reproduction, helping instead to rear the offspring of her kin—occasionally even suckling them—and generally doing her best to be tolerated in the group and to stay alive until she can become a breeder in her own right.

While studying a closely related subspecies of dwarf mongoose, O. Anne E. Rasa, of Bonn University, learned that subordinate females have an even more pressing reason to postpone reproduction. The dominant female may destroy the pups of any rival that does breed. Earlier this year, Duke University's Leslie Digby reported that there appears to be the same pattern among wild common marmosets in Brazil.

In a rare instance when a subordinate female gave birth, one of her infants was killed; the other disappeared at about the same time. For marmosets and dwarf mongooses, then, most subordinate females make the best of a grim lot by temporarily shutting down their ovaries. With luck, their time to breed does come.

Suppression of ovulation is only one of the many means for mothers to adjust the timing of their reproductive effort. In a diverse array of mammals—including bats, skunks, minks, and armadillos—ovulation occurs, but implantation of the fertilized egg in the uterine wall is delayed so as to insure birth of the offspring at the

Hormonal Cocktails for Two
by Sarah Blaffer Hrdy and C. Sue Carter

When first presented with pups, a virgin female laboratory rat generally ignores them; she may appear afraid of the tiny, squirming, naked creatures and, occasionally, may even eat them. Only after being introduced to pups many times over several days can a virgin rat be conditioned to tolerate and care for them—licking them, crouching protectively over them, retrieving them when they stray from her side. In contrast, a pregnant rat responds within minutes to pups, even prior to delivery of her own.

The idea that physiological changes might prepare the expectant mother for her new role led to a now classic experiment. In 1968 Joseph Terkel and Jay Rosenblatt, of Rutgers University, injected blood from a rat that had just given birth into a virgin female. The result was a dramatic reduction in the time it took virgins to nurture pups.

Since 1968, we have learned a great deal about what goes on inside female mammals as they prepare for motherhood. During the last third of pregnancy, a cascade of endocrinological events readies and motivates mothers. Prominent in this maternal cocktail are the steroid hormones estrogen and progesterone, manufactured by the placenta and essential to maintaining pregnancy. But since the placenta is delivered along with the baby, progesterone and, a little later, estrogen levels fall around the time of birth. By themselves, these hormones cannot account for maternal responsiveness.

Enter prolactin and oxytocin, hormones essential for milk production and nursing. Prolactin is a very ancient molecule whose original function was to maintain salt and water balance in early vertebrates such as fish. Over evolutionary time, this hormone has proved very versatile and now performs diverse physiological functions in many kinds of animals. In mammals, it is associated with caretaking behavior in both females and males.

But perhaps the quintessential mammal hormone is oxytocin. A muscle contractor, oxytocin (from the Greek for "swift birth") evolved in mammals and produces the uterine contractions of birth and milk ejection during lactation. Present when the mother first greets her emerging offspring, it continues to be released whenever she nurses. Oxytocin released into the brain is known to promote calming and positive social behaviors, such as pair bonding.

Studies of domestic sheep by Barry Keverne, Keith Kendrick, and their colleagues at the University of Cambridge provide the most complete picture we have of the behavioral effects of oxytocin. As a lamb moves down the birth canal, nerves stimulated during the passage trigger the release of oxytocin in the mother's nervous system. Only if oxytocin is present at birth or injected so that it reaches the brain at the same time a mother meets her newborn, will she bond with her offspring. If release of oxytocin is blocked, the ewe rejects her lamb. High levels of oxytocin also are found in mother's milk, raising the possibility that this hormone plays a role in making the mother-infant attachment mutual.

As important as these hormones can be in determining how responsive a mother will be, they do not act in a deterministic fashion. They both affect and are affected by a mother's behavior and her experience. Exposure to pups, for instance, can lead to reorganization of neural pathways in a mother rat's brain, making her respond faster to pups in the future, even with lower hormone levels. And some recent studies suggest that the hormones of breast-feeding may benefit a mother's mental health and increase her ability to deal with stress.

In many mammals, males, as well as adoptive virgin females, can be primed to exhibit parental behaviors. Prairie vole males, for instance, typically respond to a newborn pup by retrieving it and huddling over it. Geert De Vries, of the University of Massachusetts, found that such nurturing is facilitated by vasopressin, a hormone that in other contexts is associated with aggressive, territorial behavior.