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Avoiding Synchrony as a Strategy of Female Mate Choice

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Abstract. *It has long been thought that some female mammals (e.g., humans and Norway rats) synchronize their ovarian cycles when in close proximity. However, re-analyses of these studies have revealed serious and systematic methodological errors. In retrospect, this is exactly what should have been expected given that female mammals exhibit considerable ovarian cycle-length variability, which prevents synchrony. Despite the diversity of cycle lengths in mammals, little attention has been paid to possible adaptive functions of cycle-length in female mate choice. Thus an individual-based model of Norway rats is described here that uses actual data from an experimentally constructed habitat. Results showed that synchrony is costly to females in achieving matings with high quality males because synchrony forces female-female competition. Synchrony can be avoided by evolving longer cycles, but there are limits on cycle length due to the cost of waiting. Furthermore, it is possible for inter- and intra-female cycle length variability to be evolutionarily stable within a population; thus offering a plausible explanation for some of the diversity observed in ovarian cycle lengths in female mammals.*

Key words: Ovarian cycle synchrony; estrous synchrony; computer simulation; female mate choice; Norway rats; women; individual-based modeling.

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INTRODUCTION

Why do female mammals have ovarian cycles? The origin of ovarian cycling is unknown, but cycling may have evolved from the physiological process of follicular competition; a mechanism by which species typical ovulation numbers are achieved (Akin & Lacker, 1984; Schank, 2003). In this scenario, cycling may have evolved as a by-product of a mechanism for determining follicle number (Schank, 2003). Because evolution is opportunistic, once a phenotypic feature is present with heritable fitness consequences, evolutionary forces may exapt it for other functions (in the sense of *expatation*, Gould & Lewontin, 1979).

The diversity in lengths and processes of ovarian cycles in mammals is considerable. Adult female rats, under standard laboratory conditions, ovulate every four or five days in the absence of mating (Everett, 1989; Johnson & Everitt, 2000) but wild rats appear to have cycles that are somewhat longer and more irregular (Calhoun, 1962; King, 1939;Long & Evens, 1922). Women ovulate on average every 29.5 days with considerable variability (Chiazze, Brayer, Macisco, Parker, & Duffy, 1968; Harlow, Lin & Ho, 2000). Even mammals that are seasonal breeders or those that do not exhibit behavioral or physiological indicators of cycling have waves of follicles that develop and become atritic if successful mating does not occur (Johnson & Everitt, 2000). Rabbits, in the absence of a male, exhibit waves of developing follicles about every two days (Johnson & Everitt, 2000). For cattle, sheep, and horses, there may be several waves of follicles preceding an ovulatory wave and the length of time between ovulatory waves is two to three weeks (Johnson & Everitt, 2000).

Physiological characteristics of ovarian cycles are also diverse. In humans there is an extended luteal phase in which follicular development is inhibited for about two weeks followed by a variable period of follicular development that lasts from one to several weeks (Johnson & Everitt, 2000). In small rodents such as Norway rats, the luteal phase is non functional (i.e., does not inhibit follicular growth), and follicular development is rapid but variable typically taking 4-days in laboratory rats (Everett, 1989; Johnson & Everitt, 2000; Long & Evens, 1922). Associated with ovarian cycles are endometrial cycles, which vary considerably among mammals in their physiological characteristics and are subject to natural selection (Strassmann, 1996). For example, by shedding the endometrium through menstruation, rather

than maintaining it throughout the ovarian cycle, saves energy (Strassmann, 1996). The diversity of ovarian cycle lengths and processes in mammals indicates that natural selection has operated directly or indirectly to shape characteristics and mechanisms of ovarian cycling.

The evolution of mating systems also may have created selective forces that have altered the length, variability, and characteristics of ovarian cycles. For example, in humans concealed ovulation may have evolved to obscure the timing of ovulation (together with female receptivity throughout a cycle) to increase male parental investment (Burley, 1979; Heistermann, et al. 2001). Ovarian-cycle synchrony is another process that could have evolved once cycling evolved. Studies from the 1970s and 1980s reported that females in two rodent species (Norway rats, McClintock, 1978, and golden hamsters, Handelmann, Ravizza, & Ray, 1980) three species of primates (women, McClintock, 1971, chimpanzees, Wallis, 1985, and golden lion tamarins, French & Stribley, 1985) synchronized their cycles when living in small groups.

Several adaptive scenarios have been offered for the evolution of synchrony, but none hold up to careful scrutiny (Schank, 2001d). For example, synchrony may promote the communal care of young by females with offspring. However, female rats do not communally raise their young (Calhoun, 1962) and neither do asocial golden hamsters (Gattermann, Ulbrich, & Weinandy 2002). In humans, the length of pregnancy is more variable in days than can be overcome by synchronizing ovarian cycles, which if it occurred, would only bring cycles a few days closer. Moreover, recent empirical and methodological studies revealed no evidence for synchrony and serious errors in previous studies (Arden & Dye, 1998; Cepicky, Mandys, Hlavicka, & Sosnova, 1996; Erb, Edwards, Jenkins, Mucklow, & Wynne-Edwards, 1993; Gattermann, Ulbrich & Weinandy 2002; Monfort, Bush & Wildt, 1996; Schank, 2000a, 2000b, 2001a, 2001b, 2001c, 2001d; Strassmann, 1997, 1999; Trevathan, Burleson & Gregory, 1993; Wilson, 1992; Wilson, Kiefhaber & Gravel, 1991). The basic problem not accounted for in earlier studies was that ovarian cycles are variable and variable cycles cannot synchronize unless they converge on the same stable cycle length (Winfree, 1980). Thus, there appears to be neither evidence for nor adaptive benefit of synchrony. Does synchrony therefore have potential fitness costs for females? If so, what are the consequences for selection on ovarian-cyclicity?

In this paper, I examine these questions using data from Norway rats and individual-based modeling. I will show that (i) synchrony is costly for female fitness and (ii) that the ecological and mating systems that make synchrony costly give rise to selection for cycle length. Specifically, I will show that the evolution of cycle lengths allows females to minimize the cost of accidental synchrony (or forced synchrony due to high female population density) constrained by the fitness costs of waiting associated with increasing cycle length.

Synchrony and Chance Coincidence of Biological States

An interesting feature of cyclic biological states is that that they can match by chance (Schank, 1997). State matching can occur at any given time even for individuals with different length cycles, but this is not synchrony because state matching does not persist over cycles. In the simplest case, when biological states have the same duration and all individuals have the same cycle length, then the probability of state matching can be calculated analytically (Schank, 1997). *Nk* synchrony occurs when there are N individuals cycling through k biological states of equal duration (Schank, 1997). Laboratory rats are a good example. Sprague-Dawley rats (one laboratory strain of Norway rats) typically have 4-day cycles (though there is variability in laboratory rats; Everett, 1989; Long & Evens, 1922; Schank, 2001b, 2001c). In a 4-day cycle, it is standard to distinguish $k = 4$ biological states: estrus, metestrus, diestrus, and proestrus (Johnson & Everitt, 2000; Schank, 2001b, 2001c). Typically, these are viewed as discrete biological states with duration of 24 hours. The main reason for viewing these states in this way is that ovulation in Norway rats is under circadian regulation (Everett, 1989; Johnson & Everitt, 2000).

Suppose that $k = 4$, and we observe groups of rats with exact 4-day cycles. We can then ask what the probability is that $m_1,..., m_k = N$ rats are distributed across k biological states at a given time. The probability distribution for each such configuration is given by the following multinomial distribution (Schank, 1997):

Table 1. Configurations of *N* Individuals Across *k* Biological States and Classification into Synchrony Levels.

	N = 6, k = 4	***N = 10, k = 4***		***N = 6, k = 4***	***N = 6, k = 4***
Config. #	S_1 S_2 S_3 S_4	S_1 S_2 S_3 S_4	**Sync. Level**	**Config. #**	**Config. #**
1	2 2 1 1	3 3 2 2	2	1, 2	
2	2 2 2 0	3 3 3 1	3	3, 4, 5	1, 2
3	3 1 1 1	4 2 2 2	4	6, 7	3, 4, 5, 6, 7
4	3 2 1 0	4 3 2 1	5	8	8, 9,10,11,12
5	3 3 0 0	4 3 3 0	6	9	13, 14, 15, 16
6	4 1 1 0	4 4 1 1	7		17, 18, 19
7	4 2 0 0	4 4 2 0	8		20, 21
8	5 1 0 0	5 2 2 1	9		22
9	6 0 0 0	5 3 1 1	10		23
10		5 3 2 0			
11		5 4 1 0			
12		5 5 0 0			
13		6 2 1 1			
14		6 2 2 0			
15		6 3 1 0			
16		6 4 0 0			
17		7 1 1 1			
18		7 2 1 0			
19		7 3 0 0			
20		8 1 1 0			
21		8 2 0 0			
22		9 1 0 0			
23		10 0 0 0			

$$p(m_1,\ldots,m_k)=\left(\frac{k!}{\ell(s_1)!\cdots\ell(s_r)!}\right)\left(\frac{N!}{m_1!\cdots m_k!}\right)\left(\frac{1}{k}\right)^N \quad (1)$$

where $p(m_1,..., m_k)$ is the probability of m_i individuals being in one of k biological states, $\ell(s_1)$ is the number of biological states that have the

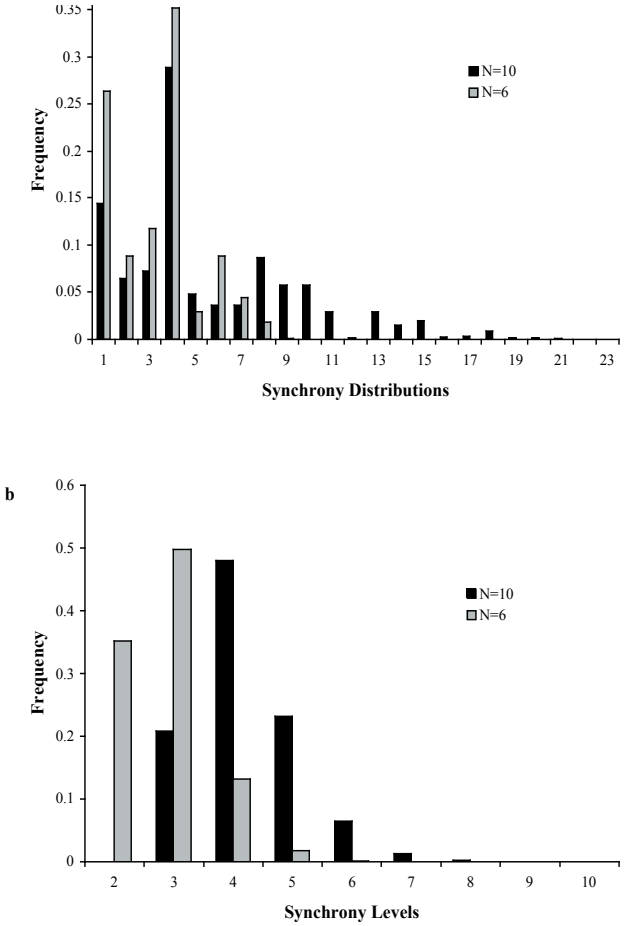


Fig. 1. Probability distributions for configurations of *N* = 6 and 10 females across *k* = 4 biological states (a). These distributions indicate that more synchronous configurations are less probable but they are multimodal in appearance. It is convenient to simplify these distributions (see Table 1). Thus, for *N* = 6, *k* = 4, there are 2 through 6 synchrony levels and for *N* = *10, k* = 4, there are 3 through 10 synchrony levels (b). Notice that as synchrony levels increase, their probability of occurrence decreases and that the most asynchronous level is not necessarily the most probable.

same number of individuals in them, and N is the total number of individuals. For example, suppose $N = 6$ and $k = 4$. The individuals could be configured over the four biological states such as <1, 2, 0, 3> (i.e., one individual in the first state, two in a second, none in the third, and three in a fourth) or <0, 6, 0, 0> (i.e., all individuals are in the same state). If we do not care which biological states individuals are distributed across (e.g., <1, 2, 0, 3> or <3, 1, 2, 0>), then equation (1) can be used to calculate the probabilities for each class of configurations and we can order all possible configuration classes of N and k as illustrated in Table 1 by the maximum number of individuals in a given state in ascending order.

In Fig 1, probability distributions are illustrated for two groups ($N = 6, 10$) of females cycling through $k = 4$ biological states. The distributions of configurations of females over biological states are very multi-modal in appearance (Fig. 1a). A heuristic for simplifying these distributions, which will be useful later, is to group all configurations that have the largest number of individuals in the same state as belonging to the same synchrony level (see Table 1). For example, all configurations with a maximum of 4 individuals in the same state are classified as level-4 synchrony (Table 1). As can be seen in Fig. 1b, such distributions illustrate that the most asynchronous level is not the most probable, but after the most probable level for a given N and k, the probability of more synchronous levels decreases rapidly. The important points are first that different levels of synchrony can occur by chance alone and second, for fixed k, increasing N, increases the minimum number of individuals in the same state.

Female Mate Choice

The development of evolutionary theory since Darwin (1859, 1874) includes a substantial literature concerning female mate choice (e.g., Parker, 1979; Clutton-Brock, 1989, 1991). The basic problem for females is how to evolve strategies that counter male strategies of manipulation (Parker, 1979). For example, male phenotypic quality is a potential fitness payoff for females. Females achieve higher fitness if they mate with males of relatively high phenotypic quality because phenotypic quality is either an indicator of “good genes” and/or good health (e.g., a relatively low pathogen load). But, how do females avoid being misled by males regarding phenotypic quality? The only way to rule out deceit is for females to make choices based on characters, which

males cannot manipulate for their benefit (Parker, 1979). A male peacock cannot grow large well-kept tail feathers if it is unhealthy. He is also likely to be a good forager (to invest the extra energy to grow and maintain large feathers) and good at avoiding predators. However, feathers cannot grow indefinitely long, so there will be tradeoffs between female choice (sexual selection) and natural selection on feather length.

Male quality is not the only factor that may influence female choice. If resources are insufficient for a female to raise her offspring on her own, then male parental care becomes a factor. In mammals, male parental care is typically less important than in birds (Jennions & Petrie, 2000). Males should invest more in the care of offspring only if a female has insufficient resources for rearing her young. Male parental care irrespective of whether a female can rear her young on her own will benefit the offspring, but if a male can obtain greater reproductive fitness by seeking more mates, then male parental care will not evolve (Clutton-Brock, 1989, 1991) unless females can manipulate males into investing in parental care. Though the reasoning is apparently straightforward, the quantitative argument underlying it has only recently been clarified (Wade & Shuster, 2002).

Even when male parental care is essential for female reproductive success, male quality is always a factor. When good parental care and male quality are not closely correlated, then female-mating strategies can become more complex (Wade & Shuster, 2002). For example, females may adopt a strategy of choosing high parental care males but "sneak" mates with high quality males though the fitness benefits remain unclear (Petrie & Kempenaers, 1998; Moore, Gowaty, Wallin & Moore, 2001). There is mounting evidence that this type of reproductive strategy is adopted in many bird species (Petrie & Kempenaers, 1998). The important point is that male quality always is an important factor in female mate choice, but overlooked in the literature on female choice are potential conflicts among females for quality males.

Male Norway rats provide no parental care. Thus, male quality is the only factor affecting female mate choice. Strategies for achieving mating with high quality males is little explored other. Mating system, ecological factors such as territories and the distribution of males and females influence the strategies that may evolve. Surprisingly, even though Norway rats are a primary research animal, relatively little is known about the ecology and social behavior of the wild Norway rat

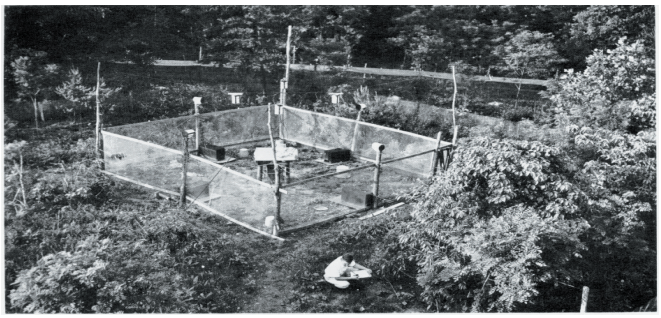
(Barnett, 1975). Calhoun (1962) conducted the only systematic naturalistic study of wild Norway rats. The Norway rat breeding system is best characterized as promiscuous, females in estrus may mate with multiple males in an evening and males may achieve matings with multiple females over time (Calhoun, 1962).

From the perspective of female mate choice theory, the problem for female rats is choosing quality males with high phenotypic quality. This suggests females need only detect reliable indicators (i.e., characters for which males cannot cheat) of male phenotypic quality and avoid male manipulation strategies. However, this analysis is not complete. It does not take into consideration that females may be forced to compete with each other for quality males. If a mating period is relatively short (e.g., an evening as with Norway rats), then several females in estrus at the same time may be competing for a few quality males if synchrony reduces the likelihood that females successfully mate with high quality males. Indeed, if females compete, the number of matings may decrease, which also may lower fitness (Gattermann, Ulbrich, & Weinandy, 2002). Therefore, I hypothesized that estrous synchrony is a state to be avoided and that ecological factors, such as the density of males and females, provide sexual selective forces for the evolution of different cycle lengths and perhaps stable cycle variability in a population in the sense of an evolutionary stable mating strategy (ESS or Nash equilibrium; Parker, 1979; Maynard-Smith, 1982).

METHOD

To test this hypothesis, I used the results of the only systematic study of the ecology and social behavior of wild Norway rats (Calhoun, 1962). Calhoun (1962), over a 27-month span from 1947 to 1949 studied wild caught Norway rats in a 100 × 100 pen (Fig. 2). Figure 2c illustrates not only the structure of the habitat but the extensive trail and burrows formed by November 1948. Calhoun (1962) discussed in detail the mating behavior of rats, the approximate number of females cycling at any given time, the number of adult males, and a categorical estimate of their rank. Using Calhoun's (1962) data and interpretations, I constructed an individual-based model to explore the consequences of

a



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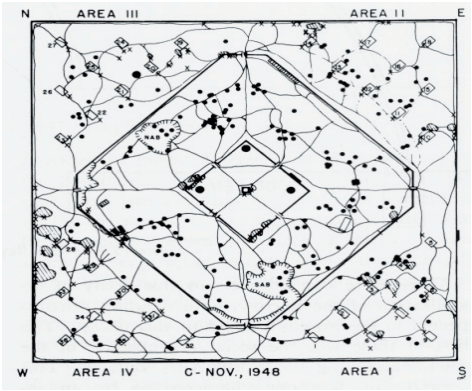

Fig. 2. Two pictures of Calhoun's (1962) wild rat habitat (a, b) and a diagram of the habitat including trails and burrow openings that I digitized and used in the simulations reported here (c).

cycle variability and synchrony among females on success in achieving quality matings and number of mates.

Movement

The model consisted of a 300 × 300 matrix of probabilistic cellular automata (see Figs. 3 & 4). Model rats ("particles") moved to adjacent cells based on probabilities calculated at each time step. Whether a rat moved to an adjacent cell also depended upon the likelihood of moving forward or turning (see Fig. 3). The probability of moving to one of eight adjacent cells was given by Eq. 2:

$$P(c_{ij}) = \frac{w_{ij} p_{ij}}{\sum_{h=I-1}^{I+1} \sum_{k=J-1}^{J+1} w_{hk} p_{hk}} \quad (2)$$

where IJ is the current location of a rat, p_{ij} is the basic probability of moving into a cell, w_{ij} weights the basic probabilities, and $P(c_{ij})$ is the calculated probability of moving into cell c_{ij}. This permitted control over the "momentum" of random walks along paths by simulated rats. If there is no weighting of directional movement (e.g., weights biased towards moving forward, see Fig. 3), model rats tend to move back and forth along a path making little progress along the path. Rats do move back and forth along paths (Calhoun, 1962), but if w_{ij}s are all the same, movement along paths appears more like an animal pacing in a cage than rats meandering on paths.

The basic probabilities, p_{ij}, (Table 2) were assigned by first digitizing and editing pixel by pixel the pen and trail map in Fig. 2c. This produced a new image illustrated in Fig 4a. I left out the nest boxes but included burrow openings, paths, fences, trees, and water locations. Within the two major mound areas, Calhoun (1962) did not mark all the burrow openings but said that they were numerous, so I added a number of burrow openings to these locations. Because the image was digitized to 300 × 300 pixels, a probability could be assigned to each cell based on the pixel value for that cell location. To prevent rats from escaping, the probability of penetrating the outer fence was always set to 0.0(Table 2).

The movement and behavior of rats also depended on their sex. In these simulations, I only modeled adult males and cycling female rats.

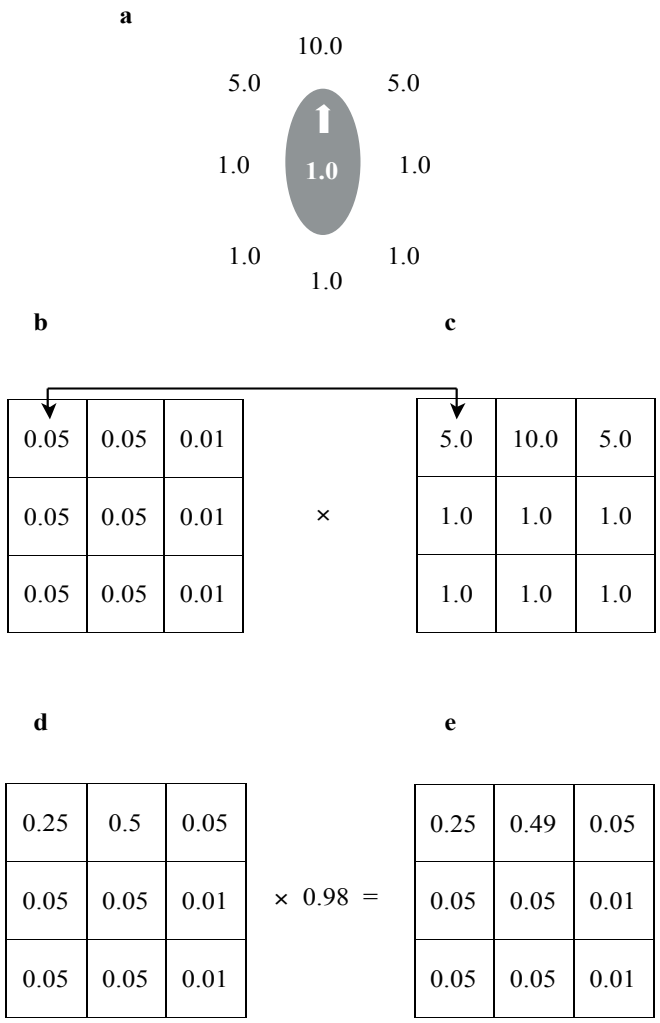

Fig. 3. A graphical illustration of how the local probability space (b) is updated as a function of weights for direction of movement (a, c). After each local probability (b) is multiplied by its corresponding weight (c), the resulting values (d) are renormalized to probabilities (e).

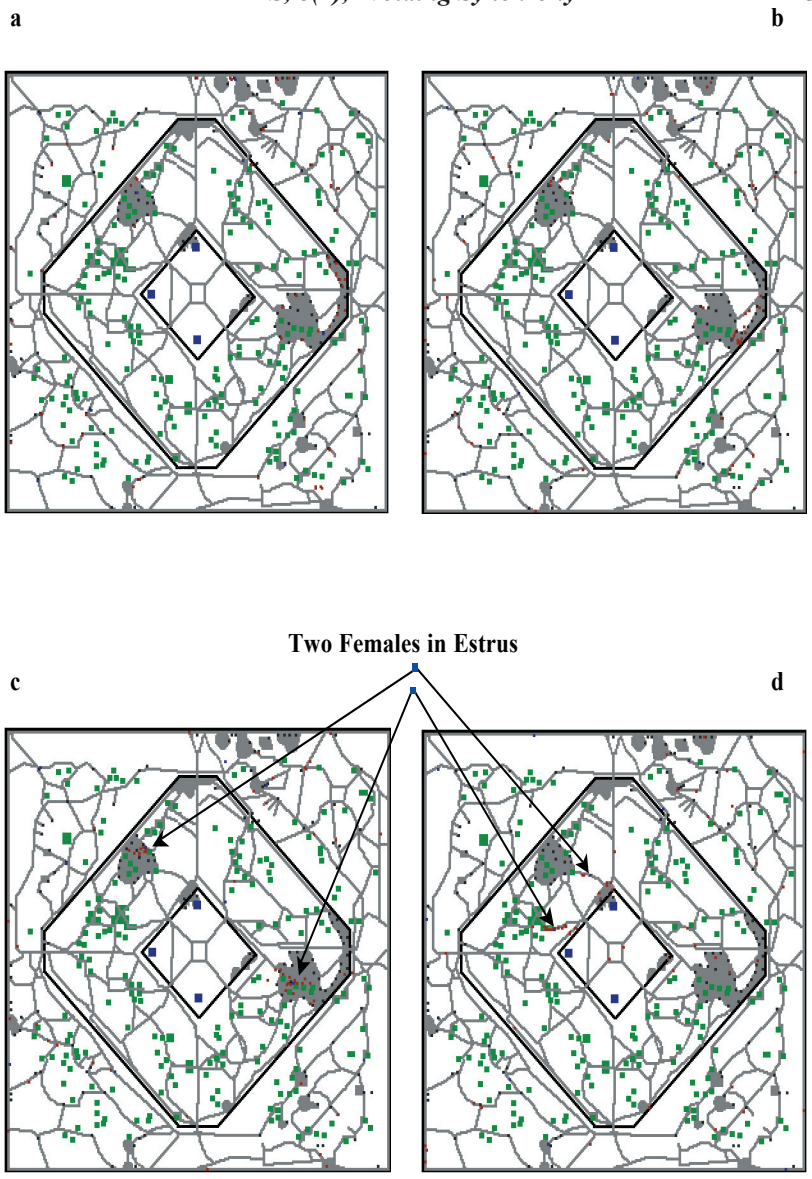

Fig. 4. The diagram of Fig. 2c digitized together with snap shots of simulations: just before the rats leave their burrows at night (a) and just after (b) followed by male rats (red) aggregating around female rats (blue, which are in heat, c, d).

Table 2. Summary of Parameters, Interpretations, Values, Their Source, and Robustness.

Parameters	*Interpretation/Values*	*Robustness*
N_m	Number of male rats: high rank, N_{hr} = 7, medium rank, N_{mr} = 12, low rank, N_{lr} = 42, N_m = 61[a]	For larger N_m or N_{hr}, less effect, but synchrony is never favored.
N_f	Number of female rats: range 5 to 10[a]	For larger N_f, effect becomes greater.
p_{ij}	ij cells probabilities based on the pixel value of the pen map[d] outer fence = .0, inner fences = .01, trees, water = .001, paths = 0.95, burrows = .5, all other spaces = .05[b]	If rats can move about and cannot escape, there is no qualitative change.
w_{ij}	multiplicatively weights adjacent and occupied cell probabilities an individual: forward = 10, left, right = 5, all others = 1.0[c]	Equal weights did not qualitatively alter results.
wf_{ij}	multiplicatively weights adjacent and occupied cell probabilities for males relative to females in estrus: towards = 5, left, right = 2.5, all others = 1.0[c]	When weights are not biased to females, quality and number of matings reduced, but synchrony is never favored.
d_{max}	maximum distance males can detect female in estrus: d_{max} = 150 cells (pixels)[b]	Decreasing d_{max}, decreases effect, but never favors synchrony.
r	female resting or "refractory" period after mating: 10 min[a]	Not varied and not expected to affect results.
$Q(i)$	male phenotypic quality distribution: high rank = 1.0,	Changes towards equality decrease effects, but

	medium rank = .75, low rank = .25[b]	synchrony is never favored.
p_{mate}	probability of mating at each time step, an average of 5 min intervals: .033 for each 10 sec step[b]	Does not qualitatively affect results

[a]Based on Calhoun's data (1962), [b]Partially based on Calhoun,
[c]Plausible but not essential [d]See Fig. 3.

Calhoun (1962) said very little about the movement of cycling females, so I assumed they moved about according to Eq 2. Males, however, move towards, follow, and attempt to mate with females (Calhoun, 1962). How male territories affected male movement was not fully described by Calhoun, but once a pack of males began to follow a female, they followed her wherever she went (Calhoun, 1962).

Rats urinate, defecate, and mark with scent glands indicating to other rats where they have been (Price, 1977). They also have an acute sense of smell for odor gradients. All of these factors can greatly complicate rat movement. In these simulations, I simplified these compli-cations by assuming that the distance to females in estrous altered the probability of a male rat moving towards her. This was accomplished by weighting the three cells next to a male but oriented closest to females (illustrated in Fig. 4) according to equation (3):

$$wf_{ij} = \begin{cases} 1.0 & \text{if female is not in estrus} \\ 1.0 & d_{fm} > d_{max} \\ w'_{ij}[1.0 - d_{fm}/d_{max}] & \text{otherwise} \end{cases} \qquad (3)$$

where wf_{ij} are weights for the movement probabilities (equation 2). Each of the adjacent cell probabilities oriented towards a female can be weighted differently wf_{ij}, but in the representative simulations below, I weighted the middle cell greater than the two adjacent cell probabilities (see Table 2). The variable d_{fm} was calculated using the distance formula

$$d_{fm} = \sqrt{(i - I)^2 + (j - J)^2} \qquad (4)$$

where *ij* is the location of a female and *IJ* is the location of the male. Thus, for males the probability of moving to or staying in cell, c_{ij}, is given by equation (5)

$$P_m(c_{ij}) = \frac{wf_{ij}P(c_{ij})}{\sum_{h=I-1}^{I+1}\sum_{k=J-1}^{J+1} wf_{hk}P(c_{ij})} \qquad (5)$$

where $P(c_{ij})$ is given by equation (2).

During the day (0600 h to 2000 h), rats remain in their burrows, starting at 0400 h, rats attempt to return to their home burrow but if they have not found it by 0600 h, they enter the first burrow they find. The equations for moving back to burrows are similar to equations (3) through (5) but are omitted because they are not essential to the results presented here.

Mating Behavior

For the purposes of these simulations, estrus is the day of ovulation. After estrus, is metestrus, then one or more diestrus states, followed by proestrus, and then estrus again. Estrus synchrony is measured in terms of the number of females in estrus on the same day over a mating cycle. Each female is in estrous only once. Presumably, if a female fails to mate, she could come into estrus a cycle later, but simulating this adds complications I have avoided here. For example, there is an unknown cost to waiting longer (see below). Mating one cycle later may provide the benefit of less female competition for males (since most if not all of the other females in the group mated), but there also may be new females now competing for mates. To avoid these complications, each female was tested only once. Females that had cycles longer than 4-days were assumed to have extended diestrous days. It is also possible to have extended estrous days (Everett, 1989). I did not include this possi-bility in these simulations because the main consequence would be to increase the cost of synchrony across females. Also, it is not clear whether extended estrus in laboratory rats is an artifact of domestic strain and/or laboratory conditions (Everett, 1989).

Specifically, at each time step Δt between 2000 h to 0400 h, females assess males in cells adjacent to or in the cell she occupies (more than one rat can occupy the same cell because rats often crawl over each other Calhoun, 1962). Following Calhoun (1962), during 1948 (p. 215),

61 adult males were present, which he classified into high, medium, and low ranking males. I assigned a number ranging from 0 to 1 to each of these classes. For example, in the simulations reported below, high-ranking males were assigned 1.0, medium, .75, and low, .25 (see Table 2). The results reported here did not qualitatively depend on the particular values chosen so long as high > medium > low. The rule for the probability of female *i* mating (when in estrus) with male *j* in a cell adjacent to her or in her cell is defined by equation (6):

$$P(i,j) = \begin{cases} 0 & \text{if time since last mating is less than 10 min} \\ p_{mate} \times Q(j) & \text{otherwise} \end{cases} \tag{6}$$

where $Q(j)$ is the quality of the highest-ranking male near her. This assumption can be relaxed with qualitatively similar results (see below).

Measuring Estrous Synchrony

For a group of N_f cycling females, maximum synchrony would occur if all the females came into estrus on the same day. Minimum synchrony would occur if none of the females came into synchrony on the same day. If the number of females, N_f, exceeds the number of biological states, k, then some females will come into estrous at the same time (see Table 1). If the estrous states of females are randomly related to each other, then all possible combinations can occur. Table 1, illustrates the possible estrous state combinations for $N_f = 6$ and $N_f = 10$ females when the number of biological states is $k = 4$. As discussed above, it is convenient to classify synchrony configurations according to the largest number of females in the same state (Table 1). When classified into these levels, the relationship among probabilities of synchrony by chance becomes clearer (Fig. 1b) and it is easier to compare synchrony for various N_f.

Simulation Procedure

At the start of each simulation, N_m adult males and N_f cycling females were randomly assigned to burrow entrances (more than one rat could be assigned to the same burrow entrance; Table 2). A daily 14-hour light and 10-hour dark cycle was assumed. Thus, on each day at 2000 h, rats left their burrows and began meandering primarily along paths according to equation (2). Drives or motivation other than sex (e.g., hunger and thirst) were not modeled in these simulations. Male rats could detect females in estrus if they were within a radius of detection as described by equations (3) to (5). If a female mated with a male, she did not mate until at least 10 minutes had past (Calhoun, 1962; also see Table 2). The number of matings and male quality were recorded, as was the number of females in estrus on the same night.

RESULTS

The more synchronized a group of females were, the lower the expected male phenotypic quality and number of mates achieved (Fig. 5). Both of these expectations decreased as a function of the number of currently cycling females (Fig. 5). Figure 5a illustrates how expected male quality decreases as a function of the level of synchrony for groups of N_f = 5 to 10 females, and Fig. 5b illustrates the corresponding decrease in number of matings. These results are qualitatively robust for a wide range of parameter values as discussed below.

Both male quality and number of matings increased as cycle length increased (Fig. 6). All levels of synchrony for N_f = 10 females were simulated with synchrony level determined by chance according to the probability distribution in Fig 1a. Figure 6a illustrates increasing male quality as cycle lengths are increased from 4 to 7 days for groups of N_f = 10 females, and Fig. 6b shows the corresponding increase in number of matings. Thus, increasing cycle length is one way to lessen the costs of synchrony. Again, these results were qualitatively robust for a wide range of parameter values.

These results imply that if the number of cycling females is relatively high, then sexual selection, due to female-female competition, should act to increase cycle length. Similarly, if the number of males or the number of higher quality males is reduced relative to the number of

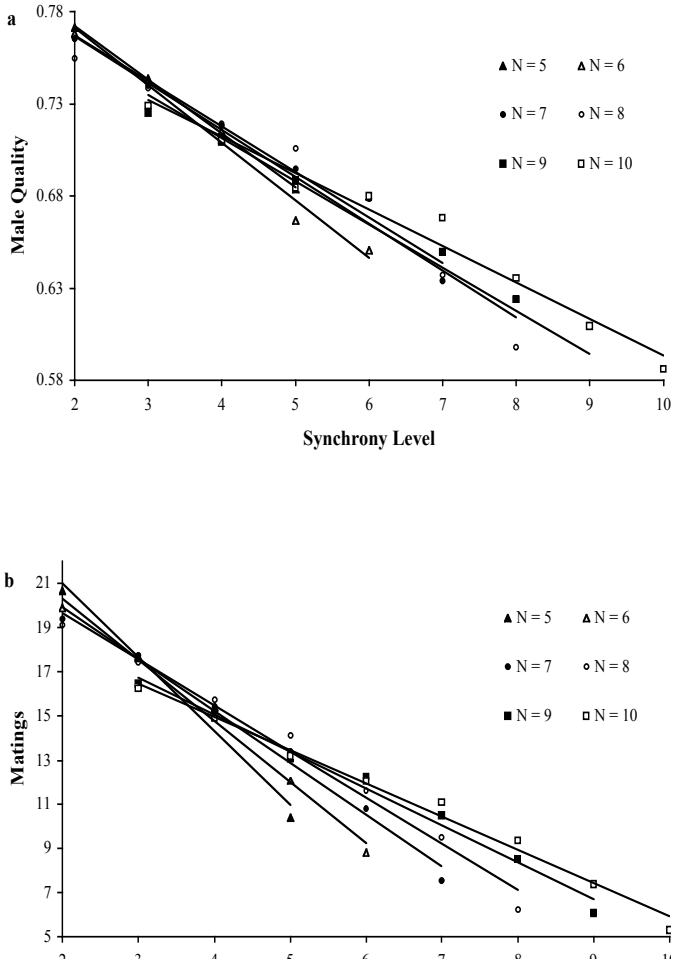

Fig. 5. Mean male phenotypic quality for N = 5 to 10, k = 4 (a) and mean number of mates for the same parameters (b). Each synchrony configuration was simulated 50 times (see Table 1) and then averaged for each synchrony levels. As illustrated, both mean male phenotypic quality and number of matings decreases with increasing synchrony. In general, increasing N increases the number of females that must be in estrus on the same day (holding cycle length constant), so both phenotypic quality and number of mates decreases with increasing N.

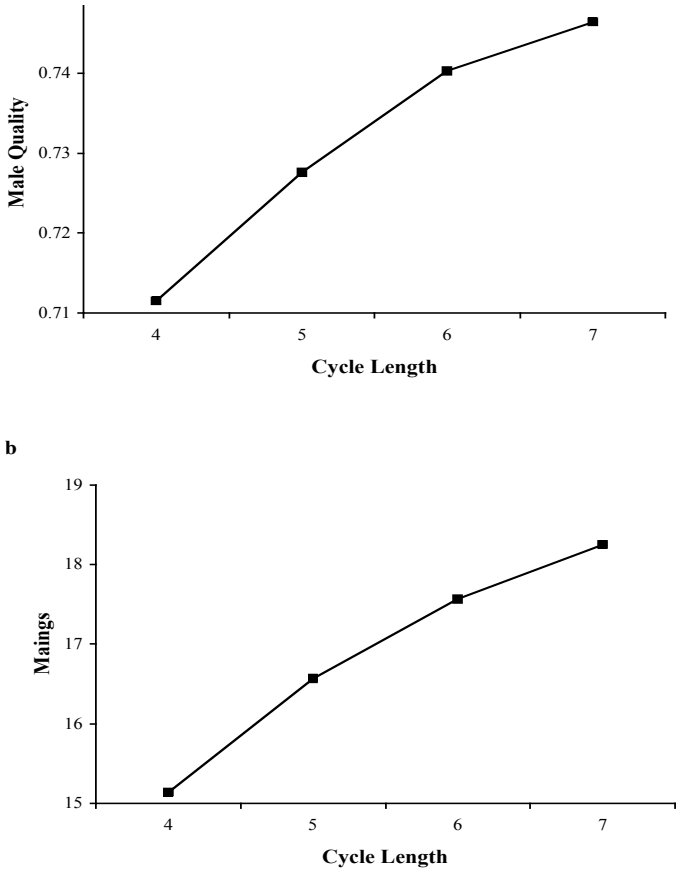

Fig. 6. The effect on mean phenotypic quality (a) and number of matings (b) with increasing cycle length, N = 10, k = 4, 1,000 simulations for each point (synchrony configuration drawn randomly from the distribution in Figure 1). As expected, phenotypic quality and number of matings increases with increasing cycle length.

females, the costs of synchrony goes up and increased cycle length is favored (unpublished simulations). However, there must be fitness costs for longer cycles. Rats have relatively short life spans of about two years (King, 1939; Barnett, 1975). Predation, parasites and disease imply that each day reproduction is delayed; there is a non-negligible likelihood of mortality and failure to reproduce. Thus, there is a cost of waiting, $C(m)$, in fitness for cycles of length m, which implies that if $m' > m$, then $C(m') > C(m)$. Now, for a group of cycling females, the fitness benefit for longer cyclers should be greater

$$F(m_i \mid m_1, \ldots m_{Nf}) \geq F(m_i \mid m_1, \ldots, m_{Nf}),\ m > m \qquad (7)$$

than shorter cyclers. Equation (7) means that the fitness of an m' cycler in a group of m' cyclers has fitness greater than or equal to an m cycler in a group of m cyclers. Fitness, F, is assumed to be a function of male quality and number of mates.

In the simplest case, where the cost, $C(m)$, of having cycle length m is constant, and assuming a constant number of males with the same male-quality distribution, then for some $m' = m + 1$,

$$F(m_i \mid m_1, \ldots m_{Nf}) - C(m) \geq 0 \quad \text{and}$$
$$F(m_i \mid m_1, \ldots m_{Nf}) - C(m) < 0 \qquad (8)$$

implying that there is some maximum cycle length, m, beyond which the cost of longer cycles becomes too great. However, we should ask whether a fixed cycle length is always evolutionarily stable in a population. Of course, changes in the fitness costs, $C(m)$, of cycle lengths or long-term ecological changes, which alter population density can alter $C(m)$ and if these changes occur frequently in evolutionary time, this could lead to variable cycle-lengths in a population over time.

It also may be that irrespective of the changes just mentioned, a fixed cycle length (pure strategy in game theoretic terms) is not an evolutionarily stable strategy (Maynard-Smith, 1982). A fixed cycle length would not be stable if it were invadable by a longer cycle-length m'. Thus, a population of mixed cyclers can evolve if there is a cycle length m' such that

$$F(m_i \mid m_1, \ldots m_i \ldots, m_{Nf}) - C(m) > F(m_i \mid m_1, \ldots m_{Nf}) - C(m) \qquad (9)$$

but

$$F(m_i|\, m_1\mathbb{N}, \ldots\, m_i \ldots, m\mathbb{N}_{Nf}) - C(m) > F(m_i\mathbb{N}|\, m_1\mathbb{N}, \ldots m\mathbb{N}_{Nf}) - C(m\mathbb{N}) \quad (10)$$

which implies that a new cycle length $m' > m$ does better in a group of m-length cyclers than an m-length cycler does against other m-length cyclers (9) but also an m-length cycler does better in a group of m' cyclers than an m'cycler does against other m'cyclers (10).

Evidence that mixed cycle lengths may maximize fitness in some ecological contexts is illustrated in Fig. 7. In these simulations, a group of $N_f = 10$ females consisted of 9, 4-day cyclers, $m = 4$, and a female with a mutant (constant) cycle length, $m' = 5$, 6, or 7 days. All mutant cyclers achieved greater male quality and number of matings than did the other 4-day cyclers. Notice also that when Figs. 6a,b and 7a,b are compared that $m' = 5$-, 6-, or 7-day cyclers did better in a group of 4-day cyclers than with other m'cyclers. Finally, 4-day cyclers did slightly better with a mutant longer cycler, than they did with all 4-day cyclers (Fig. 7a,b). Moreover, a 4-day cycler did only slightly worse in groups of 5-, 6-, and 7-day cyclers than did the longer-length cyclers (unpublished simulations). Because $C(m') > C(m)$, equation (10) can be satisfied under these conditions. These results imply that conditions (9) and (10) can be satisfied and thus populations with mixed cycle lengths (inter- or intra-female) may evolve.

How robust are these results for parameter values different from those presented in Table 2? I ran a number of simulations to determine if these results qualitatively change when parameter values were changed. In Table 2, I have summarized the results of these simulations under the column "Robustness." There were no conditions under which synchrony was favored. Even if all males had equal phenotypic quality, there was still a small effect on the number of matings, though smaller than those reported in Figs. 6 and 7. If a female mated randomly with males near her, there were still qualitatively small but similar effects for both male quality and number of mates. Any effects whatsoever are meaningful for fitness, F, because fitness is a function of reproductive success, which leads to exponential changes in populations over time. In addition, increasing the density of females with respect to males increased the effects, as did reducing the density of males and/or reducing the number

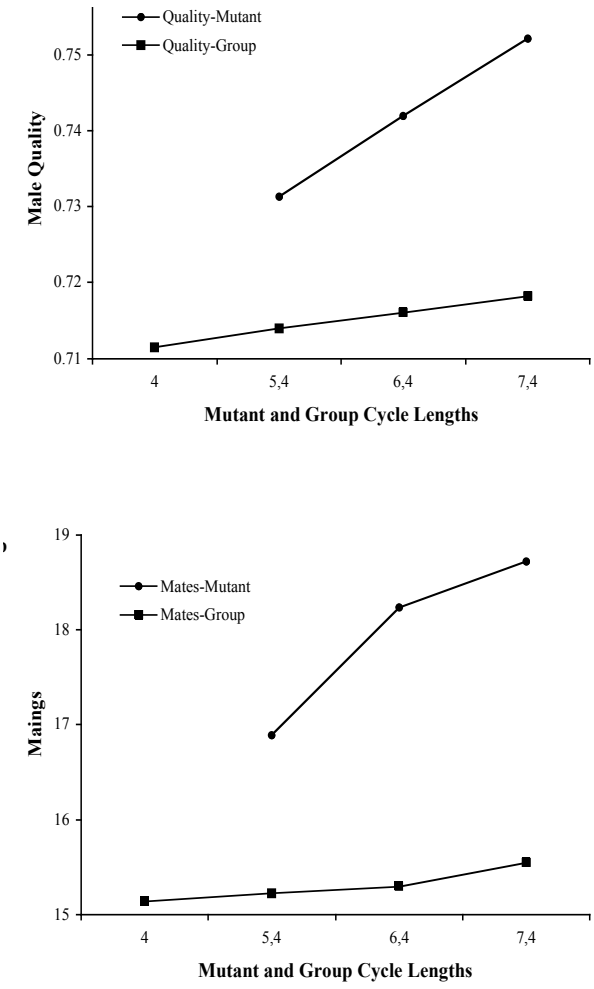

Fig. 7. Can a mutant female with cycles longer than 4-days in length invade a population such as that described by Calhoun (1962)? For groups of N = 10, k = 4, 5-, 6-, and 7-day cyclers did better with a group of 9 other 4-day cyclers both in quality (a) and matings (b). Notice, that the other 4-day cyclers did a little better with a mutant female among them. This is because the synchrony load is slightly reduced.

of quality males. None of the other parameters, if provided with plausible values (e.g., weighting movement towards estrous females), qualitatively affected the results.

DISCUSSION

Synchrony among female rats decreased expected male phenotypic quality and the number of matings, thereby decreasing female fitness. In effect, synchrony among females forces female-female competition for males, and the greater the degree of synchrony (or density of females), the greater the competition. Estrous synchrony among females is therefore a relationship to be avoided. The costs of synchrony decreased when cycle lengths were increased. Thus, increasing cycle lengths lessened the fitness costs of accidental synchrony. Longer cycle lengths are not cost free, since waiting to mate comes with some cost, $C(m)$, especially for species with short life spans and/or high mortality rates. These results lead to the prediction that, so long as the cost of a longer cycle length is not great, the sex ratio of high quality (HQ) males to females (HQ males: females) together with the density of cycling females at any given time will influence the evolution of cycle length in promiscuous breeding systems. Relatively low HQ male to female sex ratios together with high densities of cycling females will favor the evolution of longer cycles. This should be especially important in mating systems in which females cycle within a limited breeding season.

This prediction has not been tested, but Pereira's (1991) discovery that ringtailed lemur females come into estrous asynchronously during a short breeding season appears to support this hypothesis. Ringtailed lemurs have evolved a promiscuous breeding system in which groups of up to 27 individuals have been observed, typically mostly adults in a 1:1 sex ratio (Gould, 1997). By asynchronously coming into estrous, females do not compete with each other for males (Pereira, 1991).

The prediction that synchrony is a state to be avoided is also supported by recent empirical and theoretical evidence from a species previously thought to synchronize their estrous cycles. Using computer simulation, Schank (2000a) showed that Handelman's et al (1980) results on synchrony among golden hamster females could be explained as an artifact of their methodology. Subsequently, Gattermann, Ulbrich, &

Weinandy, (2002) tested whether pre-synchronized hamster females maintain synchrony when housed together. They found that when females where housed together, they significantly desynchronized their cycles, whereas females not housed together maintained synchrony. They also conducted computer simulations of the costs of synchrony and found that females obtained less matings when synchronized (Gattermann, Ulbrich, & Weinandy, 2002).

The simulations presented here have direct implication for promiscuous mating systems with little or no parental care. However, this does not characterize human mating systems, which though not purely monogamous, are not as promiscuous as rats and include male parental care. For humans, it has been argued that concealed ovulation is especially important to enhance male parental care (Burley, 1979). Specifically, if females are sexually receptive throughout a cycle and males cannot predict exactly when ovulation will occur, then males are forced to stay with a female to ensure paternity of offspring. The hypothesis of concealed ovulation has implications, which are compatible with the general findings here. First, to enhance unpredictability, females should not synchronize their cycles, because information about the reproductive status of a given female would provide information about the ovulations of other synchronous females. Also synchrony would allow a single male to dominate a group of females relative to other males, which does not enhance male parental care (because a group of females would have to share the parental care from a single male). Second, long cycles lengths and cycle variability would also enhance unpredictability because females would be less likely to ovulate on the same day. Thus, concealed ovulation may result in longer cycle than observed in purely promiscuous breeding systems with considerable cycle variability to maximize unpredictability. Evidence on cycle length and variability support this prediction (i.e., women have long cycles that average 29.5 days with considerable cycle variability between and within women; Harlow, Lin & Ho, 2000). Interestingly, Heistermann, et al. (2001) found that free-ranging primates (Hanuman langurs), which have evolved concealed ovulation, also have an average length and variability almost identical to humans.

This suggests that reports that women synchronize their cycles ought to be methodologically flawed. As discussed above, more recent studies have failed to replicate earlier results (Cepicky et al., 1996; Jarett, 1984; Trevathan et al., 1993; Morofushi et al., 2000; Strassmann, 1997;

Wilson et al., 1991). We now know that methodological errors effectively eliminated or masked cycle variability, which would prohibit synchrony (Arden & Dye, 1998; Schank, 2000a, 2000b, 2001a, 2001b, 2001c; Strassmann, 1997; Strassmann, 1999; Wilson, 1992). Such methodolog-ical errors are just what would be predicted from the theoretical results presented here.

Finally, I would like to make a more general comment on the role of individual-based modeling (IBM) in these results. IBM is much more than what-if modeling (Schank, 2001e). I have used IBM to analyze implications of Calhoun's (1962) quantitative and qualitative data on the ecology of the Norway rat. This is likely to become an important strategy for exploring theoretical implications of even long ago conducted empirical research. The results presented here have both the benefits and drawbacks of empirical and theoretical research. On the empirical side, these results are anchored in real data, which raises the problem of generality. Specifically, do these results generalize to other ecological contexts inhabited by Norway rats? Do they generalize to other promiscuous species? IBM allowed me to address this issue by varying parameters and discovering how robust these results were to parameter changes (Table 2). Individual-based models also have the benefit of allowing a researcher to explicitly model individuals and analyze these models using an experimental methodology (as opposed to deriving analytical results). This allows a researcher to focus on adding realism to individual behavior, but the drawback is that simplifying assumptions always must be made. In these simulations, details about male-male and male-female interactions at each step of mating may matter, though due to the robustness of the results presented here, the specific nature of interactions should not qualitatively alter the conclusion that synchrony is a state to be avoided.

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