# Schedule-induced polydipsia in the cotton rat (*Sigmodon hispidus*)

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Two of three wild-caught cotton rats developed schedule-induced polydipsia on fixed-time (FT) food schedules in which both level of deprivation and length of the interpellet interval were varied systematically. One cotton rat first developed polydipsia on an FT 2-min schedule at 80% body weight; the other cotton rat did not develop polydipsia until placed on an FT 3-min schedule and body weight was reduced to 70%. These data indicate the importance of systematic variation of relevant variables before concluding that a given species does not display schedule-induced polydipsia. The adaptive significance of adjunctive behaviors is discussed.

Schedule-induced polydipsia is characterized by an excessive intake of water when food-deprived animals are placed on an intermittent food schedule (Falk, 1969, 1971). Polydipsia has been demonstrated in a large number of species, including rats (e.g., Falk, 1969), mice (Ogata, Ogata, Mendelson, & Mello, 1972; Palfai, Kutscher, & Symons, 1971; Symons & Sprott, 1976), guinea pigs (Porter, Sozer, & Moeschl, 1977), Mongolian gerbils (Porter & Bryant, 1978a, 1978b), pigeons (Shanab & Peterson, 1969; Magyar, Allen, Sicignano, & Malagodi, Note 1), rhesus monkeys (Allen & Kenshalo, 1976; Porter & Kenshalo, 1974; Salzberg, Henton, & Jordan, 1968; Schuster & Woods, 1966), Java monkeys (Allen & Kenshalo, 1978), squirrel monkeys (Barrett, Stanley, & Weinberg, 1978), and humans (Fallon, Allen, & Butler, 1979; Kachanoff, Leveille, McLelland, & Wayner, 1973). Thus, schedule-induced polydipsia appears to have a great deal of generality across different species of animals, although most of the research has been with the domesticated rat (both albino and hooded).

The only reported attempt to find schedule-induced polydipsia in nondomesticated rats is by Hoppmann and Allen (1979). They found that only one of five wild-caught rats (*Rattus norvegicus*) developed schedule-induced polydipsia when tested on a fixed-time (FT) 1-min food schedule for 30 1-h sessions, and concluded that their data appeared to challenge the generality of schedule-induced polydipsia. In light of Falk's (1977) proposal on the adaptive significance of adjunctive behaviors, it is important to further test the generality of schedule-induced polydipsia in wild-caught rats. The cotton rat (*Sigmodon hispidus*) was chosen for the

present study because it is one of the most abundant rodents in the southeastern United States (Walker, 1964).

The hispid cotton rat is a grayish brown to blackish medium-sized cricetine rodent (70-100 g) that is found from tropical America northward to the central portion of the United States. The northern extent of its range in the eastern United States is near Richmond, Virginia (Pagels, 1977). The cotton rat is generally found in grassy and shrubby areas, and its home range is believed to have a radius of less than 30 m (Walker, 1964). In Virginia, cotton rats are often found in patches of Japanese honeysuckle (*Lonicera japonica*), which serve as a nesting area and provide food and cover throughout the year (Pagels, 1977). The hispid cotton rat differs both from typical cricetines (e.g., the white-footed mouse, *Peromyscus leucopus*) and from typical murines (e.g., the house mouse, *Mus musculus*, and the Norway rat, *Rattus norvegicus*) in that it possesses somewhat smaller pinnae and relatively shorter legs and tails, and the bicoloration between dorsal and ventral pelages is much less distinct. These characteristics relate to the habitat in which the cotton rat lives and its basic restriction to surface runways through grass, under shrubs, and the like, although cotton rats have been observed above ground level in honeysuckle (Wright & Pagels, 1977). The other rodents noted above, *Peromyscus*, *Rattus*, and *Mus*, all have relatively large pinnae, long legs, large eyes, and long tails, and all are distinctly bicolored. These characteristics are associated with the climbing ability of these animals (scansoriality). Other characteristics of the cotton rat in Virginia are that it is diurnal during most of the year (active night and day in the coldest part of winter), it does not hibernate, it is not known to store food, and it seems especially sensitive to low ambient temperatures and other extremes associated with winter (Kirksey, Pagels, & Blem, 1975).

In the present study, wild-caught cotton rats were tested on FT food schedules in order to determine whether or not schedule-induced polydipsia would

0090-5054/80/070015-04$00.65/0

develop. Level of deprivation and length of the inter-pellet interval were varied systematically, as these variables have been shown to be important in both the development and the maintenance of schedule-induced polydipsia (Falk, 1969, 1971).

## METHOD

### Animals

Animals were three (one male, CR5, and two females, CR3 and CR6) wild-caught cotton rats (*Sigmodon hispidus*). They were trapped in Chesterfield County, Virginia (about 12 km south of Richmond, Virginia), in Sherman live-traps with a dry mixture of rolled oats and peanut butter as bait. After capture, the cotton rats were isolated for 4 weeks and treated for external parasites with VIP Tick and Flea Powder (5% carbaryl). They were housed individually in shoebox cages (30 x 20 cm), with cedar shavings used as the bedding throughout the entire study. Purina Laboratory Chow and water were freely available. After the 4-week isolation period, the rats were moved to an animal colony room (7:00 a.m. to 7:00 p.m. light-dark cycle).

### Apparatus

Test sessions were conducted in two Scientific Prototype operant conditioning chambers (Model A-100) that were housed in sound-attenuated cubicles. A water bottle was mounted behind the intelligence panel on the right-hand side, with the metal drinking spout protruding approximately 15 mm into the test chamber. There was no response lever during the sessions. Reinforcers were 45-mg standard formula Noyes pellets. The houselight was on and white noise was present during each session. Standard electromechanical programming and recording equipment were located in an adjacent room.

### Procedure

After the 4-week isolation period, the cotton rats were maintained for an additional 20 days with free access to food and water, and they were weighed and handled daily. Next the rats were gradually reduced to 85% of their free-feeding body weights (BW, mean of the last 3 days) by adjusting their daily ration of food over an 8-day period. Water was continuously available in the home cage throughout the entire study. Table 1 shows the testing conditions and the number of sessions for each condition. Test sessions were conducted daily, with sessions terminating after delivery of the 30th food pellet, except during baseline testing, during which all 30 pellets were given at the beginning of each session. This allowed baseline measures of water consumption in response to 30 food pellets to be determined. After seven baseline sessions (30 min each), 30 food pellets were delivered according to a FT 1-min reinforcement schedule in which a pellet was delivered every minute indepen- dently of the rat's behavior. Testing with the FT 1-min schedule was conducted at 85% BW, 80% BW, 75% BW, and then at 80% BW again. The body weights were adjusted and stabilized for 4-5 days before testing was conducted at each level of depri-vation. After the FT 1-min 80% BW test condition, the interpellet interval was increased to 2 min (60-min sessions) and then to 3 min (90-min session). Baseline measures were taken again at 80% BW, with 30 food pellets given at the beginning of each 90-min session. The FT 30-min food schedule was then rein-stated, and testing was conducted at 80% BW, 75% BW, and 70% BW (4-5 days between each testing condition). Finally, baseline measures were taken again for Subject CR3 at 70% BW. Total licks and water intake were measured during each test session. Water consumption was determined by weighing the water bottle before and after each session to the nearest .5 g. Water spillage due to the handling of the bottles was subtracted before computing total session intakes. For convenience, water intake is reported in milliliters (1 g = 1 ml).

### Table 1
Mean Water Intakes (in Milliliters) for the Last Two Sessions of Each Testing Condition for Each Cotton Rat

| Schedule Condition | N | CR3 | CR5 | CR6 |
|---|---|---|---|---|
| Baseline: 85% BW (30 pellets/30 min) | 7 | .2 | .0 | .1 |
| FT 1 min/85% BW | 10 | .0 | .1 | .1 |
| FT 1 min/80% BW | 7 | .1 | .2 | .1 |
| FT 1 min/75% BW | 7 | .1 | .1 | .1 |
| FT 1 min/80% BW | 7 | .3 | .1 | .1 |
| FT 2 min/80% BW | 16 | .4 | 3.1 | .6 |
| FT 3 min/80% BW | 10 | .5 | 3.9 | .7 |
| Baseline: 80% BW (30 pellets/90 min) | 5 | .2 | .9 | 2.0 |
| FT 3 min/80% BW | 5 | .2 | 1.4 | 1.7 |
| FT 3 min/75% BW | 7 | .9 | 2.6 | 2.6 |
| FT 3 min/70% BW | 6* | 16.3 | 4.1 | 3.8 |
| Baseline: 70% BW (30 pellets/90 min) | 5† | 1.7 | | |

*Note*—N = number of sessions for each condition. Water intakes have been corrected for spillage.   *12 for CR3.   †CR3 only.

## RESULTS

Table 1 shows the mean water intake (in milliliters) for the last two sessions of each testing condition for each cotton rat. Using a criterion of a threefold increase in water consumption above baseline levels, only CR3 and CR5 developed schedule-induced polydipsia. No drinking of any consequence occurred until the FT 2-min and FT 3-min schedules were in effect for CR5 at 80% BW (3.1 and 3.9 ml, respectively). Water intake for CR5 decreased to .9 ml when all 30 pellets were given at the beginning of the 90-min baseline sessions. CR3 did not begin drinking on the FT 3-min reinforcement schedule until reduced to 70% BW. Upon return to base-line conditions, CR3's water intake decreased from 16.3 ml to 1.7 ml. Both CR5 and CR6 showed increases in drinking on the FT 3-min schedule as the level of deprivation was increased, reaching a maximum at 70% BW (CR6's water-intake levels were not three times above baseline levels, however). A similar relationship between the level of deprivation and amount of drinking is seen in domesticated Norway rats (Falk, 1969). If the session water-intake values in Table 1 are converted to milliliters per pellet, CR3 drank .54 ml/pellet on the FT 3-min schedule at 70% BW. This is comparable to that seen in domesticated Norway rats (Falk, 1969), and it exceeds that reported in one wild-caught cotton rat (McCaffrey, Pavlik, Hoppmann, & Allen, in press). CR5 drank only .14 ml/pellet, which is almost identical to the .15-ml/pellet intake of the cotton rat in the McCaffrey et al. study.

In Table 2, mean number of licks (last two sessions) are shown for consecutive 45-sec periods of the 3-min intervals for the 90-min baseline condition (80% BW) and the FT 3-min 70% BW schedule condition. The mean number of drinking bouts (a bout is defined as an interval in which drinking occurred) and water intakes are also shown. Both CR3 and CR6 had relatively flat distributions of licking in the baseline condition, whereas

**Table 2**
Mean Number of Licks (L), Drinking Bouts (B), and Water Intakes (I) for the Last Two Sessions of the 90-min Baseline Condition and the FT 3-min 70% BW Testing Condition for Each Cotton Rat

| Ani-mal | 45-sec Periods | | | | L | B | I |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | | | |
| Baseline: 80% BW (30 pellets/90 min) | | | | | | | |
| CR3 | .0 | .0 | 7.0 | 2.5 | 9.5 | 1.0 | .2 |
| CR5 | 113.0 | 40.5 | 12.5 | 4.0 | 170.0 | 6.0 | .9 |
| CR6 | 108.0 | 151.5 | 121.0 | 146.5 | 777.0 | 8.0 | 2.0 |
| FT 3 min/70% BW | | | | | | | |
| CR3 | 538.5 | 603.5 | 187.0 | 50.5 | 1379.5 | 17.0 | 16.3 |
| CR5 | 1115.5 | 109.0 | .0 | 17.0 | 1241.5 | 26.5 | 4.1 |
| CR6 | 541.0 | 480.5 | 193.0 | 74.5 | 1289.0 | 15.0 | 3.8 |

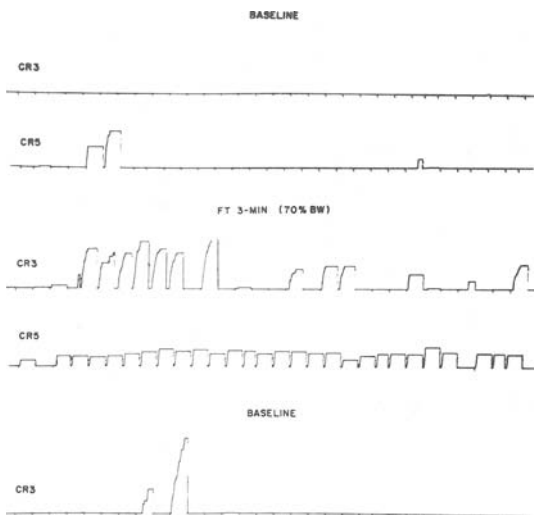*Note—Licks are shown during consecutive 45-sec periods of the 3-min intervals.*



Figure 1. Sample cumulative records for CR3 and CR5 from the last two sessions of the 90-min baseline condition (80% BW), FT 3-min schedule (70% BW), and a subsequent 90-min baseline condition (80% BW) for CR3. Each tube contact advanced the response pen, and pellet deliveries are indicated by the hatch marks. The response pen was reset to baseline with each pellet delivery. No food pellets were delivered during the baseline conditions.

CR5's licking was confined primarily to the first two 45-sec periods. On the FT 3-min schedule, all three cotton rats had similar patterns of licking, in which most of the licks were in the first two 45-sec periods (i.e., postpellet). Also, all three cotton rats showed substantial increases in total licks, number of drinking bouts, and water intake (even though CR6 did not meet the criterion of a threefold increase in water intake).

Figure 1 shows sample cumulative records for CR3 and CR5 from the last two sessions of the 90-min baseline condition (80% BW), FT 3-min schedule (70% BW),

and a subsequent 90-min baseline condition (80% BW) for CR3. Examination of these records clearly shows that the number of drinking bouts increased during the FT 3-min schedule (70% BW) and that drinking almost always occurred immediately following pellet delivery.

## DISCUSSION

The present study demonstrated schedule-induced polydipsia in two of three wild-caught cotton rats. However, polydipsia did not develop until the interpellet interval was increased to 2 min (at 80% BW) in one cotton rat, and the other cotton rat did not develop polydipsia until the interpellet interval was 3 min and its body weight was reduced to 70%. These data clearly differ from the typical results seen in domesticated rats (see Falk, 1969). Schedule-induced polydipsia readily appears in domesticated rats with interpellet intervals as short as 15 sec and at body weight levels of 85% or 90%. McCaffrey et al. (in press) also tested for the development of schedule-induced polydipsia in cotton rats. They found that only one of the wild-caught and none of the domestic cotton rats tested developed schedule-induced polydipsia. The one wild-caught cotton rat (W-4) that displayed polydipsia did not do so until it was reduced to 70% BW on an FT 1-min food schedule.

Research with several other species of animals has shown that it is difficult to obtain schedule-induced polydipsia with testing conditions under which domesticated rats readily develop polydipsia. Magyar et al. (Note 1) found that schedule-induced polydipsia did not develop in pigeons until the interpellet interval was at least 2 min in length. Porter and Bryant (1978a) showed that Mongolian gerbils did not develop schedule-induced polydipsia until the interpellet interval was 3 min. Hoppmann and Allen (1979) reported that only one out of five wild-caught Norway rats developed schedule-induced polydipsia when tested on FT 1-min food schedule at 80% BW. However, McCaffrey et al. (in press) have recently shown that these same five wild-caught Norway rats all developed schedule-induced polydipsia when their body weights were reduced to 70%.

The fact that one cotton rat (CR3, see Table 1) in the present study and one cotton rat in the McCaffrey et al. (in press) study did not develop polydipsia until reduced to 70% BW suggested that differential thresholds may exist in domesticated and non-domesticated rats (see Boice, 1973) for the development of schedule-induced polydipsia. Further evidence for this possibility was provided by McCaffrey et al. (in press), who showed that wild-caught Norway rats did not develop schedule-induced polydipsia until reduced to 70% BW. Thus, it would appear that nondomesticated rats require a higher level of food deprivation than do domesticated rats to develop schedule-induced polydipsia. McCaffrey et al. suggested that there may be differences between domesticated and nondomesticated rats in the motivational set points that control the drinking system. However, a simpler explanation may handle this apparent discrepancy. In the present study, the cotton rats were housed for about 50 days after capture before BWs were computed. The subsequent deprivation levels used for testing were based on these weights. If the deprivation levels are recalculated using the rats' initial (lower) body weights shortly after capture, then the 70%-BW levels used in testing actually represent body weight levels of about 80%. The cotton rats used in the McCaffrey et al. (in press) study were housed for 90-110 days prior to the start of the experiment. Therefore, the deprivation levels during testing were based on body weights higher than those that would have been maintained if the cotton rats had still been in the wild, instead of sitting in a small cage in which they did not have as much opportunity for exercise. This explanation could be tested by raising some wild-caught cotton rats in standard small cages

and some in cages with running wheels that would provide the opportunity for exercise.

The question still remains: Why do domesticated rats display schedule-induced polydipsia more readily than do nondomesticated rats? Falk (1977) states that "the adaptive value of adjunctive behavior consists in its maintenance of the organism's engagement with a problematic, but overall favorable, situation" (p. 331). The problematic situation is one in which the animal should remain (e.g., when feeding) but also should have a tendency toward escape behavior. Thus, the adjunctive behavior helps to maintain the animal in the favorable situation by occluding the escape behavior. Falk also concludes that there is a predictable relationship between the mobility of an animal in its foraging behavior (for food) and the relative amount of adjunctive behavior it should display. According to Falk, a species with a low mobility in its foraging behavior might be expected to show less escape behavior and, therefore, should evidence less adjunctive behavior. Conversely, very mobile foragers should display adjunctive behaviors more readily (presumably because they show more escape behavior).

We would like to propose a more parsimonious explanation for the adaptive significance of adjunctive behaviors. If a species' food supply is restricted to a small area (therefore, low mobility in foraging), then it would be adaptive for adjunctive behaviors to be displayed, since this would help maintain the animal in a favorable situation. On the other hand, if a species' food supply is scattered over a large area (therefore, high mobility in foraging), then it would be maladaptive for adjunctive behaviors to be displayed, since adjunctive behaviors would help maintain the animal in an unfavorable situation. Obviously, it is more adaptive for an animal to stay in an area with a large food supply than in an area with a small food supply. Thus, the adaptive significance of adjunctive behaviors would be to help maintain an animal in an area with a relatively dense supply of food.

Since the available data (Hoppmann & Allen, 1979; McCaffrey et al., in press; the present study) suggest that schedule-induced polydipsia is difficult to obtain in wild-caught rats, then perhaps polydipsia represents an adaptation of domesticated rats to their artificial, man-made environment. Boice (1973) has suggested that domesticated animals show both morphological and behavioral adaptations to the special demands of their unnatural environment. The domesticated rat certainly has a low mobility in foraging behavior, compared with wild rats, since it is confined to a small cage. If, as we suggested in the previous paragraph, the adaptive significance of adjunctive behavior is to help maintain an animal in an area with a relatively dense food supply (therefore low mobility), then the appearance of schedule-induced polydipsia in domesticated rats may reflect the selection pressures of domestication. Conversely, wild-caught rats that exhibit a high mobility in foraging (relative to domesticated rats) should not develop adjunctive behaviors as readily.

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