.36 (1.93)	112.76 (3.93)	5.00	5.00
	46.64 (3.40)	13.95 (1.87)	75.14 (3.67)	29.50 (1.55)	1.50	1.50
	9.62 (1.39)	46.41 (2.57)	26.17 (2.95)	79.06 (2.13)	1.50	1.50
	57.81 (7.91)	16.76 (3.56)	84.80 (3.31)	30.65 (2.96)	5.00	5.00
	18.57 (5.12)	30.54 (5.07)	33.73 (3.87)	73.14 (8.68)	5.00	5.00
	23.83 (9.25)	3.02 (1.40)	73.44 (11.81)	7.46 (3.34)	5.00	5.00

REINFORCER RATE AND MAGNITUDE

APPENDIX

(Continued)

Bird	$B_{\rm L}$	B _R	RL	$R_{ m R}$	ML	M _R
B4	$\begin{array}{c} 25.42 & (1.49) \\ 4.72 & (1.58) \\ 31.00 & (5.21) \end{array}$	$\begin{array}{c} 3.08 \ (0.33) \\ 31.80 \ (4.01) \\ 2.13 \ (0.94) \\ \end{array}$	$ \begin{array}{c} 112.10 (7.27) \\ 13.85 (3.64) \\ 96.51 (6.39) \\ 1200 (5.39) \\ 1200$	$ \begin{array}{c} 10.63 (3.09) \\ 106.28 (5.04) \\ 6.40 (2.89) \\ 0.025 \\ \end{array} $	5.00 5.00 1.50	5.00 5.00 1.50
	$\begin{array}{c} 3.90 \ (1.25) \\ 31.13 \ (2.98) \\ 10.52 \ (0.85) \\ 4.97 \ (0.61) \\ 44 \ 67 \ (2.25) \end{array}$	$\begin{array}{c} 40.22 \ (4.75) \\ 2.53 \ (0.87) \\ 34.72 \ (1.39) \\ 45.71 \ (3.53) \\ 12.65 \ (2.18) \end{array}$	$11.68 (2.91) \\83.00 (3.27) \\29.19 (2.97) \\18.01 (4.09) \\73.21 (3.26)$	$\begin{array}{c} 90.37 \ (6.71) \\ 11.79 \ (4.27) \\ 80.17 \ (1.82) \\ 73.93 \ (3.53) \\ 27 \ 23 \ (3 \ 03) \end{array}$	$1.50 \\ 5.00 \\ 5.00 \\ 1.50 \\ 1.50 $	$1.50 \\ 5.00 \\ 5.00 \\ 1.50 \\ 1.50 $
	41.59(3.11)	4.47 (1.01)	114.82(2.64)	14.48(3.28)	5.00	5.00
Part 2						
Al	$\begin{array}{c} 18.53 & (3.58) \\ 49.41 & (5.06) \\ 15.68 & (2.73) \\ 15.45 & (1.16) \\ 29.32 & (0.82) \\ 21.78 & (1.20) \\ 14.00 & (2.04) \\ 17.93 & (0.33) \\ 9.02 & (2.80) \\ 30.06 & (3.05) \\ 16.32 & (1.39) \\ 35.77 & (4.85) \end{array}$	$\begin{array}{c} 33.96 & (3.03) \\ 19.62 & (2.30) \\ 41.62 & (4.13) \\ 45.60 & (4.01) \\ 26.12 & (1.35) \\ 35.69 & (1.28) \\ 36.80 & (1.66) \\ 37.95 & (2.09) \\ 19.24 & (6.92) \\ 14.46 & (2.05) \\ 26.77 & (2.39) \\ 15.91 & (2.49) \end{array}$	$\begin{array}{c} 7.08 \ (3.11) \\ 65.56 \ (1.65) \\ 5.92 \ (2.18) \\ 11.63 \ (4.56) \\ 45.68 \ (3.46) \\ 13.03 \ (3.56) \\ 43.59 \ (10.95) \\ 59.96 \ (2.69) \\ 5.48 \ (2.51) \\ 65.85 \ (2.07) \\ 8.25 \ (2.99) \\ 43.48 \ (6.08) \end{array}$	$\begin{array}{c} 21.38 & (2.67) \\ 20.96 & (3.71) \\ 21.04 & (2.67) \\ 24.19 & (2.48) \\ 21.02 & (3.79) \\ 21.61 & (4.16) \\ 20.98 & (2.45) \\ 21.17 & (3.21) \\ 19.16 & (3.26) \\ 20.12 & (2.46) \\ 23.51 & (3.22) \\ 19.26 & (3.27) \end{array}$	$\begin{array}{c} 6.00\\ 6.00\\ 2.00\\ 6.00\\ 6.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ \end{array}$	
A2	$\begin{array}{c} 7.42 \ (1.24) \\ 19.32 \ (1.60) \\ 9.93 \ (5.12) \\ 73.48 \ (9.09) \\ 36.41 \ (4.90) \\ 30.18 \ (1.92) \\ 66.07 \ (3.55) \\ 17.43 \ (2.74) \\ 19.24 \ (6.13) \\ 39.47 \ (2.27) \\ 20.48 \ (0.78) \\ 67.36 \ (2.57) \\ 30.65 \ (3.39) \\ 55.23 \ (5.78) \end{array}$	$\begin{array}{c} 69.04 & (3.93) \\ 57.98 & (4.53) \\ 60.42 & (4.94) \\ 28.91 & (5.12) \\ 60.21 & (6.82) \\ 54.61 & (5.91) \\ 35.16 & (2.53) \\ 71.77 & (5.65) \\ 61.92 & (5.89) \\ 55.48 & (6.61) \\ 51.05 & (3.34) \\ 19.84 & (2.31) \\ 45.80 & (5.44) \\ 20.03 & (2.45) \end{array}$	$\begin{array}{c} 6.87 & (0.83) \\ 49.54 & (1.32) \\ 5.82 & (2.59) \\ 66.06 & (2.81) \\ 42.49 & (3.19) \\ 12.05 & (3.55) \\ 45.05 & (2.56) \\ 9.40 & (3.13) \\ 5.98 & (2.97) \\ 59.84 & (1.95) \\ 6.70 & (3.16) \\ 67.94 & (1.33) \\ 11.31 & (3.19) \\ 67.48 & (3.16) \end{array}$	$\begin{array}{c} 22.83 \ (3.71) \\ 22.71 \ (3.21) \\ 22.97 \ (3.60) \\ 23.81 \ (3.70) \\ 22.46 \ (3.57) \\ 21.57 \ (4.30) \\ 22.38 \ (5.05) \\ 23.18 \ (2.50) \\ 21.51 \ (3.01) \\ 23.50 \ (3.16) \\ 20.40 \ (2.98) \\ 19.19 \ (2.07) \\ 21.69 \ (2.06) \\ 19.82 \ (2.73) \end{array}$	$\begin{array}{c} 2.00\\ 2.00\\ 6.00\\ 6.00\\ 2.00\\ 6.00\\ 2.00\\ 6.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\end{array}$	$\begin{array}{c} 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\end{array}$
A3	$\begin{array}{c} 37.45 \ (3.03) \\ 21.51 \ (0.85) \\ 35.84 \ (4.29) \\ 9.23 \ (0.64) \\ 13.15 \ (4.04) \\ 40.98 \ (1.15) \\ 31.70 \ (2.43) \\ 25.79 \ (2.90) \\ 18.28 \ (5.45) \\ 44.66 \ (1.45) \\ 27.70 \ (3.70) \\ 71.99 \ (3.01) \\ 31.78 \ (1.89) \end{array}$	$\begin{array}{c} 63.21 & (3.55) \\ 77.30 & (2.55) \\ 34.44 & (5.64) \\ 71.21 & (5.58) \\ 68.15 & (3.67) \\ 36.33 & (1.77) \\ 46.15 & (3.17) \\ 40.38 & (2.97) \\ 49.84 & (4.69) \\ 27.91 & (1.72) \\ 40.45 & (6.42) \\ 18.34 & (1.78) \\ 42.74 & (3.12) \end{array}$	$\begin{array}{c} 60.00 & (2.61) \\ 4.08 & (1.80) \\ 65.91 & (2.35) \\ 5.62 & (3.22) \\ 10.81 & (3.66) \\ 42.43 & (3.37) \\ 12.09 & (3.44) \\ 41.80 & (2.85) \\ 4.10 & (1.44) \\ 41.91 & (1.59) \\ 10.69 & (3.63) \\ 71.82 & (4.35) \\ 10.38 & (2.48) \end{array}$	$\begin{array}{c} 21.68 \ (4.30) \\ 22.25 \ (2.90) \\ 18.84 \ (3.06) \\ 22.82 \ (4.21) \\ 23.04 \ (2.75) \\ 20.22 \ (2.33) \\ 23.20 \ (3.25) \\ 24.26 \ (2.95) \\ 20.07 \ (4.21) \\ 20.80 \ (2.11) \\ 20.80 \ (2.11) \\ 21.07 \ (3.24) \\ 17.95 \ (2.63) \\ 21.22 \ (2.95) \end{array}$	$\begin{array}{c} 2.00\\ 6.00\\ 2.00\\ 2.00\\ 6.00\\ 2.00\\$	$\begin{array}{c} 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\end{array}$
A4	$\begin{array}{c} 4.36 \ (0.59) \\ 50.04 \ (10.16) \\ 15.34 \ (2.10) \\ 35.90 \ (1.31) \\ 33.37 \ (2.07) \\ 37.56 \ (2.34) \\ 47.56 \ (11.34) \\ 25.55 \ (1.53) \\ 58.31 \ (1.68) \\ 26.51 \ (4.64) \\ 13.54 \ (2.14) \\ 46.33 \ (1.08) \\ 19.46 \ (1.66) \\ 12.99 \ (1.91) \end{array}$	$\begin{array}{c} 46.22 & (3.32) \\ 32.08 & (3.34) \\ 70.40 & (3.48) \\ 67.98 & (3.35) \\ 70.42 & (5.18) \\ 62.03 & (2.84) \\ 45.34 & (9.14) \\ 59.23 & (3.61) \\ 29.27 & (1.42) \\ 37.27 & (7.20) \\ 30.55 & (3.27) \\ 19.57 & (0.48) \\ 51.62 & (2.40) \\ 48.42 & (2.49) \end{array}$	$\begin{array}{c} 3.73 \ (1.39) \\ 61.37 \ (4.50) \\ 5.98 \ (2.10) \\ 60.25 \ (0.94) \\ 41.84 \ (1.72) \\ 8.20 \ (1.31) \\ 39.19 \ (7.31) \\ 12.20 \ (2.59) \\ 69.24 \ (3.50) \\ 10.84 \ (2.94) \\ 5.49 \ (2.78) \\ 44.77 \ (1.71) \\ 11.58 \ (3.29) \\ 4.37 \ (2.02) \end{array}$	$\begin{array}{c} 21.17 \ (2.15) \\ 20.29 \ (3.70) \\ 22.81 \ (3.57) \\ 20.84 \ (2.62) \\ 19.97 \ (2.18) \\ 22.73 \ (4.09) \\ 23.27 \ (5.91) \\ 21.59 \ (1.77) \\ 18.88 \ (2.26) \\ 20.15 \ (3.63) \\ 21.32 \ (4.24) \\ 20.83 \ (1.78) \\ 21.26 \ (2.47) \\ 22.80 \ (3.34) \end{array}$	$\begin{array}{c} 2.00\\ 6.00\\ 2.00\\ 2.00\\ 6.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 0\end{array}$	$\begin{array}{c} 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 6.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 6.00\\ 6.00\\ 6.00\\ \end{array}$

(Continued)						
Bird	$B_{\rm L}$	B _R	$R_{\rm L}$	R _R	$M_{\rm L}$	M _R
Part 3						
A11	18.16 (4.79) 38.29 (16.58) 10.85 (7.04) 84.61 (9.34) 27.94 (9.15) 24.63 (3.60) 60.06 (14.83) 80.74 (13.34) 13.10 (4.91) (4.91)	51.63 (9.46) 51.13 (10.71) 55.71 (11.42) 17.44 (3.08) 33.59 (7.70) 69.69 (5.58) 35.24 (7.25) 13.33 (1.81) 86 79 (11.61)	$\begin{array}{c} 17.68 & (2.36) \\ 56.56 & (5.79) \\ 4.53 & (1.56) \\ 68.30 & (0.97) \\ 5.83 & (3.40) \\ 38.21 & (4.08) \\ 10.99 & (4.03) \\ 44.68 & (2.18) \\ 7 & 97 & (3.39) \end{array}$	$\begin{array}{c} 19.88 \ (2.75) \\ 21.95 \ (2.57) \\ 22.64 \ (2.98) \\ 18.72 \ (2.33) \\ 19.45 \ (4.82) \\ 21.41 \ (2.80) \\ 20.71 \ (3.80) \\ 15.60 \ (3.45) \\ 29 \ 59 \ (3.32) \end{array}$	2.00 2.00 6.00 6.00 2.00 6.00 6.00 9.00	6.00 6.00 2.00 2.00 6.00 2.00 2.00 2.00 6.00
	$\begin{array}{c} 70.24 & (18.75) \\ 70.85 & (6.35) \\ 89.12 & (3.69) \\ 39.79 & (12.14) \\ 74.82 & (12.45) \\ 22.09 & (4.30) \end{array}$	$\begin{array}{c} 15.81 \\ (3.81) \\ 58.64 \\ (4.58) \\ 26.74 \\ (5.14) \\ 66.00 \\ (23.56) \\ 30.85 \\ (6.56) \\ 71.57 \\ (4.36) \end{array}$	$\begin{array}{c} 23.79 & (2.80) \\ 22.97 & (2.86) \\ 67.97 & (1.71) \\ 10.43 & (4.49) \\ 45.18 & (6.26) \\ 4.64 & (1.79) \end{array}$	$\begin{array}{c} 18.26 \\ (3.56) \\ 20.61 \\ (2.77) \\ 21.96 \\ (3.96) \\ 22.55 \\ (3.66) \\ 18.65 \\ (2.50) \\ 23.36 \\ (2.16) \end{array}$	$\begin{array}{c} 2.00\\ 6.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 0\end{array}$	2.00 4.00 4.00 4.00 4.00 4.00 4.00
A12	$\begin{array}{c} 22.64 \ (6.27) \\ 9.74 \ (2.62) \\ 26.30 \ (2.49) \\ 14.27 \ (2.15) \\ 55.82 \ (5.00) \\ 9.98 \ (2.16) \\ 54.20 \ (2.91) \\ 34.14 \ (4.95) \\ 17.95 \ (1.40) \\ 42.42 \ (2.63) \\ 24.86 \ (2.33) \\ 18.86 \ (2.85) \\ 48.65 \ (2.97) \\ 25.20 \ (1.57) \\ 43.44 \ (3.56) \end{array}$	$\begin{array}{c} 44.64 & (2.80) \\ 54.89 & (4.02) \\ 35.92 & (2.49) \\ 30.41 & (5.07) \\ 3.51 & (2.26) \\ 49.89 & (3.99) \\ 6.43 & (2.30) \\ 29.19 & (6.07) \\ 50.41 & (2.19) \\ 19.18 & (2.12) \\ 34.20 & (3.91) \\ 36.12 & (3.19) \\ 29.22 & (5.67) \\ 46.25 & (3.80) \\ 25.73 & (2.84) \end{array}$	$\begin{array}{c} 18.36 \ (2.21) \\ 5.30 \ (2.23) \\ 58.30 \ (1.99) \\ 5.83 \ (3.17) \\ 69.82 \ (1.92) \\ 9.53 \ (3.34) \\ 45.72 \ (2.78) \\ 10.67 \ (2.91) \\ 41.52 \ (3.23) \\ 20.88 \ (3.08) \\ 20.11 \ (2.72) \\ 11.04 \ (3.26) \\ 56.99 \ (3.15) \\ 5.71 \ (1.65) \\ 43.10 \ (4.26) \end{array}$	$\begin{array}{c} 21.66 \ (2.26) \\ 21.67 \ (2.69) \\ 21.32 \ (3.97) \\ 20.37 \ (3.42) \\ 9.26 \ (4.84) \\ 21.40 \ (2.74) \\ 14.80 \ (2.49) \\ 21.78 \ (2.69) \\ 22.43 \ (1.98) \\ 19.77 \ (2.54) \\ 22.15 \ (2.35) \\ 21.45 \ (3.14) \\ 19.87 \ (3.71) \\ 20.38 \ (2.56) \\ 21.55 \ (3.03) \end{array}$	$\begin{array}{c} 2.00\\ 2.00\\ 2.00\\ 6.00\\ 6.00\\ 2.00\\ 6.00\\ 2.00\\ 6.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ \end{array}$	$\begin{array}{c} 6.00\\ 6.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ \end{array}$
A13	$\begin{array}{c} 18.39 & (1.96) \\ 64.65 & (1.86) \\ 48.86 & (11.84) \\ 36.53 & (2.50) \\ 4.93 & (1.98) \\ 64.27 & (8.03) \\ 70.47 & (2.66) \\ 38.53 & (5.83) \\ 13.53 & (3.11) \\ 65.12 & (4.48) \\ 26.55 & (8.54) \\ 44.43 & (6.08) \\ 16.63 & (4.85) \\ 53.67 & (4.57) \\ 24.34 & (5.26) \end{array}$	$\begin{array}{c} 75.04 & (8.88) \\ 10.48 & (0.98) \\ 25.45 & (11.62) \\ 53.72 & (7.45) \\ 67.42 & (5.28) \\ 12.26 & (1.51) \\ 24.23 & (9.07) \\ 57.83 & (5.98) \\ 62.14 & (7.46) \\ 20.20 & (2.37) \\ 31.64 & (14.86) \\ 22.06 & (5.14) \\ 38.80 & (10.23) \\ 24.12 & (3.45) \\ 47.26 & (7.92) \end{array}$	$\begin{array}{c} 18.99 \ (2.98) \\ 70.12 \ (1.85) \\ 4.74 \ (2.45) \\ 53.58 \ (6.04) \\ 3.59 \ (1.96) \\ 44.37 \ (3.08) \\ 12.22 \ (2.40) \\ 39.97 \ (4.06) \\ 8.30 \ (2.23) \\ 22.64 \ (2.82) \\ 16.68 \ (3.10) \\ 42.99 \ (4.77) \\ 4.94 \ (2.40) \\ 68.18 \ (2.47) \\ 8.99 \ (2.62) \end{array}$	$\begin{array}{c} 21.03 \ (3.26) \\ 17.07 \ (1.51) \\ 14.95 \ (4.86) \\ 19.62 \ (2.71) \\ 22.79 \ (3.44) \\ 16.74 \ (2.07) \\ 18.08 \ (2.62) \\ 23.42 \ (3.83) \\ 23.33 \ (2.23) \\ 17.77 \ (3.64) \\ 18.24 \ (3.60) \\ 19.09 \ (3.32) \\ 19.57 \ (2.57) \\ 19.93 \ (2.75) \\ 20.30 \ (3.82) \end{array}$	$\begin{array}{c} 2.00\\ 6.00\\ 6.00\\ 2.00\\ 6.00\\ 6.00\\ 2.00\\ 2.00\\ 2.00\\ 4.00\\$	$\begin{array}{c} 6.00\\ 2.00\\ 2.00\\ 6.00\\ 2.00\\ 2.00\\ 2.00\\ 6.00\\ 6.00\\ 6.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ 4.00\\ \end{array}$
A14	$\begin{array}{c} 14.02 & (2.49) \\ 29.40 & (4.21) \\ 53.15 & (4.54) \\ 8.08 & (2.00) \\ 33.50 & (1.98) \\ 44.65 & (4.61) \\ 52.89 & (3.21) \\ 15.47 & (4.22) \\ 27.15 & (2.47) \\ 49.93 & (2.12) \\ 40.38 & (2.19) \\ 23.66 & (1.96) \\ 44.86 & (2.56) \\ 21.35 & (2.68) \\ 43.67 & (2.31) \\ 24.61 & (4.24) \end{array}$	$\begin{array}{c} 54.47 \ (6.59) \\ 39.06 \ (5.63) \\ 8.30 \ (1.72) \\ 51.37 \ (6.54) \\ 29.86 \ (3.74) \\ 26.16 \ (3.63) \\ 13.97 \ (1.70) \\ 46.58 \ (6.18) \\ 45.56 \ (2.77) \\ 16.48 \ (1.75) \\ 36.36 \ (3.18) \\ 44.22 \ (3.01) \\ 24.51 \ (2.05) \\ 35.90 \ (3.24) \\ 13.15 \ (1.63) \\ 35.76 \ (3.91) \end{array}$	$\begin{array}{c} 16.00 \ (3.85) \\ 6.76 \ (2.65) \\ 71.19 \ (2.39) \\ 4.51 \ (2.13) \\ 59.16 \ (2.68) \\ 11.15 \ (3.38) \\ 48.29 \ (3.93) \\ 10.32 \ (3.71) \\ 41.18 \ (3.15) \\ 22.00 \ (2.43) \\ 21.68 \ (1.49) \\ 5.73 \ (3.19) \\ 46.71 \ (2.76) \\ 5.57 \ (1.97) \\ 67.85 \ (1.65) \\ 10.09 \ (3.15) \end{array}$	$\begin{array}{c} 22.13 & (3.00) \\ 21.03 & (3.60) \\ 15.39 & (3.61) \\ 21.50 & (2.37) \\ 19.84 & (2.61) \\ 21.65 & (2.69) \\ 18.66 & (3.40) \\ 21.42 & (3.23) \\ 22.11 & (2.86) \\ 19.02 & (3.91) \\ 20.90 & (3.23) \\ 21.33 & (2.68) \\ 19.66 & (3.90) \\ 22.44 & (3.19) \\ 20.27 & (3.18) \\ 20.16 & (2.69) \end{array}$	$\begin{array}{c} 2.00\\ 6.00\\ 6.00\\ 2.00\\ 2.00\\ 6.00\\ 2.00\\ 6.00\\ 2.00\\ 6.00\\ 4.00\\$	$\begin{array}{c} 6.00\\ 2.00\\ 2.00\\ 6.00\\ 2.00\\ 2.00\\ 2.00\\ 2.00\\ 6.00\\ 2.00\\ 4.00\\$

APPENDIX