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ECONOMIC AND BIOLOGICAL INFLUENCES ON KEY PECKING AND TREADLE PRESSING IN PIGEONS

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Pigeons were studied on a two-component multiple schedule in which the required operant was, in different conditions, biologically relevant (i.e., key pecking) or nonbiologically relevant (i.e., treadle pressing). Responding was reinforced on a variable-interval (VI) 2-min schedule in both components. In separate phases, additional food was delivered on a variable-time (VT) 15-s schedule (response independent) or a VI 15-s schedule (response dependent) in one of the components. The addition of response-independent food had different effects on responding depending on the operant response and on the frequency with which the components alternated. When components alternated frequently (every 10 s), all pigeons keypecked at a much higher rate during the component with the additional food deliveries, whether response dependent or independent. In comparison, treadle pressing was elevated only when the additional food was response dependent; rate of treadling was lower when the additional food was response independent. When components alternated infrequently (every 20 min), pigeons key pecked at high rates at points of transition into the component with the additional food deliveries. Rate of key pecking decreased with time spent in the 20-min component when the additional food was response independent, whereas rate of pecking remained elevated in that component when the additional food was response dependent. Under otherwise identical test conditions, rate of treadle pressing varied only as a function of its relative rate of response-dependent reinforcement. Delivery of response-independent food thus had different, but predictable, effects on responding depending on which operant was being studied, suggesting that animal-learning procedures can be integrated with biological considerations without the need to propose constraints that limit general laws of learning.

Key words: biological effect, economic effect, contingent reinforcement, multiple schedule, response-independent food, response-dependent food, treadle press, key peck, pigeon

Herrnstein's (1970) equation states that response rate varies as a function of its relative rate of reinforcement. Stated formally,

$$R = kr_c/(r_c + r_e), \quad (1)$$

where R is rate of responding, r_c is the rate of response-dependent food delivery, k is a constant representing asymptotic rate of responding, and r_e is the rate of extraneous reinforcement. Extraneous reinforcement includes concurrently scheduled, dependent reinforcement, as well as response-independent food delivery and reinforcement from other alternatives (Herrnstein, 1970). It follows from Equation 1 that an increase in response-independent food delivery (r_e) would decrease the overall rate of responding (R). Indeed, response-independent food delivery generally decreases the overall rate of humans' button pressing (Madden & Perone, 2003), rats' lever pressing (Deluty, 1976; Rescorla & Skucy, 1969), and pigeons' key pecking (e.g., Boakes, 1973; Imam & Lattal, 1988; Lattal & Abreu-Rodrigues, 1997; Rachlin & Baum, 1972).

Equation 1 provides an excellent description of responding in different species (e.g., rats, pigeons), with different reinforcers (e.g., food, water, wheel running), and different responses (e.g., lever pressing, key pecking, treadle pressing; e.g., Belke & Heyman, 1994; for a review, see Davison & McCarthy, 1988). Equation 1 describes a pigeon's rate of key pecking as well as a pigeon's treadle pressing (Davison & Ferguson, 1978; Hanson & Green, 1986; McSweeney, 1978) even though the key peck, unlike the treadle press, is not an arbitrary response in pigeons. That is to say, there appears to be an innate, or biological, component to the pigeon's key pecking for food that is not present in treadle pressing (Brown & Jenkins, 1968; Schwartz & Gamzu, 1977; Westbrook, 1973; Williams & Williams, 1969).

The pigeon's pecking response is excited

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by and directed toward a localized visual cue if that cue differentially predicts food delivery. Gamzu and Schwartz (1973) studied pigeons under a multiple schedule of food delivery in which a green keylight component that signaled a lower rate of response-independent food delivery alternated with a red keylight component that signaled a higher rate of response-independent food delivery. They observed that pigeons came to peck the response key when it was red, the stimulus signaling the higher rate of food delivery. The red key was a differential signal for a higher rate of food and presumably came to excite the biological food response of the pigeon. Pecking did not occur when the key was not a differential predictor, that is, when the rate of food delivery was equal in each component of the multiple schedule.

Consider, now, a situation in which a pigeon is studied on a multiple schedule in which food reinforcement in each of the two components is arranged according to a VI 2-min schedule and is dependent on key pecking. If response-independent food were then added to one of the components, the biological response would be excited, increasing key pecking in the response-independent food component—termed the *biological effect*. According to Herrnstein's (1970) equation, however, key-peck responding should decrease in the component with the response-independent food because increasing its rate of delivery (r_e) decreases overall responding (R)—termed the *economic effect*.

Notice, then, that the delivery of response-independent food could have opposite effects on responding. According to the biological effect, the delivery of response-independent food increases responding if the response is a biological, food-related behavior and there is a differential predictor for the higher rate of food delivery. According to the economic effect, however, response-independent food decreases responding as predicted by Equation 1. Such conflicting predictions about the effects of response-independent food on responding may lead some to question whether accurate predictions and general laws of learning can be developed. That is, because of the biological nature of the pigeon's key-peck response, we may be unable to predict how an experimental manipulation (e.g., the imposition of response-independent food) will affect responding.

Green and Rachlin (1975) set the biological and economic effects in opposition and traced their effects on rate of responding as a function of time spent in the presence of a stimulus signaling a higher rate of food delivery. They posited that the biological effect is transient, excited at points of transition into higher rates of food delivery, and dissipates with time spent in the presence of the stimulus signaling the higher rate of food delivery. In their study, a variable interval (VI) 2-min schedule (in which food was presented, on average, every 2 min dependent on a key-peck response) was in effect during both the red and green components of a multiple schedule. In addition, a variable time (VT) 15-s schedule (in which food was presented, on average, every 15 s independently of responding) was also in effect only during the red component. Thus, in the green component, the pigeon could receive one reinforcer every 2 min dependent on key pecking. In the red component, the pigeon could receive one reinforcer dependent on key pecking and eight response-independent food deliveries every 2 min. In different conditions, the red and green components alternated every 8 s, 8 min, or 16 min, with sessions lasting a total of 32 min.

There was an increase in responding at the point of transition from the green (VI 2-min) into the red (VI 2-min + VT 15-s) component. When the components alternated every 8 s, key pecking was higher in the red component, attributed to the frequent excitation of the biological response. In the 16-min condition, key pecking was also excited at the transition from green into red; however, responding decreased with time spent in the red component as the steady-state, economic effect took over. In fact, in the 16-min condition, *overall* response rate was actually higher in the green than in the red component.

Green and Rachlin's (1975) results suggest that relatively accurate predictions about responding are possible despite the opposite effect that response-independent food apparently can have on responding. Taking into account the interaction between the economic and biological effects with the key-peck response, they were able to predict the effect on the rate of a pigeon's key pecking. A sit-

uation in which the operant response is not a biological, food-related response would further test the Green and Rachlin proposal.

Westbrook (1973) demonstrated, using a typical behavioral contrast paradigm (e.g., Reynolds, 1961), that a pigeon's rate of key pecking, but not treadle pressing, was directly affected by a shift in the stimulus-reinforcer relation. That is, when one component of the multiple schedule was shifted to extinction, positive behavioral contrast (i.e., increased responding in the unchanged component) occurred for pigeons that key pecked, whereas negative induction (a decrease in responding in the unchanged component) occurred with those that treadle pressed. Such a finding is consistent with the view that a pigeon's treadle press, unlike its key peck, is not a biologically related food response. LoLordo, McMillan, and Riley (1974) further demonstrated, under autoshaping-like procedures, that the pigeon's treadle-press response lacks the biological component of the pigeon's key-peck response. They found that rate of treadle pressing was not directly affected by the presentation of a localized stimulus signaling higher rates of food delivery, whereas rate of key pecking was influenced directly by such stimulus presentations.

In the present study, pigeons responded on multiple schedules in which the duration of the component was varied (q.v., Green & Rachlin, 1975) and in which treadle pressing and key pecking were the operant responses. If Green and Rachlin's analysis is correct, then at points of transition to higher rates of food delivery, rate of key pecking should increase (the biological effect). With time spent in the presence of the signal for the higher rate of food delivery, rate of key pecking should become a function of relative rate of response-dependent reinforcement (the economic effect). Specifically, key pecking should decrease when the additional foods are response independent but remain high when the additional foods are response dependent. In contrast, rate of treadle pressing should be relatively unaffected by transitions into the component with the higher rate of food delivery. That is, rate of treadle pressing, a nonbiologically relevant response, should be a function of its relative rate of dependent food delivery (influenced by the economic effect only), and, thus, little influenced by component duration.

METHOD

Subjects

Eight experimentally naive, male White Carneau pigeons from the Palmetto Pigeon Plant (Sumter, SC) were maintained at approximately 80% of their free-feeding body weights. Water and grit were continuously available in their home cages.

Apparatus

Each of two experimental test chambers (25.4 cm wide by 27.9 cm long by 30.5 cm high) was placed within light- and sound-attenuating enclosures with a ventilating fan running continuously. The floors were 0.64 cm stainless steel grids.

The treadle-press chamber contained two differently colored stimulus houselights. The red houselight was mounted 4 cm from the left wall, and the green houselight was mounted 4 cm from the right wall. Both lights were 2 cm from the top of the chamber, with the light deflected downward. The treadle (5.8 cm long by 5.7 cm wide) was located on the center of the panel with its front edge 1.5 cm from the floor. The steel treadle was sloped at a 40° angle to the floor and required at least 0.6 N to be activated and produce a feedback click. The feeder was located 4 cm from the right wall and provided 3-s access to mixed grains, during which time the stimulus lights were extinguished and the food magazine was illuminated with white light.

The key-peck chamber contained a response key, 2.5 cm in diameter, that could be transilluminated with red or green light. The key was located on the center of the panel, 5 cm from the ceiling. A force of at least 0.4 N was necessary to activate the microswitch and produce an audible feedback click. The feeder was situated 4 cm from the right wall and provided 3-s access to mixed grains, during which time the response key was extinguished and the food magazine was illuminated with white light.

Procedure

The pigeons were trained to peck the response key using an autoshaping-like procedure. For treadle-press training, the pigeons were trained to press the treadle by a hand-shaping procedure. All pigeons were trea-

Table 1

Summary of experimental conditions. The order in which each pigeon experienced the phases and the number of sessions for each (in parentheses) are presented.

	Phase and component duration							
	A (Baseline)		B (Independent)		C (Dependent)		D (Independent-Independent)	
	mult VI 2 min VI 2 min		*mult* VI 2 min + VT 15 s VI 2 min		*mult* VI 2 min + VT 15 s VI 2 min		*mult* VI 2 min + VT 15 s VI 2 min + VT 15 s	
Pigeon	10 s	20 min	10 s	20 min	10 s	20 min	10 s	20 min
Key Peck[a]								
73	1 (28)	2 (60)	3 (28)	4 (28)	5 (30)	6 (32)	7 (33)	8 (29)
74	1 (28)	2 (60)	5 (37)	6 (48)	4 (28)	3 (32)	8 (28)	7 (28)
75	2 (60)	1 (28)	4 (28)	3 (43)	6 (29)	5 (28)	8 (32)	7 (41)
8	2 (60)	1 (28)	6 (30)	5 (28)	3 (28)	4 (31)	7 (29)	8 (28)
31	—	—	10 (28)	9 (28)	12 (28)	11 (28)	—	—
32	—	—	10 (28)	11 (37)	12 (29)	9 (28)	—	—
33	—	—	11 (29)	12 (28)	9 (31)	10 (28)	—	—
34	—	—	9 (35)	10 (29)	11 (28)	12 (29)	—	—
Treadle Press[b]								
31	1 (28)	2 (28)	3 (45)	4 (63)	5 (34)	6 (37)	7 (28)	8 (41)
32	1 (28)	2 (28)	5 (104)	6 (107)	4 (45)	3 (45)	8 (40)	7 (89)
33	2 (28)	1 (28)	3 (28)	5 (60)	4 (93)	5 (28)	8 (29)	7 (34)
34	2 (28)	1 (28)	6 (40)	5 (51)	3 (45)	4 (45)	7 (34)	8 (28)
73	—	—	10 (28)	11 (51)	12 (45)	9 (45)	—	—
74	—	—	10 (48)	9 (42)	12 (28)	11 (30)	—	—
75	—	—	11 (38)	10 (58)	9 (29)	12 (29)	—	—
8	—	—	9 (47)	10 (46)	11 (35)	12 (33)	—	—

[a] Pigeons 73, 74, 75, and 8 were first studied under all four of the key-peck response phases, and then under two of the treadle-press phases.

[b] Pigeons 31, 32, 33, and 34 were first studied under all four of the treadle-press response phases, and then under two of the key-peck phases.

dling within three sessions. Once responding was established, the pigeons were placed on a multiple VI 30-s VI 30-s schedule for two days, followed by three days on a multiple VI 1-min VI 1-min schedule. They were then placed on the multiple VI 2-min VI 2-min Baseline schedule.

During all conditions, the signaling stimulus alternated between red and green signifying each of the two components of the multiple schedule. Components alternated either every 10 s or every 20 min. Sessions were conducted daily and lasted 40 min, excluding food delivery time. Thus, when the red and green stimuli alternated every 10 s, there were 120 10-s red components and 120 10-s green components per session. When the colors alternated every 20 min, there was one 20-min red and one 20-min green component presented daily. The component starting a session (red or green) alternated daily. Food presentations dependent on responding were occasionally not collected during the component in which they were scheduled. In such cases, they remained "set" until finally collected when that component was again in effect. Food presentations not dependent on responding (VT 15-s schedule) were always collected during the component in which they were scheduled.

The pigeons were studied under both treadle-press response and key-peck response conditions. There were four phases under each response topography condition. The phases were distinguished by the schedules of reinforcement in effect. In each phase, the pigeons were studied with the components alternating every 10 s and alternating every 20 min. Conditions remained in effect for a minimum of 28 sessions and until response rate was stable as evidenced by less than a 10% change in overall response rate in each component during the final 10 days. Table 1 summarizes the conditions during the phases, the

order in which the pigeons experienced these conditions, and the number of sessions studied on each.

In Phase A (Baseline), both the green and the red stimulus signaled a multiple (*mult)* VI 2-min VI 2-min schedule. All intervals used were determined as specified by Fleshler and Hoffman (1962).

In Phase B (Independent), the red stimulus continued to signal a VI 2-min schedule of food reinforcement dependent on responding. The green stimulus also signaled a VI 2-min schedule for responding but, in addition, food was delivered independently of responding at variable intervals averaging 15 s (VT 15 s). (Imam & Lattal, 1992, refer to a schedule that combines response-dependent with response-independent outcomes in the presence of a single operandum and stimulus as a concomitant schedule. According to their suggestion, then, the schedule in the presence of the green signal would be a concomitant VI 2-min VT 15-s schedule). Thus, on average, during 2 min in the red component the pigeon could obtain one response-dependent food reinforcement, whereas during 2 min in the green component the pigeon could obtain one response-dependent food reinforcement plus eight response-independent food deliveries.

Phase C (Dependent) differed from the previous phase in that the schedule that formerly arranged response-independent food deliveries now arranged reinforcements dependent on responding such that all food deliveries were now dependent on responding. Thus, on average, during 2 min in the red component, the pigeon could still obtain one response-dependent food reinforcer, whereas during 2 min in the green component the pigeon could obtain nine response dependent food reinforcers; one from the VI 2-min schedule and eight from a VI 15-s schedule.

In Phase D (Independent-Independent), both the red and the green stimulus signaled the VI 2-min schedule of reinforcement for responding and a VT 15-s schedule of food deliveries independent of responding. Thus, on average, during 2 min in the red and green components, the pigeon could obtain one response-dependent food reinforcer plus eight response-independent food presentations.

Pigeons 31, 32, 33, and 34 were studied on all eight conditions with the treadle-press response requirement, and Pigeons 73, 74, 75, and 8 were studied on all eight conditions with the key-peck response requirement. Following completion of these conditions, the pigeons originally studied with the key-peck response requirement were studied with the treadle-press response requirement; likewise, the pigeons originally studied with the treadle-press response requirement were studied with the key-peck response requirement. Specifically, Pigeons 31 through 34 were studied under Phases B (Independent) and C (Dependent) at both the 10-s and 20-min component durations but now with the key-peck response requirement, and Pigeons 73, 74, 75, and 8 were studied at both the 10-s and 20-min component durations under Phases B and C but now with the treadle-press response requirement (see Table 1).

RESULTS

Overall Response Rates

Reinforcement rates and response rates were calculated for each pigeon for each session, separately for the red and green components. The obtained reinforcement rates during the last 10 days of each condition remained within ± 5% of the scheduled rates. The median overall response rate for each pigeon studied on all four of the different phases of the experiment under both 10-s and 20-min component durations are presented in Figures 1 and 2 for the key-peck and treadle-press response conditions, respectively. Specifically, the individual data shown are the median response rates from the last five sessions at each 10-s component duration condition, and from the last five sessions for each color (i.e., red or green) when that color was the second component of the 20-min component duration condition. The mean overall response rates of all 4 of the pigeons during the different phases of the experiment are also shown in Figures 1 and 2.

Phase A: Baseline (mult VI 2 min VI 2 min). The upper left panels of Figures 1 and 2 show median rate of responding during the red and green components of the multiple schedule for each pigeon when equivalent schedules of reinforcement were in effect for key pecking (Figure 1) and treadle pressing (Fig-

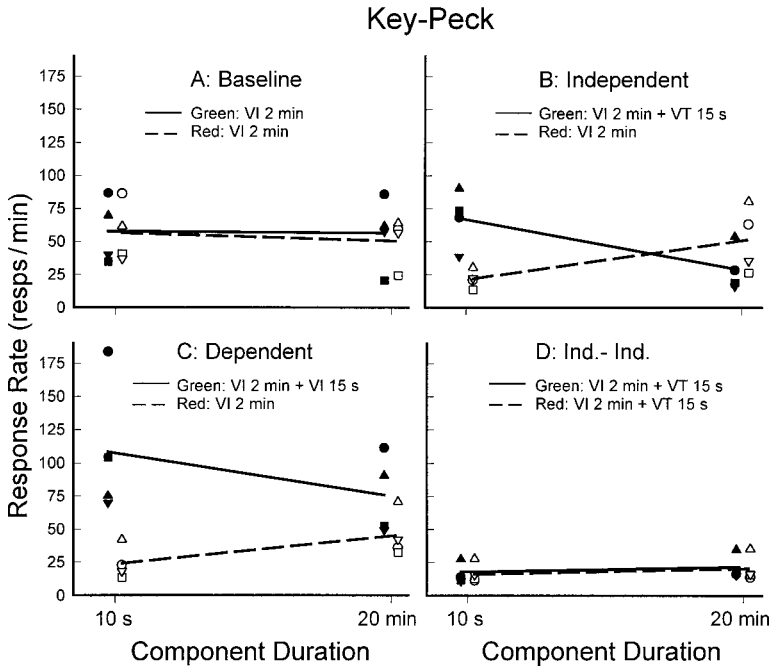

Fig. 1. Overall rates of key pecking for each pigeon in the green (filled symbols) and red (open symbols) components at 10-s and 20-min component durations for each phase. The solid line represents the mean overall rate of key pecking in the green component, and the dashed line represents the mean overall rate of key pecking in the red component. Each pigeon (73, 74, 75, and 8) is represented by a separate symbol.

ure 2). The pigeons responded at approximately equal rates during the red and green components, and there was no consistent effect of component duration on rate of responding. Although overall rate of responding was generally higher when the response was that of key pecking, the pattern of results was similar to that with the treadle-press response in that response rate during each component was equivalent.

Phase B: Independent (mult VI 2 min VI 2 min + VT 15 s). As shown in the upper right panel of Figure 1, when the response was key pecking, response rate was considerably greater during the green component (with the added VT schedule) than during the red component (without the VT) when components alternated every 10 s. When the component duration was 20 min, however, rate of key pecking was higher in the red than in the green component. Each pigeon showed this pattern of results.

Unlike the results obtained when the response was key pecking, each pigeon's rate of treadle pressing was higher during the VI 2-min red component (without the VT) than during the green (VI 2-min + VT 15-s) component at both 10-s and 20-min component durations (see Figure 2, upper right panel).

Phase C: Dependent (mult VI 2 min VI 2 min + VI 15 s). In this phase, all food presentations were response dependent. When key pecking was the operant response, rates of responding for every pigeon were always higher during the green (VI 2-min + VI 15-s) component than during the red component, regardless of the component duration (see Figure 1, lower left panel). The upward sloping function for the red component is similar to the corresponding function of the Independent Phase (compare the dashed line in the lower left panel with that in the upper right panel of Figure 1) and is also apparent for each pigeon.

When all food presentations were dependent on the treadle-press response, rate of responding was also higher in the green component than in the red component at both the 10-s and 20-min component duration for every pigeon (see Figure 2, lower left panel).

Phase D: Independent-Independent (mult VI 2 min + VT 15 s VI 2 min + VT 15 s). During

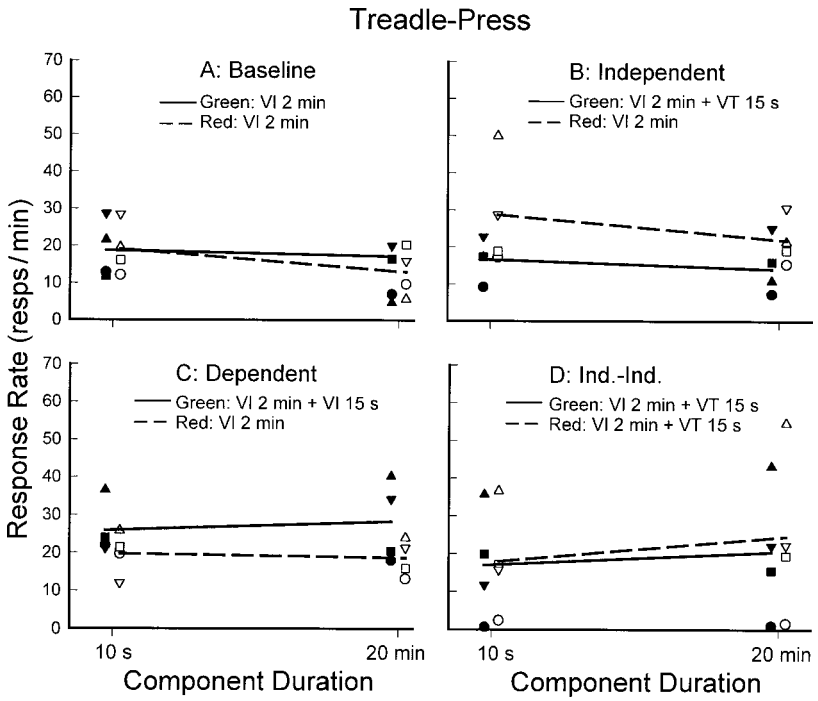

Fig. 2. Overall rates of treadle pressing for each pigeon in the green (filled symbols) and red (open symbols) components at 10-s and 20-min component durations for each phase. The solid line represents the mean overall rate of treadle pressing in the green component, and the dashed line represents the mean overall rate of treadle pressing in the red component. Each pigeon (31 through 34) is represented by a separate symbol.

this phase of the experiment, equal rates of response-independent food were superimposed on the VI 2-min schedule during both the red and the green components. As shown in the lower right panels of Figures 1 and 2, rates of responding during the red and green components were relatively equivalent, and there was no systematic effect of component duration. This pattern of results was apparent under both the key-peck and the treadle-press response conditions.

Responding Across the 20-Min Components

Rates of responding at various intervals *across* the 20-min components for each pigeon were also calculated. These values were obtained as follows: During the last 10 sessions of each condition with the 20-min component duration, the number of responses was recorded in 10-s intervals. Data from only the second half of each session were used so that the beginning of each curve represents a transition from either red to green or from green to red. For each pigeon, the number of responses was cumulated over these sessions during each of the 10-s intervals. Thus the first 10 s of the 20-min component is somewhat equivalent to the 10-s component duration condition. The total responses were then combined into longer intervals (as shown on the abscissa of Figures 3 and 4). (The logarithmic arrangement of intervals allows any rapid changes during the early portion of the component to be seen.) Then, the total number of responses was divided by the width of the interval to obtain the rate of responding during each such interval. The mean of that distribution for all the pigeons is plotted separately for the red and the green component for each 20-min component condition in Figure 3 (for key pecking) and Figure 4 (for treadle pressing). The pattern of responding is representative of the individual pigeons. For evaluation purposes, the data of 1 pigeon (Pigeon 73) from each of the four phases of its key-peck condition are shown in Figure 5, and the data of 1 pigeon (Pigeon 31) from each of the four phases of its treadle-press condition are shown in Figure 6.

Phase A: Baseline (mult VI 2 min VI 2 min).

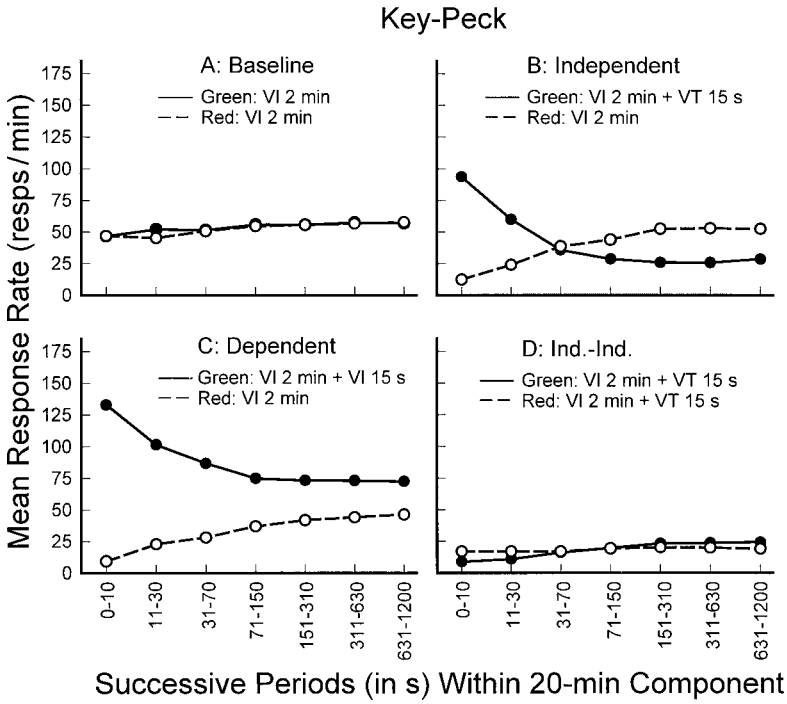

Fig. 3. Mean rates of responding across successive intervals of the 20-min component durations for each phase for the key-peck response condition. Solid lines are rates during the green component; dashed lines are rates during the red component.

The upper left panels of Figures 3 and 4 show that for both the key-peck and treadle-press response, respectively, as expected, there was no systematic change in responding within the 20-min component when it was red or green, with rate remaining relatively constant throughout.

Phase B: Independent (mult VI 2 min VI 2 min + VT 15 s). The upper right panel of Figure 3 shows key-pecking rates at various intervals within the 20-min component when the VT schedule was added to the green component. During the green component in which the VT was added, key pecking was markedly elevated during the first 10 s of the component and decreased with time, leveling out at a rate well below that during the red component. During the initial portion of the red component (without the VT), key pecking was reduced and recovered over time to a rate above that in the green component.

The upper right panel of Figure 4 shows treadling rates across the 20-min component. During both the green and red components, treadling was initially suppressed, with response rate in the red component increasing across the component duration and response rate in the green component leveling out and remaining well below that of the red component.

Phase C: Dependent (mult VI 2 min VI 2 min + VI 15 s). The lower left panel of Figure 3 shows pecking rates at various intervals during the 20-min component when the additional food in the green component was response dependent. As was the case during the Independent Phase, pecking during the initial portion of the red component was reduced and recovered over time. Pecking during the green component (in which responding produced a much higher rate of reinforcement) again showed an initial elevation in responding that decreased over time. Unlike the Independent Phase, however, responding during the green component remained at a level well above that in the red component.

As shown in the lower left panel of Figure 4, treadle pressing across intervals within the 20-min component was also higher throughout the green component than the red component (although there was suppression of

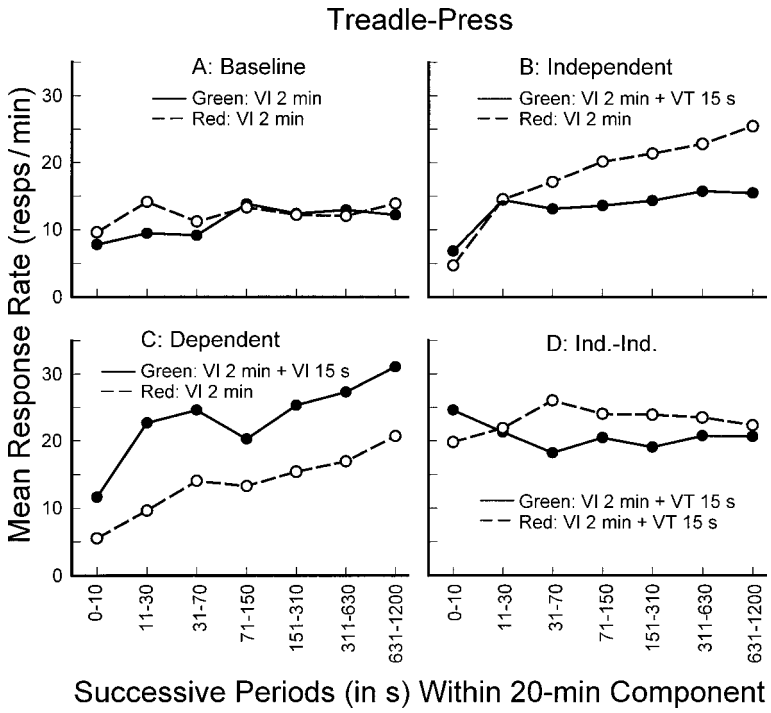

Fig. 4. Mean rates of responding across successive intervals of the 20-min component durations for each phase for the treadle-press response condition. Solid lines are rates during the green component; dashed lines are rates during the red component.

treadling at the beginning of both components).

Phase D: Independent-Independent (mult VI 2 min + VT 15 s VI 2 min + VT 15 s). Across pigeons, there were no systematic differences in rate of key pecking or treadle pressing across the 20-min component or between the red and green components when equal rates of response-independent food were added to both components. The group means are shown in the lower right panels of Figure 3 for the key-peck condition and Figure 4 for the treadle-press condition.

The pattern of results depicted for the group is evident in the individual pigeons, as represented by Pigeon 73 from the key-peck condition (shown in Figure 5) and Pigeon 31 from the treadle-press condition (shown in Figure 6).

Within-Subject Replications

The previous results were between-group comparisons. To provide a within-subject comparison, the pigeons originally studied with the key-peck response were then studied under the Independent and Dependent Phases (Phases B and C) with the treadle-press response. Similarly, the pigeons originally studied with the treadle-press response were then studied under the Independent and Dependent Phases with the key-peck response.

Pigeons 31 through 34 were first studied with the treadle-press response and then switched to the key-peck. Their results under the Independent and Dependent phases replicated those obtained with the 4 pigeons initially studied with the key-peck response conditions. The upper left panel of Figure 7 shows that overall response rate during the Independent phase, in which response-independent food was added during the green component, was markedly higher during the green than during the red component when components alternated every 10 s, but was lower when components alternated every 20 min. The lower left panel of Figure 7 shows that when all food was dependent on pecking (Phase C, Dependent), response rate was higher during the green at both the 10-s and 20-min component durations.

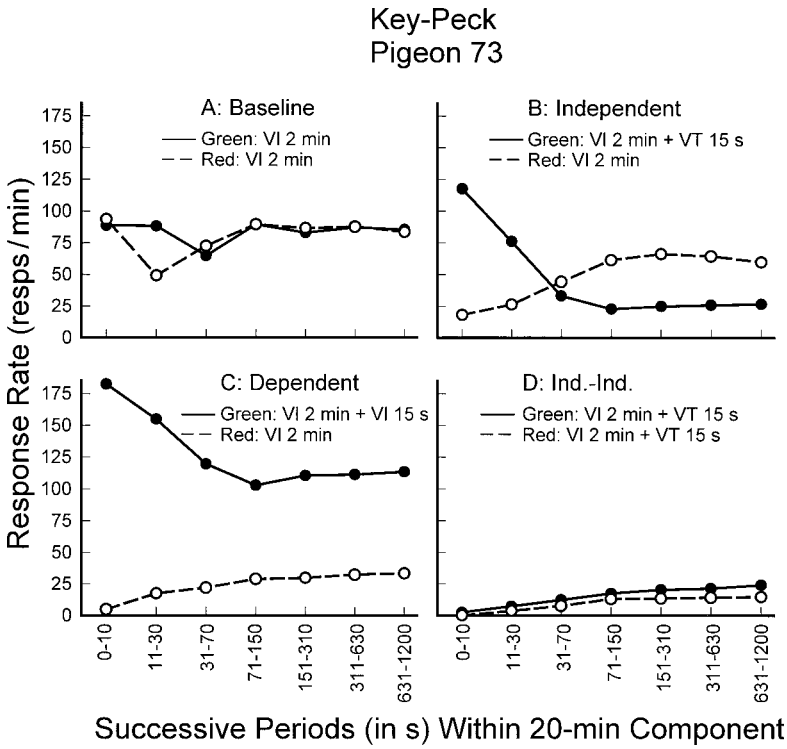

Fig. 5. Mean rate of responding across successive intervals of the 20-min component durations for Pigeon 73 for each phase of the key-peck response condition. Solid lines are rates during the green component; dashed lines are rates during the red component.

Pigeons 73, 74, 75, and 8 were first studied with the key-peck response and then switched to the treadle-press. Their results replicate those obtained from the pigeons initially studied with the treadle-press response. For each pigeon, when extra food was delivered independently of responding in the green component, treadle-press rates were lower in the green than in the red at both 10-s and 20-min component durations (see Figure 7, upper right panel). When the extra food deliveries were dependent on treadling, response rate for each pigeon was higher in the green than in the red component at both 10-s and 20-min component durations (see Figure 7, lower right panel).

The results from Pigeons 31 through 34 under the Independent and Dependent phases across the 20-min green and red components replicated those obtained with the 4 pigeons initially studied with the key-peck response. The left panels of Figure 8 show mean rate of responding across the 20-min green and red components for the key-peck response. Again, during the Independent phase (shown in the upper left panel of Figure 8), responding during the green (with the VT) was elevated during the initial portion of the component and decreased over time, whereas responding was initially suppressed and recovered during the red component (without the VT). The functions crossed for each pigeon. As can be seen in the lower left panel of Figure 8, when all food was dependent on pecking (Phase C), responding during the green also showed an initial elevation in response rate which, for every pigeon, remained above that in the red component.

The right panels of Figure 8 present mean rate of treadle-press responding across the 20-min interval for Pigeons 73, 74, 75, and 8. In general, responding in the red component was initially suppressed, followed by recovery of responding over time. This pattern was obtained regardless of whether the higher rate of food delivery in the green was presented independently of, or dependent on, a re-

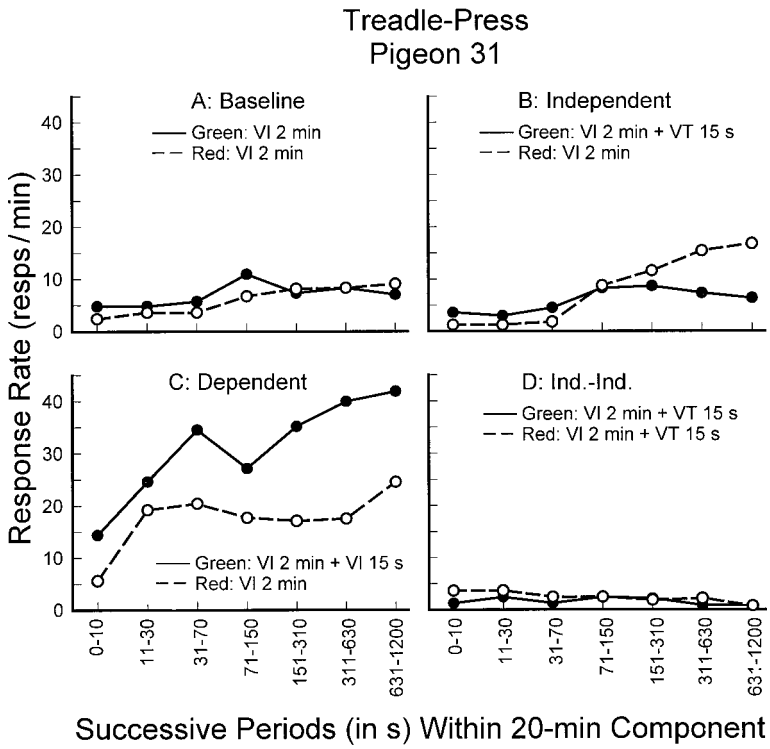

Fig. 6. Mean rate of responding across successive intervals of the 20-min component durations for Pigeon 31 for each phase of the treadle-press response condition. Solid lines are rates during the green component; dashed lines are rates during the red component.

sponse. On the one hand, during the green component when all food was response dependent (Phase C), treadle-press responding was also suppressed at the beginning of the interval and recovered over time, but rate of responding was always considerably higher than that during the red component (see Figure 8, lower right panel). On the other hand, when the additional foods were response independent (Phase B), rate of responding in the green component generally remained well below that in the red component throughout the 20-min component (see Figure 8, upper right panel).

Figure 9 presents the data across the 20-min interval for Pigeon 31 under the key-peck response requirement and for Pigeon 73 under the treadle-press response requirement. These pigeons are the same two that were shown previously but with the alternative response requirement. As is evident, the pattern of responding during the Independent and the Dependent phases shown for the group is apparent in the individual pigeons and, furthermore, replicates that seen previously with the respective response requirement.

DISCUSSION

According to the economic effect, the addition of response-independent food should be accompanied by a steady-state decrease in responding when either key pecking or treadle pressing is the operant response. Additional response-dependent food should increase steady-state key pecking and treadle pressing. According to the biological effect, a biologically relevant response should increase at the transition into a component with a localized visual signal for higher rates of food in a multiple schedule, and decrease at the transition into a component with a localized signal for lower rates of food. The increase in responding, however, should not be observed when a nonbiologically relevant response is the operant.

Together, the economic and biological ef-

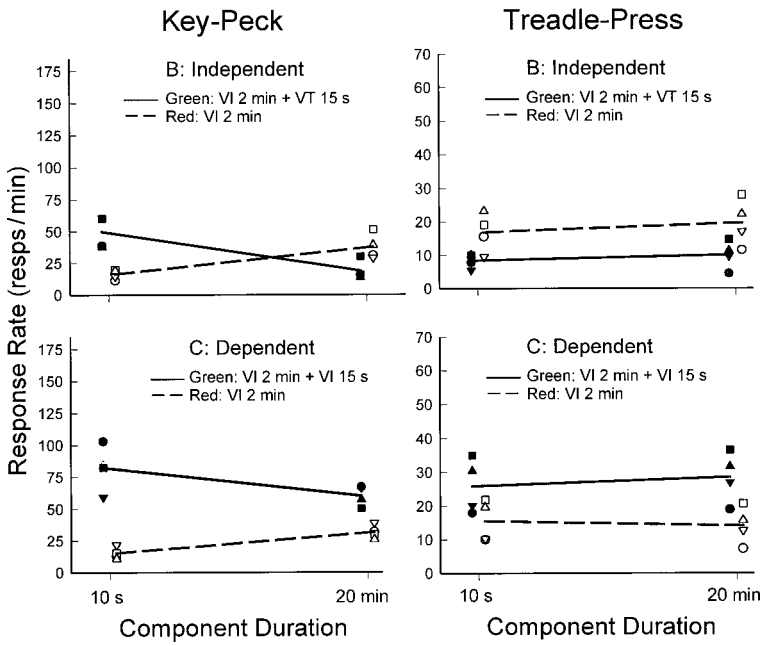

Fig. 7. Overall rates of key pecking (left panels) for each pigeon originally studied with the treadle-press response, and overall rates of treadle pressing (right panels) for each pigeon originally studied with the key-peck response, in the green (filled symbols) and red (open symbols) components at 10-s and 20-min component durations for Phase B (Independent) and Phase C (Dependent). Each pigeon is represented by a separate symbol. The solid line represents the mean overall rate of responding in the green component, and the dashed line represents the mean overall rate of responding in the red component.

fects predict different patterns of results when the operant is either biologically relevant (e.g., the key peck) or nonbiologically relevant (e.g., the treadle press), and when components of a multiple schedule are of brief duration or long duration. With *mult* VI 2 min (red component) VI 2 min + VT 15 s (green component), overall rate of key pecking should be higher in green with 10-s component durations because of the transient biological effect, but higher in red with 20-min component durations because of the steady-state economic effect. In contrast, overall rate of treadle pressing should be higher in red during both 10-s and 20-min component durations.

With all food deliveries response dependent, *mult* VI 2 min (red component) VI 2 min + VI 15 s (green component), overall rate of key pecking should be higher in green with 20-min component durations because of the economic effect, and higher still in green with 10-s component durations because the biological effect combines with the economic effect. Similarly, rate of treadle pressing should be higher overall in the green component with 10-s and 20-min component durations. Key-peck response rates *across* the 20-min component also should reflect the transient nature of the biological response, showing an increase at the beginning of the component with the higher rate of food delivery, whereas treadle-press responding should not show this initial increase.

When additional but equal amounts of response-independent food are presented in both components, *mult* VI 2 min + VT 15 s (red component) VI 2 min + VT 15 s (green component), overall rate of key pecking and treadle pressing should be relatively equivalent in the green and red component. In this case, there is no biological effect because transitions between components do not lead to higher or lower rates of food delivery. That is to say, there is no localized signal for higher rates of food delivery that would lead to an increase in the biological response.

Overall, the results of the present experiment confirm these predictions. When components alternated every 10 s during Phases

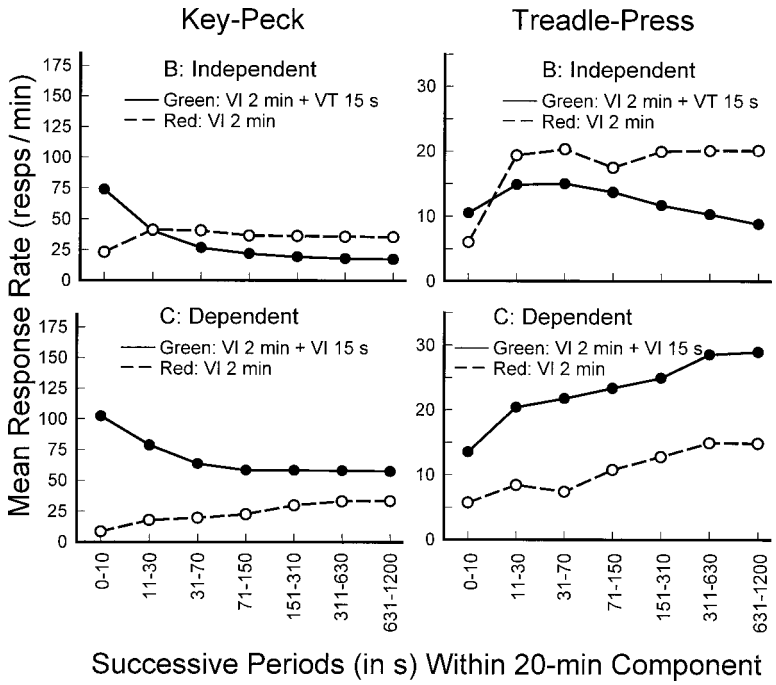

Fig. 8. Mean rates of key pecking (left panels) for the pigeons originally studied with the treadle-press response, and mean rates of treadle pressing (right panels) for the pigeons originally studied with the key-peck response, across successive intervals of the 20-min component durations for Phase B (Independent) and Phase C (Dependent). Solid lines are rates during the green component; dashed lines are rates during the red component.

B (Independent) and C (Dependent), the biological effect dominated key-peck response rate but had no excitatory effect on rate of treadle pressing. When components alternated every 20 min, the economic effect dominated the overall rate of both key pecking and treadle pressing (see Figures 1 and 2).

The results from Phase D (Independent-Independent) show that the delivery of response-independent food, by itself, does not result in higher rates of responding. This is especially clear with the key-peck response (see Figures 1 and 3) where response rates were, as expected, lower than in Phase A (Baseline) where no additional response-independent food deliveries occurred. This pattern of results was consistent across both 10-s and 20-min component durations. Less clear was the effect of response-independent food on the rate of the treadle-press response (see Figures 2 and 4) where the mean response rate was not lower under the response-independent food components of Phase D as compared to that under Phase A. Inspection of individual response rates, however, reveals that 1 pigeon (Pigeon 33) treadle pressed at a rate of two to ten times higher in Phase D than Phase A. The other pigeons responded at lower or somewhat equivalent rates in Phase D.

Figures 1, 2, and 7 reveal two major differences in responding between the key-peck and treadle-press conditions. First, whereas the biological effect dominated responding under the 10-s component duration during the biologically relevant key-peck condition, the economic effect dominated the results when the two effects were set in opposition during the nonbiologically relevant treadle-press condition (Phase B, Independent). It also is to be noted that rate of treadle pressing was sensitive to reinforcement contingencies (compare rate of treadling in Phase B, Independent, with Phase C, Dependent) (cf. Davison & Ferguson, 1978).

A second difference between the key-peck and treadle-press conditions was that the duration of the component had little effect on overall rate of treadle pressing, unlike that obtained under key-peck conditions. This

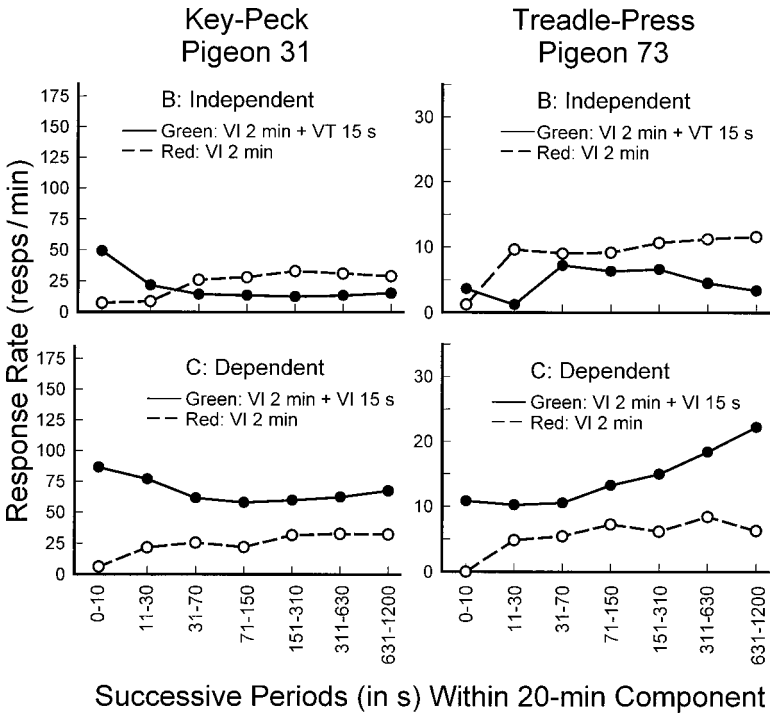

Fig. 9. Mean rates of key pecking (left panels) for Pigeon 31, originally studied with the treadle-press response, and mean rates of treadle pressing (right panels) for Pigeon 73, originally studied with the key-peck response, across successive intervals of the 20-min component durations for Phase B (Independent) and Phase C (Dependent). Solid lines are rates during the green component; dashed lines are rates during the red component.

finding is inconsistent with previous studies that found that with shifts in reinforcement, rate of key pecking or treadle pressing was inversely related to component duration (e.g., McSweeney, Dougan, Higa, & Farmer, 1986). Our failure to find systematic changes in the treadle-press response rate as a function of the change from lower to higher rates of food delivery, however, was predicted by the biological and economic effects analysis.

The distribution of responding across the 20-min interval under both the key-peck and treadle-press conditions is consistent with the biological and economic analysis. Transition to a higher rate of food delivery excites the biological response, leading to the increase in key pecking (see Figure 3). Such excitation may interfere with the emission of another, nonbiological response, thus producing the observed initial suppression of treadle responding (see Figure 4). Although we have no direct measure of the pigeons' movements towards the green houselight (which signaled the component with the higher rate of food delivery), LoLordo, McMillan, and Riley (1974) reported that the presentation of a localized visual conditional stimulus (CS) may initially suppress the treadle-press response in the pigeon because directed movements (conditional responses or CRs) towards the CS interfere with the treadle-press response.

Transition to a lower rate of food delivery initially inhibits the biological response, thus leading to a decrease in key pecking. This inhibitory effect diminishes over time. It remains unclear, however, why the transition to a lower rate of food also decreased treadle pressing, a nonbiological response. Rachlin (1973) argued that if the inhibited response (e.g., key pecking) is different from the operant response (e.g., treadle pressing) then there should be no inhibitory effect on operant responding. We suggest, however, that inhibition (like excitation) of a biological response might, under certain arrangements, produce interference with the treadle-press response. Just as a localized signal for an increase in food delivery produces movement

toward the signal, so, too, a localized signal for a decrease in food delivery may produce withdrawal from the signal (Green, 1978). When the movement away from the signal also moves the organism away from the operandum, then a decrease in responding at the transition to the lower rate of food delivery might be observed (as we found in most of our pigeons; see Figure 6).

Boakes, Halliday, and Poli (1975) also found, in both rats and pigeons, that differential changes in responding as a function of response-reinforcer contingencies (what we term the economic effect) and stimulus-reinforcer contingencies (what we term the biological effect) were predictable when the ecological validity of the operant was considered. Their study involved a different operant response for each species (i.e., lever pressing for rats and key pecking for pigeons). The present results extend the generality of their findings by using a biologically relevant and nonrelevant response within the same animal.

We have argued that treadle pressing is a nonbiologically relevant response, at least with respect to the present arrangement. It would seem reasonable, however, that the treadle-press response (or some form of that response; e.g., lifting a leg) could be an elicited response (CR) if the proper unconditional stimulus were to be identified. Under such an arrangement, the treadle-press response would have biological relevance and the present analysis would make empirically testable predictions.

A crucial issue in learning is whether a general-process approach can be sustained in which elemental processes are operable across species and situations. Species- and situation-specific results (often referred to as ''constraints on learning'') have led some to question whether general laws of learning can be developed (e.g., Bolles, 1970). An alternative approach, proposed by Domjan and Galef (1983), suggests that ecological considerations could be used to strengthen general laws of learning. They suggested that learning theorists, in part by identifying correlations between selective pressures and behavior, could in fact strengthen general laws of learning by way of an integration of the study of learning and behavioral ecology.

The pigeon's key-peck response for food is a nonarbitrary, biologically significant behavioral elaboration of a consumatory response. As such, laws of behavior derived from studies with this operant might not accurately pertain to situations involving the pigeon's treadle-press response, a response that may not be a biologically relevant food response. Indeed, our results show that the response-independent delivery of food can have significantly different effects on responding depending on the operant under study. Importantly, however, we successfully integrated basic animal-learning procedures with biological considerations, and there was no need to propose any unique, response- or species-specific learning mechanisms. Accurate predictions were possible given the interaction between the biological and economic effects.

We agree with Burns and Domjan's (2002) statement that it is necessary to ''test the generality of general-process theories outside the specific paradigms in which those theories were developed.'' We would add that it is also essential to test within the paradigms in which those laws were developed but with different operants within the same species. Such tests may allow one to distinguish between constraints that limit general laws and predictable effects that extend the generality of our laws.

The present study employed both operant (response-reinforcer) and Pavlovian (stimulus-reinforcer) procedures, yet we have avoided using these terms, preferring economic and biological, respectively. In support of our terminology, we would point to the fact that under certain of the experimental conditions the terms operant and Pavlovian did not uniquely specify the results. For example, the Pavlovian stimulus-reinforcer contingency in which a signal for a higher rate of (response-independent) food was added to one component of the multiple schedule led to significant increases in key pecking but to a decrease in treadle pressing. Moreover, pecking decreased whereas treadling increased with time spent in the component. The terms economic and biological effects were chosen because in spite of the superimposition of a stimulus-reinforcer (Pavlovian) *procedure* on a response-reinforcer (operant) *procedure,* the *effect* on responding differed depending on the response being measured. The terms biological and economic, then, are used to re-

fer to the effects of various procedures and contingencies on responding understood within an ecological framework.

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