An infant baboon follows his male protector closely. (Photo by Ryne Palombit.)
INTRODUCTION

The investigation of variation within and between primate societies has been a major focus of primatology since the 1960s [e.g., Altmann, 1962; DeVore, 1965; Wrangham, 1979, 1980; Goldizen, 1988; Uchida, 1996; Ross, 1998; Smuts et al., 1987; Sterck et al., 1997; Dixon, 1998; Kappeler, 2000]. Overlap of generations is found in all primate societies, and primate sociosexual organization ranges from “suprasolitary” (e.g., Loris), in which adult females utilize exclusive nesting or sleeping sites and do not cooperate with other adults in predator or resource defense, foraging, or parenting, to quasi-eusocial (e.g., cooperatively breeding marmosets and tamarins [see Bicca-Marques, Heymann, Saltzman, this volume]) in which related or non-related individuals, whose reproduction may be suppressed physiologically or socially, assist a primary breeder to raise offspring. The documentation of interspecific and intraspecific variation by primatologists was stimulated by Darwin’s [1859, 1871] formulations of evolutionary theory based upon his observations of variation in nature. These have made a significant impact on the broad field of animal behavior [Wilson, 1975; Alcock, 1979] which, until the 1970s, was dominated by typological thinking about animal social organization, in particular, mating systems [Brockmann, 2001].

Brockmann [2001] pointed out that Darwin [1871, 1876] not only described differences between species and sexes but also variation within the sexes, although none of the examples of within-sex variation referred to primates. Nonetheless, Darwin [1871] noted numerous instances among a variety of animal species in which different male types coexisted. He proposed that each type was associated with repro-
ductive “advantages” for the bearer. In 1972, Crook suggested that dominant and subordinate male primates generally have distinct morphological (size) and behavioral characteristics and that these corresponded to differential reproductive success. Crook argued that these within-sex differences were most likely to occur in multimale-multifemale mating systems in which competition for mates (“social selection” or sexual selection [see Crook & Gartlan, 1966; also see West-Eberhard, 1979, 1983]) was intense. Discussing Crook’s use of the term social selection, West-Eberhard [1979, p 223] defined it as “selection involving direct competition via social interaction” and noted that Darwin’s [1871] interests involved social competition broadly, including competition for mates. Under these conditions, behavioral responses are “competition-dependent” [West-Eberhard, 1979], driven by social interactions between individuals and groups relative to changing environmental regimes.

It is now widely accepted that male-male competition may be a strong selective force in polygynous and dispersed (non-gregarious), in addition to multimale-multifemale (polymynandrous), mating systems in primates [Dixson, 1998]. Moreover, “sperm competition” (competition among sperm from more than one male for the ova of a female) may be ubiquitous within the Order [Gomendio et al., 1998; Harcourt et al., 1981; see Reeder, this volume]. In the present chapter, we describe alternative reproductive behaviors in male and female primates, assess the relationship between phenotypic plasticity and conditional reproductive behavioral patterns in our examples, discuss the importance of intersexual interactions in determining alternative patterns of behavior in the opposite sex, and evaluate the potential for general principles of alternative reproductive behaviors. We make no attempt to review the primate literature but concentrate, instead, upon selective examples that highlight alternative reproductive behaviors as products of sexual selection and reproductive competition. While some authors discuss “alternative phenotypes,” where “phenotype” may pertain to physiological, morphological, behavioral, or other components of the organism’s responses to the environment, in this paper “phenotype” is employed to mean the behavioral component (i.e., “behavioral phenotype”).

### Alternative Reproductive Behaviors: Definitions and Terminology

Individuals of the same sex differ in many characteristics, and two or more reproductive behavioral phenotypes may be expressed during the lifetime of an individual and between individuals within the same population [Austad, 1984; Caro & Bateson, 1986]. Differing reproductive behavioral phenotypes are driven by sexual selection where they result in differential reproduction. Alternative reproductive behaviors, components of phenotypic evolution and patterns of intraspecific character divergence [West-Eberhard, 1979], entail all discrete strategies and tactics employed by individuals to maximize inclusive fitness [Austad, 1984]. Dixson’s [1998] review of “alternative mating tactics” in primates included only male examples, although he did note that certain data sets suggest that dominance rank may correlate with reproductive success for females as well as for males [also see Pusey et al, 1997; Clarke & Glander, 1984]. This may indicate that different costs and benefits and, thereby, different selective pressures, may affect females of differing rank. Because males are
typically considered to be the sexually selected sex (since ova are generally limiting for males [Trivers, 1972]), discussions of alternative reproductive behaviors have emphasized males [Henson & Warner, 1997; Stockley, 1997]. Whether considering males or females, however, mating behavior is expected to entail relative costs and benefits (e.g., opportunity costs, searching) which may be expressed in the following formulation:

\[
\frac{dB(n)}{dn} = \frac{dC(n)}{dn},
\]

where \( B(n) \) and \( C(n) \) are the benefit and cost curves, respectively [Janetos, 1980]. The precise shape of the cost curve cannot be predicted; however, it will be an increasing function of \( n \), the number of prospective mates examined, a process that is costly in time [Janetos, 1980]. The shape of the cost curve will usually differ for males and females since males are “time minimizers,” females “energy maximizers” [Schoener, 1971]. The expression of alternative reproductive behaviors by either sex is expected to be a function of the fitness costs associated with mating which will be sensitive to environmental constraints (e.g., physical, ecological, social).

Brockmann [2001] reviewed the evolution of “alternative strategies and tactics” with an emphasis on the invertebrate literature, and Henson & Warner [1997] and Taborsky [1998] provided an overview of the topic in vertebrates (fish). Henson & Warner [1997] noted that a distinction between the underlying rule of a phenotype (a strategy) and the expression of that rule (a tactic) is generally made. In the present chapter, we avoid the use of these terms, except where employed by particular authors, since their definitions have not been standardized in the literature on alternative reproductive behaviors and phenotypic plasticity.

Previous discussions of alternative phenotypes have fostered the nature:nurture fallacy by classification systems based upon presumed environmental vs. genetic mechanisms underlying observed behavioral variation [Brockmann, 2001]. Instead, Brockmann [2001] proposed a system of classification analogous to that employed in the literature on sex allocation (apportionment of investment between the sexes) whereby alternative phenotypes were viewed as either irreversible and fixed over the individual’s lifetime or reversible (facultative). Since we know of no cases of irreversible and fixed alternative reproductive phenotypes for primates, the present chapter will focus on alternative reproductive behaviors that are facultative and reversible. In the latter case, differences in behavior are expected to be a function of behavioral assessment by the actor of others’ response patterns [Parker, 1974; Krebs & Davies, 1993, Chapter 10]. If the resulting alternative phenotypes yield equal reproductive success, the responses are assumed to be evolutionarily stable [Krebs & Davies, 1993]. Selection, then, would influence not only the behavioral options but also the capacity for behavioral assessment, resulting in phenotypic plasticity (“flexible behavior”) for response to variations in the environment (social, ecological, or physical).

Brockmann’s [2001] descriptive approach emphasized three points derived from the literature on sex allocation. First, she observed that alternative phenotypes have
not commonly been viewed as responses influenced by environmental conditions. Instead, “conditional strategies” or “condition-dependent strategy” has traditionally referred to environmental (including social) and individual conditions affecting the behavioral patterns employed during a lifetime. These phenotypes have generally been discussed in terms of differences between individuals for the duration of the adult life stage or may involve the same individual switching from one behavioral, morphological, physiological, life history, or other option to another. The individual adopting the secondary phenotype is generally the condition-sensitive individual who has lost in or defects from social competition [West-Eberhard, 1979]. In Brockmann’s [2001] view, environmental conditions, age, an individual’s physical or reproductive condition, population density or structure, and other factors influence all alternative responses that individuals adopt if fitness is thereby increased. Thus, all alternative phenotypes may be viewed as variable and responsive to environmental or individual conditions.

The second point proposed by Brockmann [2001] concerns frequency-dependence, whereby the success of a phenotype is dependent upon the phenotypes expressed by others. She suggested that frequency-dependence is a component of condition-dependent options in sex-allocation theory and is likely to be significant in condition-dependent and/or environmentally influenced alternative behavioral patterns [also see Parker, 1982]. Continuing to argue from the sex allocation literature, Brockmann’s [2001] third point argued that combinations of phenotypes are likely to be expressed as alternative phenotypes. Thus, combined patterns of alternative reproductive behaviors may occur within individuals depending upon environmental conditions and individual characteristics. Males, for example, may combine persuasion and force during courtship.

A Comment on Mechanisms: Alternative Reproductive Behaviors and Phenotypic Plasticity

Most mammals have generalist phenotypes [Vaughan, 1978]. Although precise epigenetic rules are poorly understood [Schlichting & Pigliucci, 1998; Pigliucci, 2001], these behavioral options are thought to permit individuals to exhibit adaptive responses to changing environments without the costs of modifying the organism’s morphology. Agrawal [2001; also see Parker, 1982; West-Eberhard, 1989; Schlichting & Pigliucci, 1998; Pigliucci, 2001; Debat & David, 2001; Scheiner, 1993] has recently discussed phenotypic plasticity, emphasizing the importance of interactions between individuals in relation to phenotypic change. While genetic and non-genetic factors influencing inclusive fitness may generally interact [Brockmann, 2001], it is useful to consider them separately for a clearer appreciation of their differences.

West-Eberhard [1979] provided a subtle treatment of genetically programmed and facultative (non-genetically programmed) alternative reproductive behaviors. Most alternative phenotypes will be facultative and “competition-dependent” because most examples of alternative reproductive behaviors in the literature are “temporary, age-dependent, or otherwise...condition-dependent” responses [West-Eberhard, 1979, p 230]. As West-Eberhard [1979] pointed out, “At the facultative switch point a sec-
Alternative reproductive behavior begins to be on an average more profitable than the primary specialization, and at that point the fitness values of the two alternatives are equal.” (p 230). Thus, for the individual adopting the secondary phenotype, decreasing benefits from the primary phenotype may lead to the adoption of a secondary phenotype where this option leads to gains in fitness relative to the phenotype expressed previously. The switchpoint is that point in time and space when the individual “decides” to employ an alternative reproductive behavior rather than the primary reproductive phenotype.

A possible example for primates involves the expression of infanticidal behavior by dominant male chacma baboons, whose group tenure is relatively brief, and two alternate non-infanticidal phenotypes [Palombit et al., 2000, see discussion of this example below]. Palombit and his colleagues concluded that the infanticidal phenotype is expressed facultatively because behavior was highly variable, failing to conform to a “pure” or “mixed” evolutionarily stable strategy model. In West-Eberhard’s [1979] view, fitness benefits from facultative, “secondary alternatives” will usually be advantageous only when the benefits of the “primary specialization” decrease below some threshold value for the individual observed to switch. She argued that “secondary alternatives” will be less beneficial and more costly in terms of inclusive fitness than primary alternatives and should be adopted only where the primary specialization yields “diminished returns.” Secondary alternatives, then, should often represent “best of a bad job” options [Krebs & Davies, 1993, Chapter 10].

West-Eberhard [1979] also argued that “favorable switch conditions are competition-dependent, not simply frequency dependent” (p 230). Thus, the individual should be capable of responding to a number of factors that “can fluctuate widely and independently in nature” [West-Eberhard, 1979, p 230]. These ideas imply that facultative alternatives are favored in heterogeneous regimes where physical, ecological, and social events change frequently, possibly in opposing and unpredictable directions. As West-Eberhard [1979] stated, “a ‘condition blind’ genetic switch to a secondary (inferior) alternative often would be likely to prove less favored by long term selection than would rigid adherence to the primary specialization” (p 230).

The ratio of alternative phenotypes is fixed in models assuming genetic programming of the switch from one phenotype [West-Eberhard, 1979]. The ratio of phenotypes is “situation-dependent,” however, for facultative alternatives. These arguments assume nothing about the degree of heritability of the behaviors themselves, only the switch mechanism involved in relation to primary and secondary alternatives. West-Eberhard’s discussion permits one to assume that the behaviors might be more or less heritable and that heritability might vary between individuals with different genotypes. We propose that many, if not most, of the alternative reproductive phenotypes discussed in this chapter have a heritable component because reports in the literature document their “repeatability” within species in a broad range of environmental (including social) regimes. Similar patterns of alternative reproductive behaviors within species have been reported by numerous researchers [Smuts, 1987], although differences also occur [see Palombit, 2000; Palombit et al., 2000]. Smuts [1987], for example, noted at least one example of an individualized alternative re-
productive phenotype in a chimpanzee, stressing the importance of variations in
development, experience, and/or cognition in the expression of secondary responses.

West-Eberhard [1979] and Qvarnstrom & Price [2001] also emphasized the im-
portance of developmental effects that might favor individualized responses. For ex-
ample, Qvarnstrom & Price [2001] discussed several studies from mammals show-
ing a relationship between variations in maternal investment and offspring size and
odor, non-genetic characteristics often related to mate selectivity. They stated that,
“Individuals with a relatively good start in life...might be preferred as mates because
they, in turn, could be better able to provide their offspring (or mates) with resources....”
(p 95).

We infer from West-Eberhard’s [1979] paper that, while the capacity to switch
from one phenotype to another in relation to competitive regimes and the frequencies
of other phenotypes is heritable (i.e., the capacity for phenotypic plasticity), the fre-
cuency-dependent timing of the switch would be facultative (competition-dependent)
in most cases. Facultative responses may be characteristic of primates because obliga-
tory, frequency-dependent switching from one phenotype to another would constrain
the range of an individual’s influence over and reactions to immediate circumstances.
Furthermore, if some primates have the capacity to plan behavioral options for the
future, as has been suggested for chimpanzees and some other species [e.g., de Waal,
1989; Byrne & Whiten, 1997], obligatory switching would be disadvantageous. The
capacity to learn from past experience would seem to complement the capacity for
facultative responses to competition-dependent conditions.

OBSERVED DIFFERENCES IN PRIMATE REPRODUCTIVE PHENOTYPES

Krebs & Davies [1993] proposed that alternative reproductive behaviors within
species arise by way of intrasexual competition in response to environmental hetero-
genetic, “making the best of a bad job” (i.e., conditional strategies), and/or frequency-
dependent selection, ultimate causes favoring different intraindividual and/or
interindividual behavioral phenotypes in space and time for mate acquisition. These
factors are not mutually exclusive. In the case of frequency dependence, alternative
reproductive phenotypes are expected to represent evolutionarily stable strategies
with equivalent reproductive benefits. Dunbar [1984] proposed that male alternative
reproductive strategies yield comparable reproductive benefits in Theropithecus
gelada. This case, then, may represent an example of the evolution of alternative
reproductive behaviors by frequency-dependent selection. As Brockmann [2001] sug-
gested, however, individual phenotypes may be a function of what others are doing
most of the time, even where fitness benefits differ between phenotypes. Where theo-
retically optimal responses are not possible, the individual does the best that (s)he
can given the available behavioral options. Most studies of primates that have esti-
mated differential reproductive success report variations in fitness of alternative re-
productive phenotypes [e.g., Solis et al., 2001 and references therein; Alberts et al.,
2001; Jones, 1985, 1995] and thus may represent “best of a bad job” phenotypes.
Since alternative reproductive behaviors are thought to be negatively frequency-de-
pendent [Bell, 1997], it is expected that the rare (extreme) phenotype will often be
favored by the choosing sex [Alexander et al., 1997], possibly explaining studies for primates which fail to find a positive correlation between high rank and reproductive success [see references in Soltis et al., 2001]. Although, for fish, alternative reproductive behaviors have been studied at several levels of analysis (e.g., ecology, behavior, life-history, relative fitness, physiology, and genetics) [Henson & Warner, 1997], no primate species, with the arguable exception of the cooperatively breeding *Callithrix jacchus* [see Abbott et al., 1998], has been evaluated systematically for all of these factors.

Table I presents a preliminary schema of alternative reproductive behaviors observed and expected in male and female primates. Following the logic of Alexander et al. [1997] for insects, behavioral patterns may be viewed as a continuum from relatively passive and/or non-aggressive (persistence, copying) to relatively direct and/or aggressive (e.g., contest, force, or coercion). Alexander et al. [1997] pointed out that sexual selection entails conflict by one sex with the opposite sex who may impact the initiator’s fitness by rejection or the recipient’s fitness by force or coercion. Members of the same sex may likewise affect an individual’s reproductive success by competing for mates. Table I suggests that alternative reproductive behaviors in primates may involve physiological mechanisms (e.g., reproductive suppression; see Saltzman, this volume), “cryptic” (e.g., sperm selection; see Reeder, this volume), and non-damaging (e.g., dominance hierarchies, persistence) response patterns. Unclear from this table is the degree to which females can control the reproductive process by variations in their responses, although in a few primate species, female dominance has arisen [Kappeler, 1993; see Vervaecke et al., this volume]. The available literature, however, indicates that primate females may experience significant constraints from males in many environmental regimes [Smuts & Smuts, 1993], and leks, in which females choose freely among a range of male phenotypes and generally mate only once, do not exist in the primate Order. This suggests that, although primate females may demonstrate significant emancipation from males, probably as a result of the unpredictable dispersion of resources [see Jones & Cortes-Ortiz, 1998; Jones, 2000; Emlen & Oring, 1977], overt and direct influence over males may be significantly limited in most species.

From an evolutionary perspective, the typical copulatory posture of primates (and other mammals), as well as internal fertilization, implies intersexual conflict because males are in a position (dorso-ventral) to restrain females. This conclusion holds, also, for ventral-ventral positions with males in the superior mode. Such implicit conflict implies that force or coercion of females by males is a primitive trait in the Order and that sexual selection on male responses may incur significant costs for primate (and other mammalian) females [see Brooks & Jennions, 1999; Stockley, 1997; Smuts & Smuts, 1983]. Sperm competition, an indirect form of contest competition, also appears to be ancestral. It appears that few primate males are egalitarian [but see *Brachyteles*: Strier, 1997], although some primate females are [e.g., *Macaca maurus*: Matsumura, 1998; also see Sterck et al., 1997], an observation having implications for the evolution of alternative reproductive behaviors since egalitarianism among males, which may be favored by kin selection or ecological conditions, will
decrease reproductive competition within that sex. Likewise, female-female competition is most likely much more common than has been reported to date [see Crockett, 1984; Smuts, 1987; Kuester & Paul, 1996; Pusey et al., 1997; Jones, 2000; Sterck et al., 1997; see Saltzman and Vervaecke et al., this volume], suggesting that alternative reproductive behaviors are common in primate females as well as males.

**Male Alternative Reproductive Behaviors**

Alternative reproductive behaviors within and between individual male primates have been relatively well documented [e.g., Smuts, 1987; Dixson, 1998; Watts, 2000; Horwich et al., 2000; Palombit et al., 2000], although this topic has rarely been the primary topic of investigation. Palombit et al. [2000; see Palombit, this volume] reported infanticidal and non-infanticidal phenotypes among male chacma baboons. These authors showed that infanticide is a primary specialization of a high-ranking male whose tenure as dominant is usually brief, and duration of a male’s tenure was positively correlated with mortality of infants born subsequent to a takeover. Thus, individual characteristics of males influenced patterns of infanticide [also see Clarke et al., 1994]. Male “friends” of mothers of infants, who were the targets of aggression by infanticidal males, influenced outcomes of events between dominant males and infants, since friends intervened defensively in these situations to protect infants. There was also a category of non-friend males that intervened defensively. These latter phenotypes significantly decreased the likelihood of death or injury to infants. Palombit et al. [2000] concluded that “the brevity of alpha male tenure...is a likely proximate cause of infanticide” (p 146) and that the patterns of behavior exhibited by friends are costlier than those of non-friend and, possibly, infanticidal males (p 147). How friends and non-friends benefit reproductively from their behaviors is unclear from this study, although the sexual selection hypothesis [Hrdy, 1974] was supported for the infanticidal phenotype.

Primate males can vary in their “mating mode” [Taborsky, 1994], both within and between species, including within and between individuals. Dixson’s [1998] review indicated that these differential responses will often be a function of age and dominance rank. Jones [1995] described facultative reproductive phenotypes for mantled howling monkeys (*Alouatta palliata*) in tropical dry forest of Costa Rica. She identified five age and rank-related alternative reproductive behaviors, including two forms of consort behavior, consorts within sight of other group members, and consorts away from the group. Consortship, a form of mate-guarding behavior [Dixson, 1998], was most likely to be performed by high-ranking males, similar to reports on other species [Dixson, 1998; Tutin, 1979]. Dixson [1998], however, pointed out that the relationship between the consort phenotype and male reproductive success is unclear. In mantled howlers, since dominant males obtain most of their matings with females in “peak” estrus [Jones, 1985], the presumed time of ovulation, this phenotype may be a highly successful one for males who employ it. Other male mating phenotypes observed in *A. palliata* were “sneaker,” “appeaser,” and “fighter” [Jones, 1995]. Each of these alternatives, exhibited by subordinate males, was observed once in this study.
Studying Japanese macaques (Macaca fuscata), Soltis et al. [2001] also observed sneaker tactics by lower-ranking males, which they interpreted as conditional responses to avoid direct competition with males higher in rank. Using DNA analysis, these authors found that the sneaker phenotype was much less successful reproductively than more aggressive phenotypes employed by dominant males, although some of the variance in male reproductive success was a function of female choice of subordinate and non-troop males. Dominant males monopolized females, although the mating success of these males was negatively impacted by the increased numbers of females and female ovulatory synchrony. These and other studies [see references in Soltis et al., 2001] indicate that alternative reproductive behaviors may be especially characteristic of multimale-multifemale mating systems in primates and, possibly, other mammals, although alternative male phenotypes have been observed in polygynous species as well [e.g., Dixson, 1998; A. pigra: Horwich et al., 2000]. These studies lead to a general conclusion that alternative reproductive behaviors should be adopted when the benefits to inclusive fitness of the alternative phenotype outweigh the costs of the primary phenotype(s) adopted by the most successful reproductives in a population.

Costa Rican squirrel monkeys [Saimiri oerstedii: Boinski & Mitchell, 1994; Figure 1] display two phenotypes in relation to group tenure. Males may either remain in their natal group to breed or, less commonly, disperse as a young age cohort, cooperating to invade another established group from which they expel resident males. The infrequent occurrence of the latter strategy might occur in response to environmental heterogeneity (e.g., ecological and density effects), making the “best of a bad job,” or frequency-dependence for young males sensitive to rates of interaction with conspe-
cifics within and between groups. Sexual dimorphism in age and size is a significant feature of most primate populations [e.g., Plavcan & van Schaik, 1997], and alternative reproductive phenotypes may be expected to differ as a function of these distributions which will correspond to variations in reproductive value, a hypothesized determinant of some behavioral responses [e.g., Hrdy & Hrdy, 1976; Jones, 1996].

Taborsky [1998], studying fish, identified two classes of male mating phenotypes: bourgeois and parasitic. Bourgeois males are those that monopolize females, or the resources that they require for successful production of offspring, regardless of the mode of monopolization. Parasitic males, on the other hand, exploit the investment of bourgeois males by adopting strategies and tactics besides monopolization (e.g., “sneaker”). This scheme may be helpful for other vertebrate taxa, including primates. For example, in the mantled howlers discussed above, the copulation classified as “sneaker” occurred during group movement when the dominant, guarding male was preoccupied. Similar phenotypes have been described for other primate species [Dixson, 1998; Smuts, 1987]. Both Dixson [1998] and Smuts [1987] described “follower” phenotypes in which males associate with one or more groups and may obtain copulations more or less opportunistically [also see Horwich, 1983]. Both follower, sneaker, and “bachelor” [see Watts, 2000] phenotypes may generally be classified as parasitic.

Males may also vary in their expression of mate choice. In one group of Costa Rican mantled howlers in riparian habitat of tropical dry forest [see Jones, 1980], the dominant male rejected females seven times out of 36 solicitations by females. The mid-ranking male, rejected once out of 31 sexual solicitations. The subordinate male was never observed to reject sexual solicitations by females who solicited him 25 times [Jones, unpublished data]. This pattern of results indicates that dominant males are choosier than subordinate males and/or that the time budgets of dominant males are more constrained than those of subordinate males. Rejection of females’ solicitations may also be employed by males to guard against cheating by females (e.g., “pseudoestrus”), and dominant male mantled howlers, who receive more sexual solicitations from females in “peak” estrus than subordinate males [Jones, 1985], may be at greater liberty than subordinate males to employ information about female quality (e.g., stage of estrus) associated with female signals (e.g., genital signals and displays [Jones, 1985]).

Taborsky [1994] also argued that, in addition to mating mode, males will vary in their degree of paternal care [Wright, 1990; Woodroffe & Vincent, 1994]. Owens [1993] and Qvarnstrom & Price [2001] discussed models that describe how and under what conditions males make decisions to invest in young. Parental care in primates may be viewed along a continuum from lesser to greater investment with males in some species displaying a dispersed (i.e., non-gregarious) mating system, providing no investment in offspring (e.g., Loris), at one extreme, and the remarkable, bird-like example of Varecia variegata [see van Schaik, 2000] and cooperatively breeding male callitrichids at the other. Paternal effects may be direct (e.g., access to resources) or indirect (genetic) and may interact, significantly influencing offspring attractiveness and quality.
In a report on the polygynous red howling monkey (*A. seniculus*) in Venezuela, Agoramoorthy & Rudran [1993] showed that immature males may disperse from their natal groups with or without a father or a brother. In this species, cooperation between relatives for access to females in group takeovers is associated with longer tenure, and, presumably, greater reproductive success, compared with males who usurp a group of females on their own [Pope, 1990]. Pope’s [1990] work showed, further, that coalitions associated with longer tenure may be formed between males natal to a group, another alternative phenotype in this species. Agoramoorthy & Rudran [1993] argued that kinship also influences two other male phenotypes, males who commit infanticide and males who do not, since infanticide is less likely where a male transfers into a group whose sire is his relative.

In polygynandrous mantled howling monkeys (*A. palliata*) in Costa Rica, males demonstrate two patterns of group takeover [Glander, 1992]. Males may either fight or not fight for group entry. In some cases, the invading male is a relative, sometimes the son, of the alpha male in the established group, and, in these cases, the fighting phenotype has not been observed. Observed alternative patterns of paternal investment yielding differential inclusive fitness among males may be influenced by genetic and physiological factors as well as social learning. Clarke [1990], for example, described several variable aspects of the developmental psychology (e.g., temperament and socialization) of Costa Rican mantled howlers that might correspond to later decisions regarding paternal investment, reproductive competition, and mate selectivity.

In addition to mating mode and parental care, Taborsky [1994] argued that males may vary in their propensity to engage with other males competitively. Concerning the latter point, the ability of primate males to assess the resource-holding potential of other males is expected to vary as a function of resource dispersion, individual traits (e.g., intelligence), as well as other factors outlined by Smuts [1987] and Horwich et al. [2000]. While it is rarely clear whether aggressiveness and other risk-taking behaviors favor high rank or whether high rank provides a male the option to be aggressive, success in competitive contests and displays is a well documented component of male reproductive success for many primate species [Smuts et al., 1987].

Similar to the results of Soltis et al. [2001], Alberts et al. [2001] found that the ability of male savannah baboons (*Papio cynocephalus*) to monopolize females is density-dependent, a function of the number of females in a group. Differential reproductive success among males was also found to be a function of age-dependent fighting ability and individual differences. Rank correlated significantly with these factors and demonstrated a “queing” effect whereby males persisted for varying periods of time to achieve high rank. Males also differed significantly in their length of tenure as dominants. Alberts and her colleagues argued that these results may apply generally. Qvarnstrom & Forsgren [1998; also see Qvarnstrom & Price, 2001] proposed, however, that cues for female choice may often benefit subordinate males where choice traits fail to signal male quality and/or where costs to females outweigh benefits. Such conditions may be most likely in heterogeneous regimes and may favor subordinate males.
Female Alternative Reproductive Behaviors

Although primate females do not display monopolization of mates in the same sense that males may, abundant evidence now exists to demonstrate that primate females are more than simply donors to males and immatures [e.g., Hrdy, 1999; Crockett, 1984; Smuts, 1987; Kuester & Paul, 1996; Abbott et al., 1998; Jones, 2000]. Female-female competition, however, is still widely interpreted in terms of competition for food rather than mates [e.g., Silk, 1993]. It might be expected that alternative female reproductive phenotypes will be expressed wherever access to males is limited [Henson & Warner, 1997] and wherever males vary in attractiveness, quality, and/or control of resources required by females for reproduction. Henson & Warner [1997] proposed that female behavior will also vary with age or size where costs and benefits (e.g., of mate choice or of female-female competition) vary ontogenetically. In mammals, female adaptations, including physiological and behavioral traits (e.g., parenting effort), will be severely constrained by demands to maximize energy [Schoener, 1971]. Thus, females may exhibit a lower degree of overall phenotypic plasticity than males, although female phenotypes may be expected to be particularly creative in relation to their offspring and kin.

Nicolson [1987, p 333-337], discussing interindividual variations in maternal investment, suggested that alternative phenotypes are a partial function of maternal rank, age, parity, and reproductive performance [see West-Eberhard, 1979, p 230]. Characteristics of infants are also expected to influence maternal behavior and, in primates, only the influence of offspring sex has been broadly investigated as a factor in generating alternative female phenotypes [Nicolson, 1987]. Clarke [1990] reported that infant mantled howling monkeys feed in accord with their mother’s rank, a maternal effect that might influence infant quality, having long-term consequences for the mother’s and offspring’s future reproductive success. Clarke [1990] documented that female A. palliata display different “mothering styles” and that females respond differently to male and female offspring, consistent with the roles played by adult males and females in mantled howler society. Studies are required from the field to identify the range of alternative behavioral phenotypes exhibited by females in relation to parental investment and to correlate these differences with fitness.

A primary difference within and between females is the tendency to mate with a single male during an estrous or menstrual cycle and the tendency to mate with multiple males, inducing sperm competition [see Reeder, this volume]. Most females probably choose to mate multiply under certain, yet undefined, conditions. Data for birds [Gowaty, 1994] and humans [Gangestad & Thornhill, 2001] suggest that females may be most likely to mate with more than one male during their fertile period, findings that require further investigation in nonhuman primates [see Jones & Cortes-Ortiz, 1998]. Associated with multiple mating, primate females are known to adopt sneaker phenotypes, since copulations with extra-group males and with males other than the guarding, dominant male, have been reported [Boesch, 2001; Soltis et al., 2001; Watts, 2000; Horwich, 1983; Agoramoorthy & Hsu, 1999; C.B. Jones, personal observation]. Differences within and between females is also evident in female propensity to mate within a group or away from the social unit [e.g., chimpanzees:
Alternative Reproductive Behaviors

Tutin, 1979; mantled howlers: Jones, 1995, 1997a]. Alternative phenotypes have been observed in female fish as well [Henson & Warner, 1987].

Since males may offer good genes, resources, or both to females, and since males may vary in their ability to deliver these benefits, females are expected to compete for access to males of highest quality. However, little is known about male primate indicators of quality other than cues that are useful to females in making mating decisions. Females may interrupt copulations of other females and suppress their reproduction wherever gains in inclusive fitness can be realized. The cooperatively breeding callitrichids are the classic example for primates of alternative female reproductive phenotypes involving reproductive suppression of subordinates by dominants displayed in response to female-female competition for direct reproduction and for male investment [see Abbott et al., 1997; Dixson, 1998; see Saltzman, this volume]. Female-female competition in sexual contexts, particularly interruption of copulations and copulation attempts, has also been reported for several other primate species [see citations in Smuts, 1987; Jones & Cortes-Ortiz, 1998; see Vervaecke et al., this volume]. Smuts [1987] also discussed several other female mating patterns in her 1987 chapter that may vary within and between individual females, in particular, the tendency to initiate sex, generally with varying patterns of sexual solicitation, and refusing sex [also see Dixson, 1998; Jones, 1985].

In one study of mantled howling monkeys in riparian habitat of tropical dry forest, males were found to solicit females significantly more frequently than females solicited males, and the highest ranking males were most likely to solicit females signaling genital swelling and color cues, the presumed time of ovulation [Jones, 1985]. Females were observed to reject solicitations by the dominant male only 5 times [C.B. Jones, unpublished data] out of 16 sexual solicitations observed [Jones, 1985], possibly indicating a high degree of male control over females at certain stages in their estrous cycles. However, forced copulations were attempted but were observed to succeed only once [Jones, 1985; unpublished data]. Similar patterns were observed in Venezuelan red howlers [Agoramoorthy, unpublished data]. Male mantled howling monkeys may utilize sexual solicitations, and females may respect them, because most copulations involve precopulatory feeding by females at a food source defended by a male [Jones, 1995; Jones, 1997a]. In the same study, precopulatory feeding was associated with 75%, 73%, and 57% of the dominant, second-ranking, and lowest-ranking male’s copulations, respectively [C.B. Jones, unpublished data]. In a group of mantled howlers in deciduous habitat of tropical dry forest [see Jones, 1980], precopulatory feeding by the female took place in 60% and 100% of the dominant and subordinate male’s mating, respectively [C.B. Jones, unpublished data]. Thus, females and males differ in their tendencies to permit (males) or demand (females) precopulatory feeding. Strengthening the speculation that these food bouts are nutritionally significant to females is the observation that precopulatory feeding almost always involved high-quality food (i.e., new leaves, flowers, or fruit) rather than old leaves [C.B. Jones, unpublished data]. In these examples, females may parasitize male resource holding potential and courtship ("prenuptial feeding") and may or may not respond by accepting intromission [Jones, 1997a]. Multiple mating by
female mantled howlers [Jones & Cortes-Ortiz, 1998] may occur because females gain direct benefits from males, a condition that may in part explain alternative mating behaviors by females of this species.

Intersexual Interactions and Their Consequences for Alternative Phenotypes

Henson & Warner [1997; also see Watts, 1996] proposed that “intersexual dynamics” influence the evolution of alternative reproductive behaviors because of inherent conflicts of interest between the sexes, resulting in the mating system [Birkhead, 1993]. According to Alexander et al. [1997], these conflicts are a function of the decoupling of insemination and fertilization whereby it benefits males to control the former and females, the latter. This conflict establishes the conditions for an evolutionary “arms race” between the sexes, which results either in resolvable chases that are evolutionarily stable or in unresolvable chases that are unending [Alexander et al., 1987; see West-Eberhard, 1979]. As Alexander et al. [1997] pointed out, uncoupling is in the female’s interests since she is primarily invested in the fates of zygotes and since she may choose to mate multiply. The apparent ubiquity of multiple mating in primates and, it is presumed, subsequent sperm competition, strongly suggests that primate females have yet undiscovered mechanisms for influencing the timing of fertilization and thereby gaining the upper hand in this conflict with the opposite sex [see Reeder, this volume]. Males in some primate species have evolved responses to decrease the likelihood of multiple mating by females such as sperm plugs [see Dixson, 1998] and post-copulatory guarding [e.g., A. palliata: C.B. Jones, unpublished data; A. seniculus: G. Agoramoorthy, unpublished data], and variation between males might be detected in these aspects of their phenotypes. These male traits, neither of which has been investigated systematically in primates, might be correlated with alternative reproductive behaviors of males and might influence female choices. For example, bourgeois males may be more likely to deposit more effective sperm plugs and to mate guard. Either of these phenotypes might have differential costs and benefits for females selecting a mate.

Further, Dixson’s [1998] discussion of sperm competition suggests that sperm might differ in quality, including motility and length [see Tregenza, 2000; Anderson & Dixson, 2002], within males at different points in time and/or between males, possible outcomes of the sexually selected chase between the sexes. If so, these variations may correlate with other male traits signaling male quality which may serve as cues to females. However a recent study of Soay sheep (Ovis aries) [Preston et al., 2001] reported a counterintuitive finding that dominant males may obtain more copulations than subordinate males but may be less successful in sperm competition due to a depletion of sperm reserves. Thus, subordinate males sired more offspring than expected. Testicular circumference and number of sperm ejaculated were negatively correlated. While these data were preliminary and several important differences exist between promiscuous Soay sheep and species of primates (e.g., phylogeny, social organization, behavior), Preston et al. [2001] identified an area of research that demonstrates adaptive differences in male traits corresponding to alternative phenotypes that has not been investigated in primates. Nonetheless, these and other alternative
reproductive patterns by males (e.g., persuasion, force, coercion) indicate that, to varying degrees, males have evolved traits in response to female control of fertilization.

The extent to which either sex dominates the conflict between them will be a function of several constraints: physical (e.g., climate), biotic (e.g., resource dispersion and predation pressure), and social (e.g., interaction rates). For primates, there may be a continuum of female control of fertilization — from species in which females dominate males to species in which females appear to be coercively dominated by males most of the time. It would also be expected that, where males are dominant to females, females will prefer multimale-multifemale to single male groups [e.g., *Gorilla*: Robbins, 1995] because the former permit females a greater degree of freedom in mate choice. The relative extent of male domination may influence the evolution of alternative mate choice phenotypes in females, depending on the differential costs and benefits to female mate selectivity.

Henson & Warner [1997] discussed several ways in which females might influence male alternative reproductive phenotypes derived from the observation that, in some conditions, it might benefit females to express mate choice and that, in others, it may not. Costs and benefits of female choice, according to these authors, will be a function of the extent to which male phenotypes differentially influence female inclusive fitness. Henson & Warner [1997] suggested that, under frequency-dependent selection of male alternative behavior patterns, females have little to gain from mate choice since male alternatives yield comparable fitness benefits. However, female mate choice will be maintained, they argued, if males vary in the direct benefits (e.g., resources) that they provide. We suggest that wherever males are despotic and male dominance hierarchies have arisen, males will differ in their ability to monopolize females or resources required by females for reproduction. In these conditions, females may have been favored to yield some of their control over reproductive events to males.

This scenario, however, will be influenced by the relative degree of reproductive skew (the apportionment of reproduction within groups; see Hager, this volume) among females. Where females are egalitarian, having relatively equivalent reproductive success among them, few or no pressures may have operated to utilize male resource defense, assuming that females gain access to critical resources by their own devices [see Strier, 1997]. The environmental correlates of these differential patterns are unclear. However, it has been speculated for *A. palliata* that female emancipation is associated with extreme heterogeneity of limiting resources making females non-defensible for males [Jones & Cortes-Ortiz, 1998; Jones, 2000]. These ideas might be tested by a study of demes of *Theropithecus gelada* if, as Dunbar [1984] suggested, alternative male phenotypes in this species yield comparable fitness benefits.

Henson & Warner [1997] argued that females should display choice between male alternative reproductive phenotypes where these alternatives correspond to direct fitness benefits (e.g., access to resources). Males, for instance, may vary in their paternal investment [see Taub, 1984] which may impact infant survival and female fecundity. Similarly, infanticide risk may influence female alternative reproductive
behaviors [van Schaik, 2000, 2001]. Henson & Warner [2000] also pointed out that, if females benefit from mate choice, they should prefer males who exhibit aggressive restraint toward them. These authors showed, however, that some fish studies have demonstrated an association between predation risk and mating mode by males. Where predation risks are high, males are likely to adopt coercive phenotypes; where the consequent risks are low, males are more likely to display courtship. These patterns might apply as well to primates and should be investigated.

Other means whereby females can influence male alternative reproductive responses include increasing the reproductive skew among males by favoring large males – leading to alternative phenotypes in smaller males [Henson & Warner, 1997]. These authors noted that female responses may be deleterious to female fitness if males exhibiting the alternative phenotype are males of low quality or otherwise exhibit traits with negative impacts upon female fecundity (e.g., disruptive mating). It is possible, for example, to imagine infanticide evolving as a counterstrategy by some males in response to extreme preference by females for males most likely to invest in paternal care, reinforcing Henson & Warner’s [1997] caveat that it is important to consider the costs as well as the benefits of mate choice.

Alternative male phenotypes can influence the evolution of alternative reproductive behaviors in females [Henson & Warner, 1997]. In particular, males may use force, coercion, persuasion, or parasitic phenotypes to decrease female control over fertilization. These behavioral patterns are well-documented in primates [e.g., Smuts & Smuts, 1993; Smuts, 1985; Jones, 1985, 1995, 1997a; Soltis et al., 1997a, b] and may have evolved in response to female mate choice favoring males of the highest quality and/or attractiveness. Similar to their argument for females, Henson & Warner [1997] proposed that mate choice by males will arise where female phenotypes differentially influence male fitness, for example, where female primates differ in physical quality or stage of estrous or menstrual cycle. Choosiness by males might also be adaptive where males are limited in the rate of sperm production [Henson & Warner, 1998; see Dixon, 1998]. According to Henson & Warner [1998], female mate choice might favor forced copulations by particular males or classes of males rejected by the opposite sex which might establish an intersexual chase whereby females are selected to tolerate coercion or intensify or change modes of mate choice. Such a chase might explain many of the examples discussed by Smuts & Smuts [1993]. Henson & Warner [2001] also suggested that variations between males in paternal investment might favor female alternatives such as assuming a greater investment in offspring care or “demanding” male investment.

The arguments of Henson & Warner [1997] indicated that male reproductive phenotypes leave females with three options: retaining their phenotypes and accepting the tradeoff of associated costs and benefits, increasing their resistance to male control of fertilization and its aftermath, or increasing their maternal investment. One might also imagine a scenario in which male behaviors favor females’ decreasing their investment in offspring as may have occurred in A. palliata [see Altmann, 1959; Clarke, 1990; Jones, 1997b]. Female collared flycatchers (Ficedula albicollis) adjust reproductive effort facultatively in response to time of breeding and male traits...
[Qvarnstrom et al., 2000], a relationship that should be investigated in primates. Finally, Henson & Warner [1997] suggested that female alternative reproductive behaviors may be expressed even in the absence of alternative male phenotypes, where females of high quality favor males of high quality, leaving low-quality females to mate with low-quality males. Clarke’s [1983] finding that high-ranking female mantled howlers were more likely than subordinate females to mate with the dominant male might represent an example of this facultative adjustment to subordinate status. Kuester & Paul [1996] proposed that this pattern is common among primates.

### Dispersal as an Alternative Reproductive Behavior in Males and Females

Varying patterns of dispersal are documented for primates [Pusey & Packer, 1987; Jones, 1980, 1996, citations in Jones, 1999; Pope 1990, 1992; Glander, 1992; Brockett et al., 2000; Watts, 1996]. In some species, both males and females disperse; in others, one sex (usually female) is generally philopatric. Dispersal may be primary, when individuals transfer between reproductive units once in their lives, or secondary, when individuals move more than once between groups. Individuals may transfer as immatures or adults, and dispersal may occur independently or with one or more conspecifics of the same or opposite sex. Males unsuccessful at entry into new groups may become peripheral to established reproductive units, displaying varying patterns of access to females [e.g., Watts, 1996, 2000; Cords, 1987]. Other emigrating individuals may establish new reproductive units in unoccupied habitat (colonization) or, where population densities are high, within the home ranges of existing groups.

Dixson [1998, Figures 4.10, 4.11, 4.12; also see Horwich et al., 2000, Figure 1; Watts, 2000] provided a schematic overview of strategies and tactics employed by male primates for dispersed (non-gregarious), polygynous, and multimale-multifemale mating systems which demonstrates the importance of dispersal in the course of searching for and locating females. Dixson’s treatment showed that primate males, unlike many insects, fish, birds, and other mammals [see Emlen & Oring, 1977], are generally non-territorial, a condition probably related to the non-defensibility of resources required for females to reproduce. A clear alternative reproductive phenotype for males of all three mating systems, however, is males who disperse from their natal groups, and males who do not. Since Dixson’s [1998] diagrams and the primate literature indicate that most males disperse (although age of dispersal may vary within and between species), male philopatry is clearly the derived condition. Dispersing males may spend a varying period of time searching alone (e.g., A. palliata) or in all-male groups (e.g., Cercopithecus ascanius) and may ultimately colonize open habitat (e.g., A. seniculus), join existing groups (e.g., Saimiri sciureus), or invade existing groups either singly (e.g., Gorilla) or with other males (e.g., Erythrocebus patas).

Dispersal is an alternative reproductive behavior because its expression may vary within and between individuals over time and space. Patterns of dispersal reflect discrete decisions by individuals, their kin, or other group members where conspecifics share limiting resources [Parker & Stuart, 1976] and may function in part to avoid inbreeding [Pusey & Packer, 1987] and/or avoidance of ecological competition.
with relatives [see Perez-Tome & Toro, 1982]. Recent work on fig wasps showed that the benefits of cooperating with kin may be outweighed by its costs where ecological constraints are severe [West et al., 2001], a condition that may lead individuals to cooperate with unrelated conspecifics or to breed alone. Dispersal may be viewed as one component of an organism’s overall pattern of assessment employed to maximize inclusive fitness, and the primate literature shows that decisions to disperse can be a function of individual (e.g., age, sex, rank, physical condition, relatedness) as well as environmental (e.g., population density, habitat type, season) states.

The differential costs and benefits to inclusive fitness of dispersal may themselves favor alternative phenotypes, not only variations within and between individuals in their propensity to transfer out of their natal groups, but also with respect to their phenotypes after dispersal. Immigrants, for example, may be destined to low rank, requiring adjustments to subordinance such as helper phenotypes [e.g., cooperatively breeding callitrichids: see Keller, 1995]. Where opportunities to immigrate or to colonize are prevented by ecological constraints [e.g., food limitation and/or habitat saturation: see Keller, 1995], reproductive skew is expected to be high [e.g., Reeve & Emlen, 2000; see Hager, this volume], a relationship amply demonstrated in insects, birds, and vertebrates [see Keller, 1995].

Reproductive skew in cooperatively breeding marmosets is high because a group generally contains only a single female breeder. This condition is thought to be correlated with severe ecological constraints favoring helping behavior by subordinate females whose reproductive benefits are primarily a function of assisting the reproduction of the dominant, breeding female [e.g., Ferrari, 1993]. In the related Callimico goeldii, for whom ecological constraints are more relaxed, reproductive skew is decreased and social (reproductive) relations among females less differentiated [Porter, 2001]. Reproductive skew models, which predict high skew under conditions of greater ecological constraints, indicate that primate species in which female dispersal is rare [e.g., Macaca, Papio: see Pusey & Packer, 1987, Table 21-1] will demonstrate high skew among females and differentiated reproductive roles (e.g., “allomothering,” adoption). The literature on females of these species tentatively support this view [Macaca: S. Altmann, 1962; Papio: Hall & DeVore, 1965; Hausfater, 1975; J. Altmann, 1980]. Females in these and other species noted by Pusey & Packer [1987] appear to have lost the ability to initiate new groups. This derived condition has been observed as well in ant queens, which Keller [1995] attributes to very high dispersal costs. Because females are “energy maximizers,” and males are “time-minimizers” [Schoener, 1971], males are less constrained by ecological factors than the opposite sex. Reproductive skew models show that ecological constraints and other factors (e.g., coefficients of relationship) influence the apportionment of reproduction within groups [see Reeve & Emlen, 2000; Reeve & Ratnieks, 1993; see Hager, this volume].

Female dispersal in ants and primates

Recent theoretical papers in the field of sociobiology have concluded that “there are important differences between different systems, but there are also abstract features that unite them” [L. Hurst quoted in Whitfield, 2002; also see Gross, 1996;
Heinze & Keller [2000] discussed aspects of ant reproductive biology unemphasized in previous literature. In particular, they argued that low relatedness within ant colonies is likely to result from queen turnover rather than multiple-mating by queens. Queen turnover occurs when old queens are replaced by unrelated younger ones from within or outside the colony. Heinze & Keller [2000] suggested that this phenomenon raises the question of why workers tolerate queen turnover, since queen turnover lowers their indirect (genetic) benefits. This topic is of general import wherever relations between dominants and subordinates are discussed and wherever unrelated individuals coexist in groups. Heinze & Keller [2000] argued that workers should accept a new, unrelated queen only when survival of the sexual brood is thereby increased.

The analogous relationship in primates, whereby unrelated females are tolerated as immigrants in some taxa (e.g., *Alouatta*), has not been tested for its effects on offspring survival. Heinze & Keller pointed out that a queen’s optimal response will be a function of the relative costs and benefits to her of founding a new colony versus the likelihood of acceptance into an existing colony and that colony infiltration constitutes social parasitism, since a social parasite exploits others directly (e.g., by aggression) or indirectly (e.g., with deception) for her own advantage [Trivers, 1985; Bourke & Franks, 1995; Bertram, 1983]. Immigration of unrelated individuals into established groups, therefore, may generally be considered a form of social parasitism (e.g., *Alouatta*). If social parasitism has the potential to select for workerless caste systems as an energy-saving strategy, as suggested by Heinze & Keller [2000], then energy constraints may explain why caste systems have not evolved in other taxa (e.g., primates and most other mammals [but see Jones, 1996, 1997a]).

Morphological differences between queens, in particular, differences in fat reserves, may underlie founding strategy [Heinze & Keller, 2000]. Fatter queens may be more likely to found colonies while queens without significant fat reserves may be more likely to infiltrate established colonies. Support for such differences in queen morphs have been found in *Solenopsis* [Heinze & Keller, 2000]. Like female ants, howler females may join existing groups or establish new ones [Jones, 1980; Glander, 1992; Crockett, 1984; Pope, 1992; Fedigan et al., 1998; see references in Brockett et al., 2000]. Mantled howling monkeys may represent a primate species in which morphological differences between females differentiate dispersers from non-dispersers [see Zucker et al., 2001].

**TOWARDS GENERAL PRINCIPLES OF ALTERNATIVE REPRODUCTIVE BEHAVIORS**

General theories in biology are comprehensive formulations of phenomena within and between species. Particular emphasis has been placed on the modeling of foraging behavior [e.g., Krebs et al., 1981; Krebs & McCleery, 1984; Arsenos et al., 2000]. These attempts provide guidelines for theoretical modeling of other biological processes, including alternative reproductive behaviors. In general, complex phenomena are collapsed to simple decision rules dependent upon energy requirements [Krebs et al., 1981; Arsenos et al., 2000].
Gross’s (1996) graphical model (Box 1) stresses the importance of energy (resource dispersion and quality) in the evolution of alternative reproductive behaviors by way of its influence on fitness payoffs of varying phenotypes. Gross’s graphical model, based on ESS formulations, differs from most models of optimal foraging, however, in that ESS models measure variations in fitness while optimality models do not [see Krebs & Mc Cleery, 1984]. Both types of models, however, assume that individuals make decisions sensitive to proximate conditions, in the case of Gross’s [1996] model, factors pertaining to individual rank (status-dependence) and the decisions of other individuals (frequency-dependence), ecology, and demography. While Gross’s model assumes genetic programming of the switch to the secondary phenotype from the primary alternative, increased realism, compared to many other models, by its attempt to identify the primary factors influencing alternative reproductive phenotypes. Models of alternative reproductive behaviors may in the future be refined to rely primarily upon the costs of energy and time expenditure as a function of reproductive and related decisions, including the costs of dispersal.

Gross [1996] pointed out that the theoretical modeling of alternative tactics is incomplete. In particular, he argued that a need exists for theoretical modeling “to combine frequency- and status-dependent selection and solve for their joint equilibrium” (p 95). Gross indicated that status-dependent selection is a function of the relative fitness of alternative phenotypes, which are expected to be a function of “the competitive ability or ‘state’ of individuals in the population” (p 95). He continued, “Individual state always differs because of environmental influences (e.g., disease, trauma, energy), genetic variance (e.g., recombination, mutation) and stage of development (e.g., ontogeny, age). When through social interactions these differences in state also determine the fitness that can be obtained from a phenotype, then the individuals differ in their status.” (p 95, emphasis in original). Gross [1996] argued that social interactions drive individual phenotypic variation within the sexes and emphasized that game theory and the evolutionarily stable strategy (ESS) concept may be utilized to analyze “how and why selection favours alternative phenotypes” (p 92).

Box 1 displays Gross’s [1996, Box 4, p 96] view of how ecology and demography influence the payoff matrices of individuals interacting in frequency- and status-dependent regimes. This model implies “negative” frequency-dependence whereby fitness declines as the frequency of a given type increases [Bell, 1997]. Fitness declines because, as individuals of one type increase, resource competition (e.g., competition for mates) among those types will increase with consequent decreases in numbers of the more abundant type [Bell, 1997]. Where the curves intersect in both graphs, alternative phenotypes are adopted in response to the frequency of the primary behavioral pattern, with consequent effects upon phenotypes (X or Y), and these are shown to be dependent upon phenotype frequency, status, or demography. As Gross [1996] observed, the switchpoint must balance selection pressures that may be in opposition, such as individual status and the frequency of an individual’s phenotype. It may benefit a male, especially one rising in status, for example, to switch his behavioral pattern from sneaker to consort in response to negative frequency dependence (i.e., conditions favoring the rarer phenotype) if consort behavior is the less common phenotype.
**Box 1: Ecology and demography**

Ecology and demography may influence pay-offs or fitnesses of the frequency- and status-dependent fitness functions in two ways. First, ecology and demography influence whether the fitness functions from alternative phenotypes intersect, a necessary condition for the evolutionary origin of the alternatives. Second, ecology and demography influence where the intersection takes place, and thus the ESS distribution of alternatives in the population. The fitness function for a phenotype will vary with ecological circumstances that determine its functionality, such as suitability to a habitat or need for food resources, and also its costs, such as predators and parasites. In frequency-dependent selection (a), the fitness of phenotype X changes relative to Y with the introduction of a non-parasitized male that prefers X over Y. This has the effect of increasing the ESS frequency $f^*$ or ESS $f^*$ of the Y phenotype from $f_1^*$ to $f_2^*$. In status-dependent selection (b), ecological factors are now hindering phenotype Y relative to X, and the ESS switchpoint $s^*$ moves to a lower status, from $s_1^*$ to $s_2^*$. The Y phenotype will therefore be restricted to yet lower status individuals in the population, and also to fewer individuals.

Now hold ecology constant and consider demography, for example density. In (a), the fitness of phenotype X changes relative to phenotype Y because an increase in population size and thus density causes greater interference to X than Y, perhaps because X tries to monopolize females by excluding extra-group males. Thus $f^*$ increases and more individuals will become phenotype Y. In (b), demography has a greater influence on Y than X, and the switchpoint moves down and favors an increase in phenotype X. Ecology and demography can also work in concert. [Model reprinted From Trends in Ecology and Evolution 11, Gross MR, Alternative reproductive strategies and tactics: diversity within sexes, p 96, 1996, with permission from Elsevier Science. Legend modified with permission.]
Specific examples help to clarify the model. In frequency-dependent selection (a), assume that phenotype X is a female who is more likely to mate with multiple males during a fertile period and phenotype Y is a female who is more likely to mate with a single male at ovulation. Assume that a male without sexually transmitted diseases is introduced into a population who prefers to mate with female phenotype Y. The frequency of Y in the population will increase as a direct result of increased survivorship and fecundity of phenotype Y (from $f_1^*$ to $f_2^*$, circle below graph “a”).

In status-dependent selection (b), assume that phenotype Y is a monogamous daughter prevented by ecological constraints from emigrating from her natal group to breed independently. She “decides,” instead, to remain in her natal group as a reproductively suppressed helper to obtain indirect reproductive benefits (phenotype X), and phenotype Y will be reduced in the population, restricted to fewer individuals (from $s_1^*$ to $s_2^*$, curve below graph “b”). In the sense that this example applies to cooperatively breeding animals, another phenotype (Z), that of dominant breeders suppressing the reproduction of subordinate helpers, will also increase in the population.

Where demographic factors (e.g., population density) are the dominant selective forces, consider the following. In (a), assume that phenotype X is a polygynous (harem) male intolerant of other males. Assume that, as population density increases, male interaction rates increase leading to increased attempts by males without established groups and with a higher threshold of tolerance for polygynandrous assemblages (phenotype Y) to enter polygynous units. Interference from Y causes X to fight Y to incur serious injury or death to defend his female group or leads to the tolerance of Y by X, thus increasing phenotype Y in the population [e.g., A. pigra: Horwich et al., 2000; see Moore, 1999].

In (b), assume that females without offspring suffer fewer deleterious effects than females with offspring. Such conditions might increase alternative female phenotypes such as resistance to male advances (phenotype X) and favor these behavioral patterns over those displayed by females eager to copulate (phenotype Y). Gross’s [1996] graphical model, then, appears to have direct application to realistic examples of primate behavior. It would be productive to investigate switchpoints and relative fitnesses in these and related examples for an understanding of the influence of demography and ecology in generating alternative reproductive phenotypes.

Studies of ecology and demography are central to the literature of both insects and primates [Blum & Blum, 1979; Thornhill & Alcock, 1983; Rubenstein & Wrangham, 1986; Smuts et al., 1987; Choe & Crespi, 1997 a; Kappeler, 2000]. These research programs are derived from common theoretical paradigms, in particular, Emlen & Oring [1977; also see Bradbury & Vehrencamp, 1977; Wrangham, 1980] and the “spatiotemporal” concept of the “operational sex ratio” [Emlen & Oring, 1977] which predicts male options for monopolizing fertilizable females [see Nunn, 1999]. Gross’s [1996] graphical models indicated that general principles may be obtained from preexisting qualitative and quantitative work. In Keller’s[1995] words, “...the same conceptual framework can be used to study the social organization of insect and vertebrate societies. Ecological factors, together with inter-
nal factors, such as relatedness, determine the degree of within-group conflict, partitioning of reproduction and the stable social structure of animals, independently of whether they are ants, birds, or mammals. The time for two research traditions to proceed independently in seeking explanations for the evolution of group-living and eusociality in insects and vertebrates is over."

CONCLUSIONS AND PROSPECTS

On the surface it might appear that the differences among animals, particularly with respect to genetics, morphology and breeding systems, would obviate any attempt to formulate general principles. For example, most eusocial insects are haploid (males):diploid (females) while mammals are diploid. Models of adaptive behavior, however, are based upon the function of disparate mechanisms in the attainment of individual reproductive success, thus permitting a search for general rules that underlie variations in behavior. In this chapter we have attempted to show that Gross’s [1996] graphical model is realistic and that a more formal model is possible. Numerous questions remain unanswered, however, particularly with respect to methods of measuring the intensity of reproductive competition within and between groups as well as the influence of intraindividual and interindividual variability in responsiveness to coefficients of relatedness within groups, ecological constraints (e.g., environmental stochasticity) upon individuals and groups, the dynamics of dominance relations, the distinction between mate preference and mate choice, and conflicts of interest among group members. Additionally, formal models of reproductive skew and life history strategies (schedules of fecundity and mortality) represent more complex descriptions of phenotypic variability that are related to and may incorporate models of alternative reproductive behaviors [Heinze & Keller, 2000].

A further challenge for quantitative modeling of alternative reproductive behaviors is that female responses are driven by the distribution, abundance, and quality of limiting resources and that this “spatiotemporal” dispersion of females determines their monopolizability by males or some subset of males within and between groups [Emlen & Oring, 1977; Brown et al., 1997; Sterck et al., 1997; Nunn, 1999; but see Kudo & Dunbar, 2001]. The decisions that females make may have significant consequences for the genetic architecture of populations. A female’s reproductive program will include not only her decision to breed in her natal group, to infiltrate an existing group, or to found a new group but also, possibly, the ratio of male to female offspring produced in a group [see Watson et al., this volume]. That similar rules of interindividual organization apply across species as a function of resource dispersion and quality has been demonstrated in numerous studies [e.g., Emlen & Oring, 1977; Bradbury & Vehrencamp, 1977; Wrangham, 1979,1980; Rubenstein & Wrangham, 1986; Choe & Crespi, 1997a, 1997b]. Nonetheless, because individuals, particularly males, will tolerate significant costs in the quest for individual reproductive success, ecology is not omnipotent, especially over the short-term, and in species with the capacity to alter the environment to their own advantage [e.g., ants, humans; see Lewontin, 2000]. A formal model of Gross’s [1996] graphical one will be required to
include a cost function to represent the extreme disadvantages in time (males) and, most importantly, energy (females), of reproductive allocation. It is thus important to recognize that female decisions (phenotypes) influenced by ecological conditions will affect genetic conflicts of interest within groups, and general principles of alternative reproductive behaviors should lead to predictions about how individuals resolve conflicts of interest to their own advantage as a function of rank and ecological conditions. Since these latter variables may change within an individual’s lifetime, theories should be sensitive to ontogenetic variations.

A further assumption of existing models is that the decisions that females make influence the apportionment of reproduction (“reproductive skew”) within groups (see Hager, this volume). Models of alternative reproductive behaviors are related to models of reproductive skew since coefficients of relatedness within groups will influence the reproductive decisions that individuals make and, thereby, the costs and benefits of alternative phenotypes. Reproductive skew models are expected to be sensitive to competitive regimes which will influence the advantages or disadvantages of competing with kin and the costs and benefits of alternative reproductive phenotypes. General principles of alternative reproductive behaviors would also predict male behavior, although the influence of ecological factors upon males is expected to be an indirect function of female decisions.

Finally, West-Eberhard [1979] discussed alternative reproductive behaviors as intraspecific character divergence, pointing out that this state may lead to specialization and “obligatory” divisions of labor. Such mutual dependence is incipient in A. palliata where females, in particular, old, reproductively inferior females, leave their established groups in apparent search of high quality food patches benefiting all group members [Jones, 1996]. This temporal (age-dependent) division of labor may entail significant risks (e.g., from predation or fatigue) for female foragers and may represent a facultative phenotype sensitive to costs and benefits of age, dominance rank, and reproductive value [West, 1967; West-Eberhard, 1967, 1975; Hrdy & Hrdy, 1976]. As individual reproductive value decreases, (genetic) benefits from assisting the reproduction of conspecifics (social behavior) may increase because (genetic) costs of social behavior decrease with decreased benefits from individual reproduction.

“Primitive” sociality [West-Eberhard, 1979], in which group members compete directly and task or role specialization is flexible or absent, characterizes most primate species and, except for the quasi-eusocial callitrichids, “higher levels of social integration” are absent among primates. West-Eberhard [1979, p 233] proposed that advanced sociality is a function of “(1) increased genetic homogeneity (genetic convergence of interests), (2) increased efficiency of suppression and control of reproductive competitors (imposed convergence of interests), and/or (3) increased mutual dependence due to a common dependence on the presence of other group members, or mutually exclusive task specialization (mutualistic convergence of interests).” Although “suppression and control of reproductive competitors” by persuasion, force, or coercion are highly developed in many primate species and represent emergent characteristics resulting from reproductive (social) competition and sexual (social)
selection, these mechanisms appear to have been countered by the benefits of rule-
governed behavior that is strikingly individualized [see, for example, Widemo &
Saether, 1999]. The differential causes and consequences of interindividual and
intraindividual behavioral variation among primates and organisms with similar traits
require investigation in order to assess the costs and benefits of individualized facul-
tative decisions influencing reproduction in heterogeneous regimes.

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