

84 Discriminative Parental Solicitude and the Relevance of Evolutionary Models to the Analysis of Motivational Systems

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ABSTRACT Behavioral biologists customarily distinguish between proximate causal analyses of the mechanisms underlying action, and ultimate (selectionist) analyses, which invoke the adaptive functions (fitness-promoting consequences) for which behavior has evolved. Cognitive neuroscientists, operating in the proximate mode, have paid little attention to selectionist theories. However, proximate causal research is inevitably guided in part by implicit assumptions about adaptive function; and selectionist theories, which make such assumptions explicit and develop their implications, can help generate novel, testable proximate causal hypotheses.

This thesis is illustrated with theory and research on parenting. Selectionist models suggest certain variables (certainty of parenthood, offspring quality, opportunity costs) that evolved parental motivational systems may be expected to track, sometimes providing considerable detail about the form of expected functional relationships. Recent studies demonstrate the utility of these models in the search for cognitive and neural mechanisms.

Why do female rodents become aggressive when lactating? A psychophysiological approach to this question might entail exploring the roles of particular hormonal regimens (e.g., Mayer, Monroy, and Rosenblatt, 1990), sensory inputs (e.g., Stern and Kolunje, 1991), and brain structures (e.g., Hansen et al., 1991). A rather different approach entails asking such questions as whether maternal aggression is specifically directed against genuine threats to the pups, and whether it is

effective in protecting them (e.g., Elwood, Nesbitt, and Kennedy, 1990).

Evolutionists commonly refer to psychophysiology's explorations as *proximate causal* analyses, while the second approach, characteristic of behavioral ecology, concerns *adaptive function* or *ultimate causation*. At least since Tinbergen (1963a), animal behaviorists have painstakingly distinguished these two modes of explanation, and rightly so, since many fruitless controversies have been fueled by incomprehension of the distinction. It does not follow, however, that proximate and ultimate analyses can or should be pursued in isolation from one another. The adaptationist theoretical approach of behavioral ecology has much to offer researchers engaged in proximate causal analysis of behavioral control mechanisms. That, in a nutshell, is the thesis of this chapter.

Some writers dismiss adaptationist theorizing as unscientific speculation, but although it is true that ultimate causation hypotheses do not generally submit to experimental testing as straightforwardly as proximate causal hypotheses, this dismissive stance is counterproductive. The most resolutely mechanistic physiologist relies on complex assumptions about adaptive function, so proscription on adaptationist theorizing amounts to insistence that these assumptions remain inexplicit and unexamined. As Mayr (1983) has stressed, every important discovery in physiology and other proximate causal fields of biology has been predicated upon the researchers' interpretations of the func-

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tional significance and adaptive design features of the systems under study. Contemporary gut research, for example, is predicated on the understanding that extracting nutrients from ingesta is what the gut is for. This seems obvious and not at all speculative, but the gut's function was not always obvious, and serious investigation of gut physiology was scarcely possible until it *became* obvious. Uncontroversial orienting assumptions about adaptive function are founded in hard-won knowledge; only after basic adaptive functions are correctly apprehended can the research enterprise bloom. There could be no neuroscience, for example, until the relatively recent discovery that information processing is what nerve tissue is for.

Unfortunately, the assumptions about adaptive function that guide research programs in cognitive neuroscience and related disciplines are not always sound. Neither are they always explicit, and this hinders critical scrutiny of them. Making notions of adaptive function explicit and exploring their implications is precisely what the evolutionary models of behavioral ecology are meant to do, and their implications about potentially fruitful directions for proximate causal research can be both straightforward and novel. We shall illustrate this thesis with examples from the domain of parental motivation and behavior.

Evolution by selection and the proximate-ultimate distinction

The adaptive complexity of living things was once the most compelling reason to believe that supernatural powers intervene in our world. Darwin and Wallace (1858) destroyed this theological "argument from design" by discovering a natural process that produces adaptive complexity without intelligence or intention: the continual generation of heritable variation in the characteristics of individuals, followed by a nonrandom differential survival and reproductive success of the variants. Darwin called the latter differentials "natural selection."

Darwin's theory implied that the adaptive function of all traits is ultimately reproductive. Traits proliferate because they contribute to the relative reproductive success of their bearers compared to other members of the same populations. "Survival value" is a popular way of referring to adaptive significance, but it is misleading because personal survival is not the crite-

riion of adaptation. Selection favors whatever traits enhance the proportional representation of their carriers' alleles in future gene pools. It follows that creatures have evolved to enter willingly into life-threatening contests for mating opportunities, to deplete bodily reserves to nourish dependent offspring, to allocate benefits discriminatively with respect to closeness of relationship, and in general to expend their very lives in the pursuit of genetic posterity (fitness).

Darwin clearly understood that natural selection is primarily a process of competition within species. Nevertheless, for a century after him, most behavioral biologists routinely misunderstood this point, blithely imagining that selection equips conspecific animals with the shared purpose of perpetuating their species. This "greater-goodism" (Cronin, 1992) cannot easily be reconciled with the orthodox neo-Darwinian conception of adaptive function as effective contribution to the competitive ascendancy of one's genotypic elements over their alleles. But for decades no one seemed to notice. Greater-goodism dominated discussions of the evolution of social phenomena until demolished by Hamilton (1964) and Williams (1966), and it continues to sow confusion in fields untouched by Darwinism.

Greater-goodism illustrates how unexamined false assumptions can impede research. Konrad Lorenz, for example, so thoroughly and uncritically accepted it as to assert that the "aim of aggression" is never lethal (1966, 38), a claim he insisted he had derived from "objective observation of animals." Although Lorenz was familiar with a literature containing many field observations of fatal fights, he dismissed all such reports as instances of pathology or "mishap." Lethality was expurgated from Lorenz's analysis of aggression and became invisible to his readers. Indeed, he has been widely cited as having documented the sublethal restraint of animal aggression in nature and the unique murderousness of humankind, notions wildly at odds with actual field observations of animal conflict.

Niko Tinbergen, who shared the 1973 Nobel prize with Lorenz and Karl von Frisch for their roles in establishing ethology as a science, paid more careful attention to the problem of transforming ideas about adaptive significance into explicit, testable hypotheses. He championed the view that explanations in terms of proximate cause and adaptive function are equally valid, distinct, and complementary (Tinbergen, 1963a), and in so doing he helped to found the approach of

modern behavioral ecology. Tinbergen (1963b) asked, for example, why nesting birds carry the eggshells away after their young hatch, his premise being that selection would have eliminated such behavior unless it had fitness benefits sufficient to offset the costs in time, energy, and temporary absence from the vulnerable hatchlings. So he devised experiments to test whether eggshell removal served a sanitary function, disposed of dangerous sharp objects, or made nests less conspicuous to predators; only the latter function was supported.

Extensive formulation and testing of explicit models of adaptive function proliferated after Tinbergen's early efforts, and in the initial flowering of this approach, its practitioners sometimes declared their autonomy from the enterprise of characterizing proximate causal mechanisms. According to the introduction to an excellent sociobiology textbook, for example, "data from studies of proximate causation usually have only limited value for understanding ultimate causation, and vice versa" (Wittenberger, 1981, 4). Efforts to divorce ultimate and proximate analyses are futile, however, as may be illustrated by consideration of a classic problem in optimal foraging theory.

How should a forager exploit resources distributed in depletable patches? An elegant ultimate causation theory maintains that the forager should leave partially depleted patches to seek fresh ones when the instantaneous rate of food-getting from the present patch equals the highest gross rate of return that can be attained over the total time that is spent both foraging within patches and traveling between them or searching for them (Charnov, 1976). *How* the animal should assess a patch's instantaneous rate of yield, induce the habitat-specific mean interpatch travel time, et cetera, are proximate details that are outside the theory's purview. But trouble begins when we try to decide what would constitute a potentially falsifying test of the theory. Foragers do not always perform perfectly, so how is one to decide whether errors reflect a mere shortfall of information to guide behavioral decisions or a more basic flaw in the optimality analysis? This question inevitably led to hypotheses about information processing and decision rules (e.g., Green, 1984). What information is available to the animal, and how should it be processed to estimate relevant parameters of the situation and make adaptive behavioral decisions? How would the answer change if increased memory

loads and computational demands were treated as costs? Thus, optimal foraging theorists have come to address issues like the optimal investment of time or effort in information gathering (Stephens and Krebs, 1986), and the form of optimal forgetting functions for obsolescing information (Healy, 1992). As these issues have been raised and addressed, the general question has been subtly transformed into one that is neither simply adaptationist nor simply proximate, but an amalgam of both: What would an optimal cognitive program for solving this patch-foraging problem look like, and how do actual cognitive programs compare with that theoretical ideal?

Charnov's (1976) patch-foraging theory never was a theory of how animals will behave. It was a task analysis: a theoretical characterization of the essential features of an adaptive problem confronting animals that forage for patchily distributed foods. Natural selection may be expected to have equipped animals with solutions to problems like this, and these evolved solutions are often most usefully described at a cognitive level, as algorithms for information processing and behavioral decision making (Cosmides and Tooby, 1987). Optimal foraging is not unusual in this regard; cognitive formulations are increasingly prominent in other subfields of behavioral ecology and sociobiology, for similar reasons (e.g., Hepper, 1991; Davies, 1992). What, after all, is it that selectionist models and "ultimate explanations" purport to predict and explain? Nothing more nor less than the organization of evolved proximate causal structures.

In attempting to free physiology from vitalism, Claude Bernard (1865) maintained that although "the nature of our mind leads us to seek the essence or the *why* of things ... experience soon teaches us that we cannot get beyond the *how*, i.e., beyond the immediate cause or the necessary conditions of phenomena" (p. 80). Bernard remained oblivious to Darwinism until his death in 1878 (Olmsted, 1938), and so have many of his intellectual descendants for another century. To this day, there are physiological psychologists who cite Bernard's dictum with approval, and to whom it would be anathema to suggest, for example, that predation risk reduction is in any sense the reason why a gull removes eggshells from the vicinity of its nest.

Sober (1983) has proposed that psychology's antipathy to explanations in terms of adaptive function de-

rives from a message inferred from the victory of Newton's blind physics over Aristotle's teleology, namely that "a science progresses by replacing teleological concepts with ones that are untainted by ideas of goals, plans and purposes" (p. 115). This stance, Sober continues, "received further impetus from the Darwinian revolution in biology," because Darwin replaced a purposeful creator with a purposeless mechanism. But if the Darwinian revolution truly contributed to psychology's naive emulation of physics, then that influence entailed a great irony. By providing a thoroughly materialistic explanation for the previously incomprehensible fact that living things have "goals, plans and purposes" instantiated in their structures, Darwin's discovery actually rendered obsolete the sort of doctrinaire antagonism to purposelike concepts exemplified by Bernard's dictum. The creative feedback process of selection justifies invoking the consequences of biological phenomena as part of their explanation: What they achieve is, in a very real sense, why they exist.

Sober is certainly correct in claiming that psychology has been lukewarm about concepts that smack of teleology, but the Darwinian revolution has had little overt relevance to the debate. Those, like Tolman (1932), who rebelled against the doctrinaire exclusion of purposive concepts, were inspired more by the manifest goal-directedness of their subject animals than by an appreciation of the efficacy of natural selection. And when "goals and plans" resurfaced during the cognitive revolution against behaviorism (Miller, Galanter, and Pribram, 1960), they were inspired more by the growing sophistication of cybernetic devices than by an understanding of evolutionary adaptation. The result is that many cognitive scientists have continued to operate with only a superficial understanding of what the psyche is organized to achieve (Barkow, Cosmides, and Tooby, 1992).

Symons (1987) has argued that psychology's failure to exploit evolutionary thinking has impeded progress only in certain limited domains. Researchers in areas like sensation, perception, memory, and motor control rely on complex assumptions about the purposes of the mechanisms they study; indeed, the very delineation and naming of a mechanism for study typically entails parsing the psyche into low-level tasks such as the maintenance of perceptual constancies. These scientists make progress when their functional parsings of the psyche are sound (Tooby and Cosmides, 1992), but according to Symons (1987), sound functional parsings

are often attainable without recourse to the modern gene-selectionist theory of evolution:

Selectional thinking sheds little light on perceptual-constancy mechanisms because an ideal design for such a mechanism probably would be the same whether the mechanism's ultimate goal was to promote the survival of genes, individual human bodies, or *Homo sapiens*; for precisely the same reason, selectional thinking sheds little light on organismic goals as vague as *not being hungry* or *not being frightened*. It is only when *it really matters* that the brain/mind was designed to promote the survival of genes . . . that psychology is likely to benefit significantly from Darwin's view of life. (Symons, 1987, 130)

Symons then argues that the domain within which "it really matters" that psychological mechanisms have evolved to promote genetic posterity is that of the "mechanisms of feeling," especially social and sexual feeling.

Although it may indeed be the case that explicit evolutionizing would contribute little to analysis of a perceptual constancy mechanism, Symons's argument greatly understates the breadth of psychological domains within which "selectional thinking" is relevant. His own choice of examples—"organismic goals as vague as *not being hungry* or *not being frightened*"—may be used to illustrate the point.

Feeding research is founded in a sound conception of immediate adaptive function: The controls of feeding behavior are organized to extract energy and nutrients from foodstuffs in accord with organismic needs. But if researchers imagine that mere energy balance or survival is the sole criterion of functionality, and fail to recognize that these are subsidiary goals in a more complex motivational structure that functions to promote gene replication, then their analyses of how organisms go about "not being hungry" will suffer. Consider, for example, the fact that broody hens, who are cryptic while incubating their eggs in nests on the ground, experience a programmed decline of 18% in target body weight during incubation (figure 84.1). This radical modulation of the state of "not being hungry" functions to minimize exposure of the nest to predation when the hen gets up to feed, and it does so at considerable cost to her own bodily condition and survival prospects. This is one of many examples of adaptive anorexias (Mrosovsky and Sherry, 1980), in which the mechanisms determining an animal's inclination to feed are sensitive not only to internal energy reserves but also to cues of the likely fitness costs of taking time out from other adaptive activities.

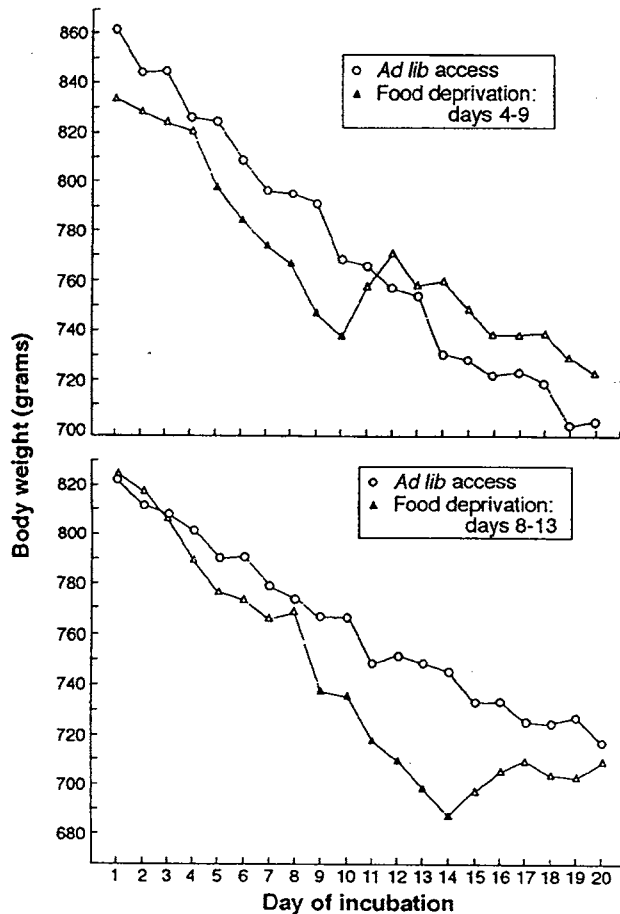


FIGURE 84.1 Adaptive anorexia. Broody jungle fowl hens with ad lib food access lose weight steadily over the 20-day incubation period. If totally deprived of food for 6 days beginning on day 4 (top panel) or day 8 (bottom panel), the birds lose weight more rapidly, then regain weight for 2 or 3 days when food is reinstated, in effect returning to their “programmed” trajectory of weight loss. (From Sherry, Mrosovsky, and Hogan, 1980, figures 6 and 7.)

Similarly, the “vague” organismic goal of “not being frightened” has complex causality that is unlikely to be elucidated without recourse to selectional thinking. A male stickleback fish guarding his nest full of eggs, for example, will stand his ground against an approaching predator longer, and dart at the predator more bravely, the more eggs he has in the nest (Pressley, 1981). In effect, the greater fitness value of a larger brood elevates the statistical probability of death that the little fish is prepared to accept. One correlate of brood size, which might be the cue modulating fear versus bravery in this case, is carbon dioxide production by the eggs, and if so, then it is likely that this cue will prove to mitigate fearfulness only in egg-guarding

males. One could never understand (and would be unlikely to discover) such contextual variation in the controls of fearfulness without the basic Darwinian insight that even personal survival is a subordinate objective to that of genetic posterity.

Thus, although the functional design of mechanisms subserving ends like perceptual constancy may indeed be studied and explained without recourse to Darwinism, as Symons (1987) maintains, it seems that almost any “motivational” mechanism will be misunderstood until it is scrutinized in the light of selection theory. This proposition applies to hunger, to fear, and to most of the subject matter of cognitive neuroscience and psychology, including even much of perception. Organisms have not been designed by selection merely to maintain energy balance, repair their tissues, and outlive their fellows. They have been designed by selection to replicate their genes, largely though not exclusively by the debilitating and risky enterprises of sexual reproduction and parental investment.

Parental motivation and discriminative solicitude

Parenting is a prominent component of the behavioral repertoires of many animals, including people. Throughout human prehistory, most women (and perhaps even men) devoted the majority of their waking hours to foraging for, educating, guarding, and otherwise nurturing their young. Yet psychologists have had remarkably little to say about the sources of variation in parental efforts and inclinations. When we prepared a paper on the topic for the 1987 Nebraska Symposium on Motivation (Daly and Wilson, 1988c), for example, we noted that the 34 previous volumes in the series contained not a single paragraph specifically concerned with parental motivation. It seems that psychologists have shied away from this important domain of motivation for want of a theoretical framework from which to approach it. The requisite framework is of course the Darwinian view of behavioral control systems as having been organized by a history of selection to promote fitness.

Parental behavior has obvious, direct links to fitness: Offspring are the vehicles of parental fitness. However, not all offspring are equally capable of translating parental nurture into increments in the long-term survival of parental genetic materials. It follows that selection favors discriminative mechanisms of parental psychology: mechanisms that allocate “parental in-

vestment" (Trivers, 1972) with sensitivity to available cues of the statistically expected consequences for parental fitness. For example, selection will favor preferential investment in one's own young as opposed to the young of others, in viable young as opposed to lost causes, and in needy young as opposed to those for whom the investments would be superfluous (Wilson and Daly, 1993).

Parental investments take various forms including direct transfers of heat and nutrients, foraging and food delivery, and protection (Clutton-Brock, 1991). Different forms of parental investment may be temporally disjunct and hence causally distinct, as when lactation succeeds gestation, but the functional commonality among diverse investments provides a rationale for expecting that there will often be some commonality of causation as well. Any offspring whose characteristics make it a good bet to yield fitness for one sort of parental investment will usually be a good bet for other sorts, too. Doubt that a particular youngster is indeed the parent's own, for example, reduces the expected parental fitness payoffs of both feeding the youngster and defending it against predators. Divestment from lost causes should similarly apply in parallel to all manner of parental investments. Thus we may expect parental motivational systems to contain processes and structures that function as if mediated by a unitary parameter of offspring-specific parental love or solicitude, which is influenced by a variety of parental, offspring, and situational cues of fitness value (i.e., of the offspring-specific expected contribution to parental fitness), and which influences in its turn a variety of parental activities.

Even offspring-specific parental investments cannot be adaptively dispensed solely on the basis of cues of offspring fitness value, however. The smaller or younger of two siblings might profit more from a food delivery, for example, and hence be the preferred recipient for such a parental investment, even though the larger or older sibling has the higher fitness value and would be the preferred recipient of parental defense in an antipredator context. Parental solicitude may be expected to be complexly contingent upon variable attributes of the parent, the young, and the situation, because both expected fitness and the expected impact of a given parental investment on expected fitness are contingent upon these variable attributes. In particular, parental solicitude can be predicted to vary adaptively in relation to (1) phenotypic and situational cues

affording information about the certainty of parenthood (whether the offspring is indeed the parent's own); (2) phenotypic and situational cues affording information about the offspring's reproductive value (expected future fitness); and (3) the fitness value of the available alternatives to present parental investment.

CERTAINTY OF PARENTHOOD An offspring's expected contribution to parental fitness is the product of its reproductive value and its relatedness (r) to the putative parent. In the case of outbred sexually produced offspring, $r = 0.5$, but this value is in effect probabilistically reduced in the case of uncertain parentage.

Indiscriminate allocation of parental benefits without regard to cues of actual parentage would be an evolutionary anomaly. Consider a famous allegation of just such indiscriminacy. Mexican free-tailed bats roost in dark caves in aggregations that can number in the millions. Within hours of giving birth to her single pup, the female leaves it hanging in a crèche while she goes foraging. The crèche may contain several thousand infants per square meter, and they sometimes crawl a meter or more between nursing bouts. Noting these facts, and having demonstrated both that pups would attach to any female held near them and that the females would not then remove the pups, Davis, Herreid, and Short (1962) concluded that female Mexican free-tailed bats act as an anonymous "dairy herd."

This conclusion demands our skepticism, because it is not plausible that lactation could be evolutionarily stable (Maynard Smith, 1976) in such a case. The nursing bat incurs both energetic depletion and predation risk in order to deliver 16% of her body weight in milk each day. If milk were truly a communal resource, selection would surely favor the female who deposits her pup in the care of the dairy herd, dries up, and opts out. Doubting the dairy herd theory for this reason, McCracken (1984) genotyped mothers and infants in the field, and found that while some mismatches indeed occurred, 83% of mothers were actually feeding their own pups. A 17% incidence of nursing nonrelatives represents a substantial failing of discriminative parental investment, but not such an egregious failing as to select against lactation (Beecher, 1991).

The adaptationist expectation of offspring-specific parental solicitude stands in opposition to a prevalent conception of mammalian maternal motivation.

Rosenblatt (1990), Pryce (1992), and many others treat maternalness as a state that is nonspecific with respect to its object. This conception is certainly not a generally applicable one, and its popularity appears to be attributable to happenstance: Maternal solicitude is indeed remarkably indiscriminate in the laboratory rat, and this species has dominated research for no other reason than its convenience. However, the rat's relative imperviousness to the individuality of young turns out to be a peculiarity of a minority of mammals, with a particular ecology.

Mexican free-tailed bats search out, recognize, and selectively nurture their pups in the free-for-all of the crèche (McCracken and Gustin, 1992). Seals that deliver and nurse their pups in close proximity attack unrelated pups who try to suckle, even as they nurse their own (e.g., Trillmich, 1981). Hoofed mammals who raise precocious young in mobile herds do likewise (e.g., Poindron and Le Neindre, 1980). Rats are different: They seem oblivious to the own-versus-alien distinction, and blithely give suck to whatever pups they find in their nests, including even those of other species. Why? Rat pups, unlike bats, seals, and goats, are immobile and sequestered in defended burrows, with the result that mixing of young does not occur in the absence of experimental intervention. The rat mother in nature dispenses nurture selectively to her own young, using her nest site as the cue by which she recognizes them. Moreover, when the growing pups of burrow-dwelling rodents become mobile so that mixing of youngsters is an imminent possibility, mothers then come to recognize their pups as individuals and will no longer accept fosterings (e.g., Holmes, 1984).

The risk that unrelated young will elicit misdirected parental investment varies even among closely related species. Bank and cliff swallows, for example, nest colonially, whereas the closely related rough-winged and barn swallows nest more dispersedly. Newly flying young sometimes return to the wrong nest in the two colonial species, but seldom or never in the dispersed species; moreover, fledged young who are still being fed by their parents aggregate in crèches in the colonial species but not in the dispersed. Thus, the demand for parental discrimination of own versus alien is clearly greater in the colonial species, and Beecher (1990) reports that they indeed recognize their own offspring by voice whereas the dispersed species do not.

Beecher and colleagues have furthermore predicted and demonstrated that selection for offspring recogni-

tion in colonial swallows has affected the attributes of both the chicks and their parents. The calls of colonial species chicks are intrinsically more discriminable than those of dispersed species chicks, as shown both by informational analyses of the physical properties of the calls (Beecher, 1988) and by superior discrimination of the calls of colonial species chicks by adults of either nesting type, as well as by other animal species (Loesche et al., 1991; Loesche, Beecher, and Stoddard, 1992). Adaptation on the parental side is indicated by the fact that adult cliff swallows (colonial) outperform adult barn swallows (dispersed) on these tasks, even when the calls to be distinguished are those of barn swallows (Loesche et al., 1991). Selection will not always favor such complementarity of parental and offspring adaptations, however, and Beecher (1988, 1991) has further discussed the circumstances, such as orphaning, in which there may be simultaneous selection in favor of parental discrimination capability but against the evolution of distinctive "signatures" in the young.

As noted above, the physiology of mammalian mothering has been studied primarily in rats and other burrow-dwelling rodents, who, like the dispersed-nesting swallows, have not experienced a history of selection for rapid discriminative attachment to their own young. There is one intensively studied mammalian species, however, that has experienced precisely such selection: the sheep. An individualized bond between ewe and lamb is typically established within three hours of parturition (Poindron and Le Neindre, 1980). Many elements of the complex neuroanatomy and chemistry of maternal motivation are similar in sheep and rats, and perhaps even across the class Mammalia (e.g., Kendrick et al., 1992). Other things vary among species, such as the specific central effects of oxytocin (Lévy et al., 1992), which plays a taxonomically broad role in parturition but has more species-specific effects on sexual receptivity (hardly surprising when one considers that rats, for example, become sexually receptive after giving birth whereas sheep do not).

Most interesting in the present context are the ewe's adaptations to the specific problem of individualized maternal responsiveness. Kendrick, Lévy, and Keverne (1992) found that single neurons in the mitral cell layer of the olfactory bulb never responded preferentially to lamb odors in late pregnancy, but that more than half had switched to doing so soon after birth,

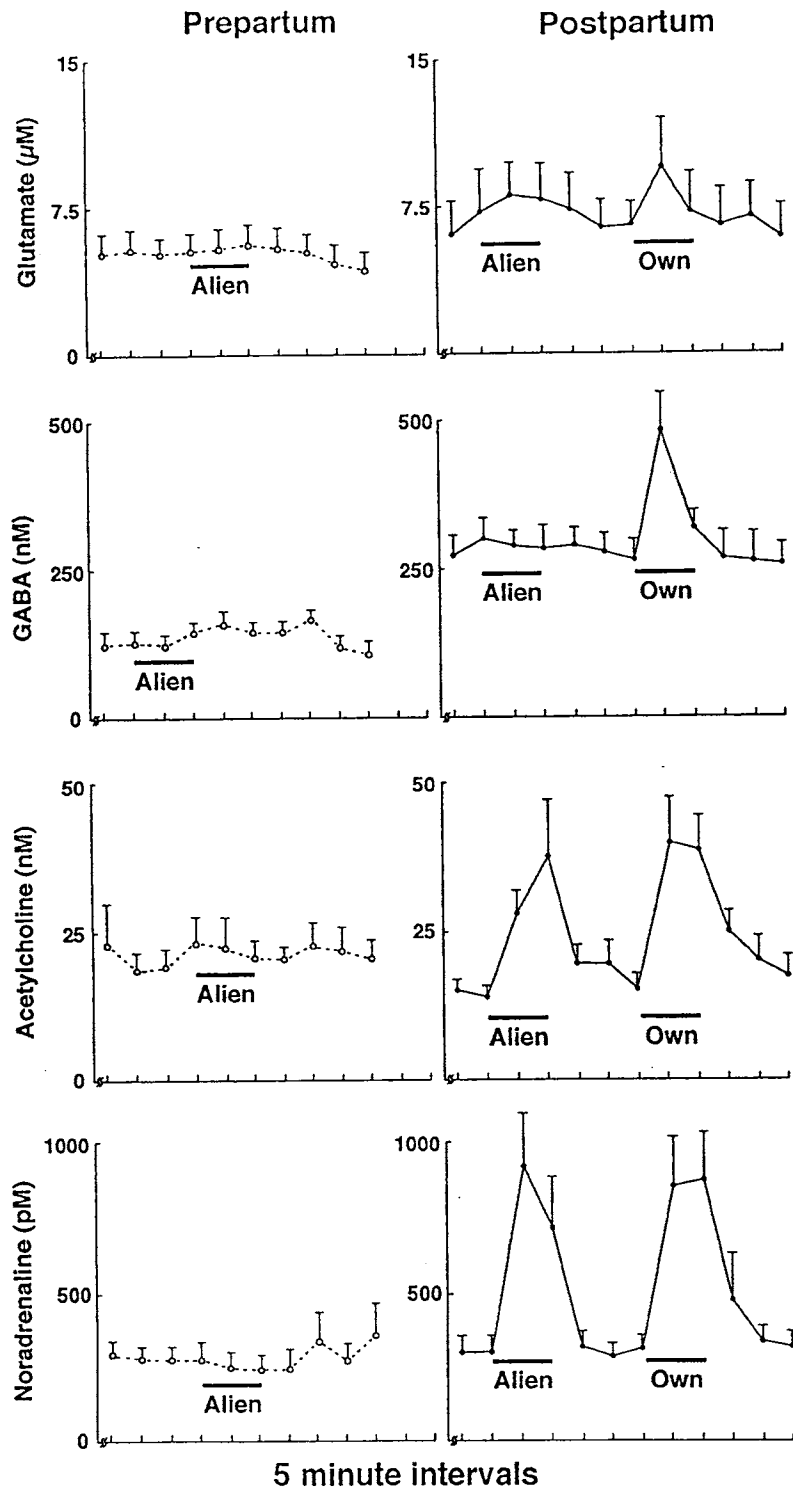


FIGURE 84.2 Discriminative response to own offspring on the day of birth. Concentrations of glutamate, GABA, acetylcholine, and norepinephrine (mean \pm SEM) in microdialysis samples taken at 5 min intervals from the olfactory bulbs of nine sheep during 10 min exposures to lamb odors

(black bars), within 24 hrs prepartum and postpartum. Although postpartum data are portrayed in the order alien lamb, own lamb, order of presentation was in fact randomized. (From Kendrick, Lévy, and Keverne, 1992, figure 2.)

male's best or only option across a wide range of values of paternity probability.

Surprisingly, there is no evidence that nonhuman males ever use offspring phenotypes as paternity cues. Human males certainly do, however (Daly and Wilson, 1988c). One corollary is intense interest in the resemblances of newborn babies to putative paternal kin, and relative noninterest in their resemblances to maternal kin (Daly and Wilson, 1982; Regalski and Gaulin, 1993). A possible adaptation in human mothers is strong motivation to discover paternal features in their babies (Daly and Wilson, 1982; Robson and Kumar, 1980); pregnant women's fantasies suggest that this motive begins to be felt before birth (Leifer, 1977). What has yet to be investigated is to what degree, if at all, human paternal affection and investment are affected by resemblance. There is much anecdotal evidence of complete divestment in response to phenotypic evidence of nonpaternity (Daly and Wilson, 1988c), but no systematic study has been made of the phenomenon. Of more general interest, perhaps, is the likelihood that even in the absence of conscious paternity doubt, the psychological mechanisms affecting parental affection may be sexually differentiated, with resemblance to self relevant to fathers but not mothers (Daly and Wilson, 1981).

A rather obvious implication of the notion that selection favors parental discriminativeness is that parental inclinations may fail when adults find themselves in loco parentis to unrelated young (Rohwer, 1986). Remarkably, this possibility seems not to have occurred to social and medical scientists seeking the sources of variable child abuse risk, until Wilson, Daly, and Weghorst (1980) showed that stepchildren are vastly overrepresented as victims. Differential risk is especially large when the criterion of abuse is unequivocal and extreme, that is, in cases of child homicide (figure 84.4). Excess risk to stepchildren cannot be attributed to poverty, coresidency from birth, maternal age, brood size, incidental traits of persons who remarry, or any other suggested confounding (Daly and Wilson, 1985; Wilson and Daly, 1987; Flinn, 1988). Much converging evidence indicates that violence against stepchildren is simply one extreme reflection of a large difference in the (undoubtedly overlapping) distributions of genetic parental and stepparental affection (Wilson and Daly, 1987; Daly and Wilson, 1991, 1993). Although the evidence is scanty, adoptive parenthood appears to be much less problematic than stepparenthood. One possible interpretation is that the contemporary Western practice of adoption by nonrelatives is an evolutionary novelty against which the evolved parental psyche has

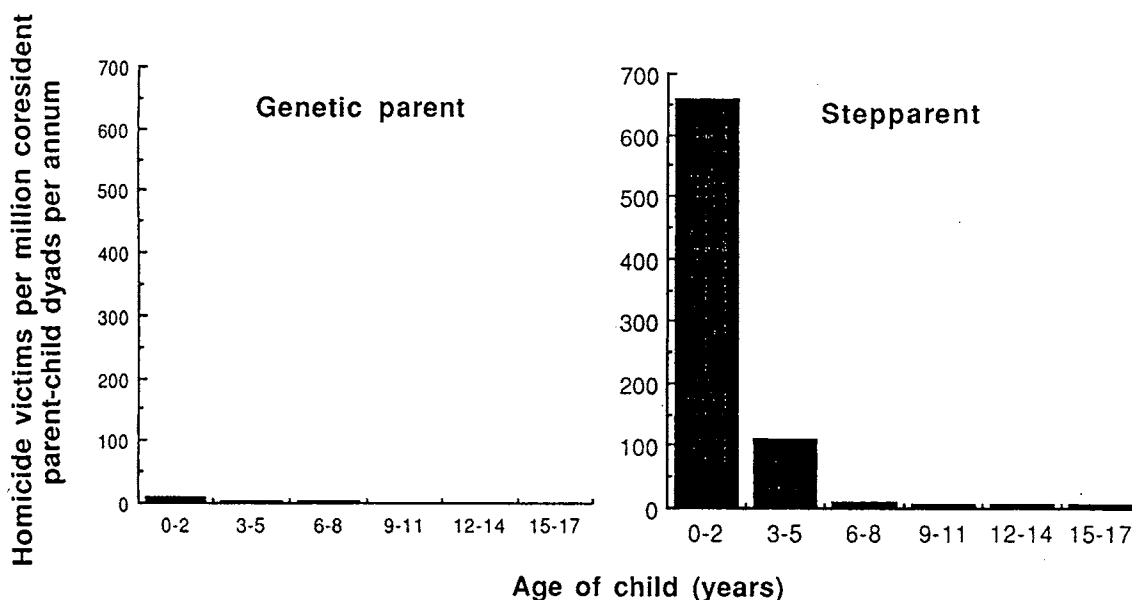


FIGURE 84.4 Rates of filicide, according to age of victim, by genetic parents ($N = 341$ victims) versus stepparents ($N = 67$ victims) in Canada. Data represent all filicide cases

known to Canadian police forces between 1974 and 1983. (From Daly and Wilson, 1988a, figure 1.)

no specific defenses, so that the psychology of genetic parenthood is more readily engaged than in the case of stepparenthood, which has been a recurring adaptive problem because of parental mortality and/or marital dissolution for as long as hominids have formed biparental unions.

In some animals (though clearly not in people), males routinely dispose of their predecessors' young when they can gain earlier use of their new mates' maternal investments for the benefit of their own young by so doing (Hausfater and Hrdy, 1984). This antithesis of parental solicitude must also be adaptively discriminative with respect to probability of paternity, and a diversity of mechanisms apparently exists. As with modulations of positive investments, there is no evidence that males of any nonhuman species use offspring phenotype as a paternity cue in infanticidal decisions. In some species, such as gerbils, males selectively spare young associating with or carrying odor cues of females with whom the male has mated (Elwood and Kennedy, 1993). Others, such as mice (vom Saal, 1985) rely less on the individual identities of past mates than on a remarkable timing heuristic. Intravaginal ejaculation is the necessary and sufficient condition for male mice tested with stimulus pups to switch from infanticidal to parental responses. However, the switch does not typically occur for many days after mating, until shortly before the male's own pups would be born (vom Saal, 1985). In effect, the male clocks the female's pregnancy, without cues from her and by a distinct neural timing mechanism; the duration of pregnancy remains constant in real time when day length is artificially modified, but the male's "pregnancy clock" counts light-dark cycles instead (Perrigo, Bryant, and vom Saal, 1990). As in the case of the specificity of sheep mitral cell responses, this sophisticated physiological mechanism was discovered as a direct result of adaptationist theorizing.

REPRODUCTIVE VALUE OF THE YOUNG An act of parental investment like food delivery cannot be considered a straightforward index of discriminative parental solicitude. The offspring receiving more parental investment in a delimited observation period is not necessarily the offspring that the parent values more. An older offspring, for example, may be better able to feed itself and hence less in need of parental feeding than a younger sibling, though the older has higher reproductive value (age-, sex- and phenotype-specific expected

future fitness), and hence higher fitness value to the parent. Where we might expect the parent to reveal its greater valuation of the older offspring is when confronted with the choice of saving only one. This choice is hard to operationalize in nature, but a related paradigm has become popular for measuring variations in parental valuation of offspring. The method is that described earlier with reference to the male stickleback's greater valuation of a larger brood: How much risk to self is the parent prepared to accept to defend its helpless young from a predator dangerous to both?

An adaptive parental psyche may be expected to tolerate more risk to self in defense of young of greater reproductive value. One determinant of reproductive value is brood size. Another is offspring age, since the reproductive value of immature animals increases over time at least until maturity, by simple virtue of surviving successive periods of potential prereproductive mortality. Studies of nestbound young who remain helpless unless defended are especially germane here, since they avoid confoundings of offspring reproductive value with changes in self-defensive or escape capabilities; many such studies have been conducted with birds and fishes, and the general result, albeit with many complications, is that parental defense indeed increases as offspring reproductive value increases (Montgomerie and Weatherhead, 1988; Redondo, 1989).

Maternal aggression in laboratory rodents is presumably an analogous manifestation of parental readiness to defend the young, and Maestripieri and Alleva (1991) have shown that it varies with brood size as predicted from reproductive value theory. Oddly, however, maternal aggression does not appear to increase as helpless young age, and the adaptive significance of the time course of maternal aggression in these species remains obscure. One possibility is that the changes are adapted to changing threats from infanticidal conspecifics of both sexes rather than to predators (Daly, 1990).

In the human case, parentally perpetrated infanticide can be treated as a reverse assay of parental solicitude for which it has some of the same advantages as parental defense. Any factor that may be expected to influence parental investment allocations should also be relevant to the likelihood of lethal divestment, regardless of whether infanticide is a fitness-promoting adaptation or an incidental and maladaptive epiphenomenon of parental unconcern with the offspring's

welfare. According to a systematic review of rationales for infanticide in nonstate societies where it is not criminalized, human infanticide is primarily a response to cues of low infant reproductive value, namely bad circumstances such as famine at the time of the birth or defects in the child itself (Daly and Wilson, 1984); the principal rationale for infanticide outside this category is dubious or inappropriate paternity.

Human infanticide also provides an instance of the hypothetical test of parental solicitude suggested above: Which do you save when one must be sacrificed? The answer is that mothers confronted with this dilemma save the older child, whose reproductive value is usually greater. A common rationale for infanticide is maternal overburdening when the birth interval is too short; nowhere do people solve this problem by disposing of the toddler (Daly and Wilson, 1984).

In the absence of mishap, a child's reproductive value increases steadily from birth until at least puberty. With modern medicine, the early increase is muted by declines in infant and juvenile mortality, but where mortality and fertility are closer to the levels that must have prevailed for most of human history, the prepubertal increase in reproductive value is not trivial. We would thus expect parental feelings to have evolved such that parents will seem to value offspring increasingly with age, and we might therefore expect to see an age-related decrease in the likelihood of lapses of parental solicitude. Increased parental solicitude with offspring age may be difficult to detect because the offspring's dependence is waning at the same time, but parental valuation of the young can again be assayed by the parent's declining willingness to tolerate or expose the young to lethal risk. One apparent manifestation of such an age-related change is a monotonic decrease in the risk of filicide (Daly and Wilson, 1988a, 1988b), which continues to near zero as the offspring approaches maximal reproductive value in young adulthood. Not merely the direction of change, but the specific shape of the age-related filicide curve tracks ancestral reproductive value schedules remarkably well (Daly and Wilson, 1988b). It is especially striking that children become increasingly immune from parental lethal action as they mature, since this maturation entails increasing competitiveness in their interactions with nonrelatives, and an increasing overall risk of becoming involved in lethal interpersonal conflict,

both as killer and as victim (Wilson and Daly, 1985; Daly and Wilson, 1990).

ALTERNATIVES TO PRESENT PARENTAL INVESTMENT

The final class of determinants of variable parental response to be considered is alternative uses of parental resources. Polygynous red-winged blackbirds that have sired young in different nests commonly help provision only one brood, at least for a period of days, and they correctly prefer the brood where their efforts best promote their fitness (Yasukawa, Leanza, and King, 1993). Broods that were neglected when there was a more profitable option become effective elicitors of paternal investment when that more profitable option disappears.

Less obvious than this sort of parental allocation problem is the trade-off between parental investment and other fitness-promoting activities, such as the pursuit of additional matings, or the use of available physiological resources for growth and tissue repair with expected fitness benefits in the future. As parents age and senesce, their own residual reproductive value declines, and future alternatives may deserve less weight in present parental decision making. In the parental defense paradigm discussed above, there is some evidence that parents accept greater risk as their own reproductive value declines (Montgomerie and Weatherhead, 1988; Thornhill, 1989), although effects are less clear than those of offspring reproductive value. Efforts to show effects of parental reproductive value on parental investment decisions have been somewhat bedeviled by the fact that aging animals change in other possibly relevant ways as their reproductive value declines. Greater parental effort with age could be confused, for example, with effects of experience that make the parent more effective without really incurring greater risk to self or otherwise investing more; however, parental experience effects do not seem to explain away increases in parental effort with age in jungle fowl (Thornhill, 1989) or California gulls (Pugesek, 1983, 1987).

Human females have an unusually discrete end to the potentially reproductive life span, and so we might expect a woman to exhibit a decrease, with age, in any tendency to devalue a present offspring in terms of its compromising effects on her future. It follows that the risk of maternally perpetrated infanticide might decline as a function of maternal age, and so it does

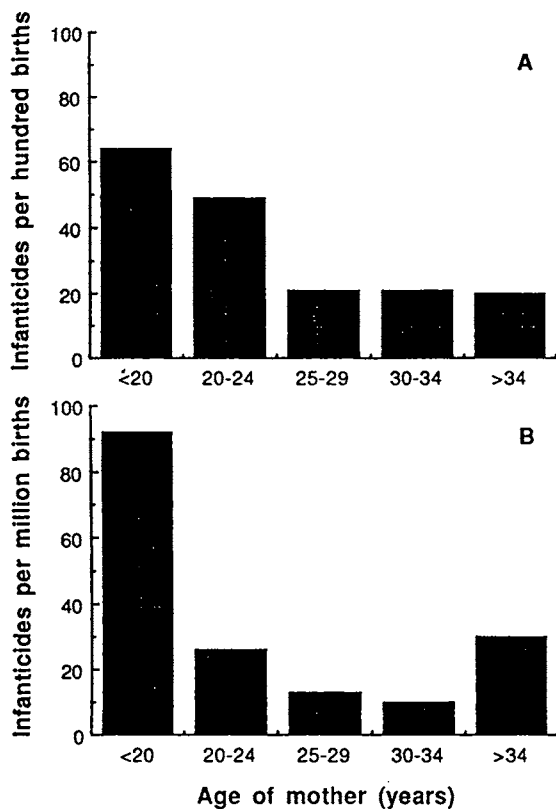


FIGURE 84.5 Rates of infanticide by mothers as a function of maternal age, among (A) Ayoreo Indians of South America ($N = 54$) and (B) Canadians ($N = 87$). (From Daly and Wilson, 1988a, figure 3, with data in (A) from Bugos and McCarthy, 1984.)

(figure 84.5). We would expect that many of the variables that are relevant to changes in maternal solicitude (or lapses therein, as in the case of maternal filicides) should be similarly relevant for fathers. However, women's reproductive life spans end before those of men, so the utility of alternative reproductive efforts declines more steeply as a function of age for women than for men. Moreover, dependent children impose different opportunity costs on mothers and on fathers: A nursing infant constrains mother's immediate alternative reproductive prospects much more than father's, and the magnitude of this differential impact upon mother versus father declines with time since birth. These considerations suggest that a mother's valuation of a child relative to her valuation of herself is likely to rise more steeply with time since the child's birth than is the corresponding quantity for the father. If filicides constitute a sort of reverse assay of parental

solicitude, it follows that filicide rate should decline more steeply for mothers than for fathers, and it does (Daly and Wilson, 1988b).

A three-stage theory of maternal bonding

The idea that variations in parental solicitude are the outputs of motivational systems designed by selection to modulate parental efforts has implications for the controversial topic of maternal bonding. The theoretical considerations reviewed above suggest that the development of child-specific parental love is likely to involve at least three separable processes with different time courses: (1) an initial assessment of the newborn's fitness prospects on the basis of both its quality and the situation; (2) discriminative attachment to the baby as an individual; and (3) a much more prolonged and gradual deepening of individualized love.

INITIAL CUES OF NEWBORN'S FITNESS PROSPECTS The first process to be expected is an assessment, immediately after birth, of the child and of how its qualities and present circumstances combine to predict its prospects. Conspicuous signs of low viability increase maternal inclination to divest; in the modern West, births of children with major defects commonly evoke immediate shocked rejection by the parents (e.g., Drotar et al., 1975), a rejection that would have led to quick abandonment in ancestral settings (Dickeman, 1975). Where genetic counseling and termination of pregnancy are available, parents commonly want to abort seriously defective fetuses (e.g., Leschot, Verjaal, and Treffers, 1985). Beliefs that deformed infants are ghosts or demons (or the progeny thereof) are found sporadically throughout the world and are invoked to justify infanticide. Analogous superstitious allegations about well-formed, healthy babies are essentially nonexistent, implying that so-called superstition cannot be dismissed as ignorant foolishness, but functions instead as an ideological buttress of difficult but functional choices (Daly and Wilson, 1988a).

Conspicuously defective newborns are rare, of course, but maternal responsiveness in the immediate postpartum period also varies with subtle cues of the infant's quality and health (e.g., Mann, 1992). Small, premature babies incur increased risk of abandonment or abuse (e.g., Hunter et al., 1978) and when such babies are likely to die, parents may distance them-

selves emotionally and fail to participate in the infant's hospital care (Newman, 1980). Emotional distancing has also been described among impoverished Brazilian mothers of weak, sickly infants who are expected to die (Scheper-Hughes, 1985). It should be noted that low birth weight in North America is associated with low socioeconomic status, maternal youth, large family size, and close birth spacing (e.g., Zuckerman et al., 1984), but size and vigor of a newborn may be salient cues modulating the development of parental solicitude. In an observational study of low-birth-weight twins, the healthier twin was more effective in eliciting maternal responsiveness at 8 months of age, and factors such as duration of postpartum separation or the incidence of positive interactions with the mother did not account for the mother's differential treatment of the twins (Mann, 1992).

Within the first few hours after birth, healthy human infants exhibit a precocious social responsiveness—eye contact and selective attention to maternal speech—which may be an adaptation for advertising quality and eliciting maternal commitment during this assessment phase. If circumstances are dicey and the mother is in any way ambivalent, poor responsiveness might tip the scales toward disinclination to raise the child.

There has been considerable controversy about the effects of mother-infant contact in the immediate postpartum period on the quality of the mother-child bond (e.g., Klaus and Kennell, 1976; Herbert, Sluckin, and Sluckin, 1982). Effects of circumstantial variables other than the contact itself have been taken as evidence against a specialized bonding adaptation, but from a selectionist perspective, it would not be surprising to discover that extra postpartum contact has little ameliorative effect on mothers when circumstances such as poverty, lack of paternal support, and other indices of maternal overburdening cue poor fitness prospects. More work is needed to assess whether situational and other variables (such as the mother's residual reproductive value as measured by her age) interact with and modify the effects of particular postpartum experiences. Moreover, modern medical techniques of fetal assessment can provide mothers with information relevant to the hypothesized assessment phase of bonding even before birth, with effects on the time course of "maternal-fetal bonding" as assessed by questionnaire (e.g., Caccia et al., 1991); it is an open question whether prenatally and postnatally received information on offspring quality have essentially similar impact or are

instead processed differently as a result of hormonal or other events surrounding parturition.

Many new mothers experience a brief period of the "blues" within the first few postpartum days (e.g., Cutrona, 1982; Hopkins, Marcus, and Campbell, 1984). A lesser but considerable number experience a more debilitating postpartum depression. Such depression is apparently especially likely when the mother is young, single, at odds with the father, or otherwise lacking social support (e.g., Cox, Connor, and Kendall, 1982; Cutrona, 1982; Hopkins et al., 1984), and when the infant is suffering from poor health (e.g., Blumberg, 1980; Grossman, Eichler, and Winickoff, 1980). These circumstances are very similar to the infanticide circumstances described in the ethnographic literature (Daly and Wilson, 1984). Women suffering from extreme postpartum depression are sometimes characterized by clinicians as delusional, but the typical content of the "delusions" seems not at all fantastic: concern about inability to care for the baby, fear of not having enough love for the baby, and guilt aroused by infanticidal thoughts (e.g., Herzog and Detre, 1976).

DISCRIMINATIVE BONDING TO OWN OFFSPRING Parents are highly sensitive to their babies' distinctive features, recognizing them by voice (e.g., Formby, 1967) and by smell (Porter, 1991) with only minimal exposure. Some have implied that these abilities represent psychological adaptations for discriminative bonding, but, of course, people are very good at recognizing individual faces generally (see *J. Cognitive Neurosci.* 3[1], 1991), and persons other than mothers may be just as good at discriminating babies by smell (Porter et al., 1986). Whether there is a specific heightened postpartum infant recognition ability is still to be determined.

Rather than having merely to recognize her own baby, the "task" confronting the new mother is to develop an individualized commitment to it, such that she is emotionally prepared to invest heavily in its welfare without being at the same time vulnerable to parasitism by children generally. Many new mothers report an initial feeling of indifference to their babies (perhaps reflecting the initial assessment phase as well as the lack of individuation), but very few feel the same way by one week postpartum (e.g., Robson and Kumar, 1980). After having had close contact with their infants over the first few days, mothers commonly report developing a feeling that their baby is uniquely wonderful (e.g., Klaus and Kennell, 1976).

A GRADUAL DEEPENING OF PARENTAL LOVE The third predictable process of parental attachment is a much more gradual one: The strength of parental love may be expected to grow with the child's increasing reproductive value, especially over the first few years when there is the steepest increase in that value. Fleming et al. (1990) analyzed the content of women's utterances at intervals over 16 postpartum months, and found that the mothers talked more and more positively about their infants over time; the effect was not merely due to changes in maternal condition or situation, as the same measures with respect to self and to husband did not exhibit similar trends. Postpartum growth in the salience and importance of the infant was also reflected by "an increasingly large proportion of women reporting such things as feelings of closeness to their infants, being pleased with their infants' development, or enjoying child-care activities" (p. 141).

The information that parents garner from their continued monitoring of offspring quality should affect the depth and time course of their love and commitment, especially while infant mortality risk remains high. Since parental effort is a resource to be invested, not squandered, chronic changes in the infants' responsiveness and robustness, consequent upon the effects of malnutrition, dehydration, and pathogens, can be expected to dampen parental love, in spite of the infant's greater need. In many societies, newborn babies are not immediately named or officially acknowledged by the community, a practice more or less explicitly linked to their uncertain future. Naming bestows personhood and facilitates the individuation of affection. (Indirect evidence for this claim can be found in observations that naming children after relatives is effective in inspiring namesake investment and inheritance; Smith, 1977; Furstenberg and Talvitie, 1980.) The postpartum delay in recognizing infants' personhood corresponds to a period of high mortality risk, perhaps with the effect of facilitating difficult decisions of divestment and lessening the emotional pain should the infant die (Mull and Mull, 1988; Schepher-Hughes, 1985). It is something of a cliché to claim that the valuation of children is a recent Western cultural invention, introducing tales of child brutalization and parental indifference in history and in other societies as support; those making this argument fail to appreciate that seeming callousness is an understandable response to circumstances that make children poor prospects for survival and reproduction, and that the same mothers

who seem indifferent to the plight of one child in one context can be profoundly nurturant to others born in more auspicious circumstances (e.g., Bugos and McCarthy, 1984).

Concluding remarks

Evolutionary theory is not a substitute for proximate causal analysis, but a valuable aid thereto: Understanding how selection operates and what behavioral control mechanisms have been designed to achieve affords innumerable hints to their probable organization. Improved maternal efficacy over the life span, to take one example, has routinely been assumed to reflect the acquisition of skills and/or knowledge, and the "immaturity" of young mothers. However, selectional thinking suggests that such changes over the reproductive life span may often reflect adaptive changes in maternal inclinations as maternal reproductive value and opportunities change. This alternative view suggests many possible lines of research about the contingent modulation of parental solicitude.

Selectional thinking provides reason to believe that the individualistic focus of cognitive neuroscientists will illuminate family relations better than more sociological approaches. The popular focus on families as "systems" and their members as components thereof cannot be correct, insofar as it elevates the so-called system's objectives above those of its actors and ignores the fact that family members are agents with only partially congruent interests. A quarter century of criticism of greater-goodism in biology has clarified why individual organisms are the appropriate level in the hierarchy of life at which to impute integrated agendas, and why the analogizing of larger groups to self-interested individuals typically fails.

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