

# Parentage and the evolution of parental behavior

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Parentage is the proportion of juveniles in a brood that are offspring of potential care givers. We analyzed how reductions in parentage affect the evolution of parental behavior using a static optimization model. The main benefit of parental effort was an increase in the survival of offspring, and the main costs were reduced opportunities to seek additional matings or to parasitize neighbors and/or reduced survival. Both the costs and benefits included terms for relatedness to young. The effect of parentage depended on (1) whether parents responded in ecological time (facultative response) or in evolutionary time (nonfacultative response), (2) whether the cues enabling assessment of parentage permitted discrimination among offspring, and (3) whether parentage was the same among different groups of juveniles (unrestricted) or varied between them (restricted). When parents did not know their own parentage and mean parentage was the same for all matings, reduced parentage affected the costs and benefits equally, so, as in several previous models, there was no effect on the optimal level of parental effort. Parentage did affect optimal parental effort when mean parentage to the present brood differed from that to young from alternative or future matings. Lowered parentage reduced optimal parental effort when the cost of parenting was missed opportunities for extrapair copulations or brood parasitism or when parentage was consistently higher in alternative or future matings. Nonlinear changes in parentage with age gave complex trajectories of parental effort, with individuals of different ages having similar parentage but exhibiting different levels of parental effort. Correlations between parentage and other variables in the model (such as opportunities for additional matings) sometimes masked, but never eliminated, the effects of parentage. When parents could discriminate their own young in a brood, overall parental effort was reduced, but nepotism was increased. When parents could not discriminate their own offspring but had general cues about average parentage to the brood, effects varied depending on the costs and benefits of parental behavior. When parental behavior was costly to care givers, parentage had more effect than when parenting was not costly. Likewise, parentage had less effect when care greatly increased offspring survival than when care was less necessary. Our analyses reconcile conflicting results from previous models and suggest a general framework for analyzing parental behavior within populations and among higher taxonomic groups. *Key words:* paternity, maternity, parental investment, uncertain parentage, relatedness, optimization models, extrapair copulations, intraspecific brood parasitism. [*Behav Ecol* 4:66–77 (1993)]

Parental behavior varies in frequency and intensity among taxa, between the sexes, and within and among individuals in populations (reviewed by Clutton-Brock, 1991; Gross and Sargent, 1985; Gubernick and Klopfer, 1981; Silver et al., 1985). Under Hamilton's (1964) rule ( $rb - c > 0$ ), the evolution of parental behavior appears to depend solely on the costs to the parent ( $c$ ) or the benefits to the young ( $b$ ) because relatedness ( $r$ ) between adults and the young they attend should be the same for all juveniles and both parents. Recently, however, it has become apparent that juveniles are not all equally related to the adults who behave as their parents. Multiple mating by females, which can reduce the relatedness of males to young, is widespread among vertebrate orders in which parental care occurs, including amphibians (Halliday and Verrell, 1984), reptiles (Devine, 1984), fishes (Conzanz, 1984; Gross, 1979), birds (Birkhead, 1987; Birkhead and Møller, 1992; McKinney et al., 1984; Westneat et al., 1990) and mammals (Ginsberg and Huck, 1989; Møller and Birkhead, 1989). Intraspecific brood parasitism, which can affect the

relatedness of both sexes or females only to dependent young (Gowaty, 1985), has been documented in about 100 species of birds (Andersson, 1984; Rohwer and Freeman, 1989; Yom-Tov, 1980), in some insects (Müller et al., 1990; Tallamy, 1985), and possibly in fish (Thresher, 1985). The implication is that adults frequently face the prospect of tending broods containing some unrelated young.

Parentage is often offered as the explanation for variation in parental behavior. Alexander (1974, 1979), Alexander and Borgia (1979), Blumer (1979), Perrone and Zaret (1979), and Ridley (1978), among others, argued that because adults (usually males) should not invest in unrelated young, reduced paternity can explain inter- and intraspecific differences in male parental care. For example, the often-noted correlation between parental care and external fertilization in fishes and frogs may result from greater certainty of paternity in externally as opposed to internally fertilizing species.

Early modeling attempts (Table 1) countered this logic, indicating that parentage should have no effect on parental behavior. In particular, Maynard

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Table 1

## Models of the effect of parentage on parental behavior and some of their critical assumptions

Reference	Type of model	Costs of parental behavior	Assessment of parentage	Parentage same for all matings?	Conclusions
Maynard Smith (1978)	ESS*	Opportunities for polygyny	No	Yes	No effect of parentage
Grafen (1980)	Marginal value	Opportunities for remating	No	Yes	No effect of parentage
Werren et al. (1980)	ESS	Opportunities for promiscuous matings	No	No	Some effect of parentage
Winkler (1987)	Static optimization	Residual reproductive value	No	No	Parentage has effects
Whittingham et al. (1992)	Static optimization	Alternative matings	Yes	No	Parentage has effects
Xia (1992)	ESS	Opportunities for remating	No	Yes	Parentage has effects
This paper	Static optimization	Alternative matings and residual reproductive value	Yes and no	Yes and no	Effects are dependent on conditions

\* ESS, evolutionarily stable strategy.

Smith (1978) argued that reduced paternity to one brood would not affect whether a male should desert to re-pair with a new female (see also Grafen, 1980). This analysis assumed that (1) paternity was the same for all broods, (2) individuals could not assess their own parentage, and (3) the only cost of behaving parentally was missed opportunities for re-pairing. Many subsequent authors have accepted these assumptions and Maynard Smith's conclusions (e.g., Alcock, 1989; Gross and Sargent 1985; Gross and Shine, 1981; Wittenberger, 1981), although Xia (1992) recently came to a different conclusion when he relaxed assumption 1 and allowed paternity to vary randomly among matings.

Werren et al. (1980) took a slightly different approach. While accepting Maynard Smith's assumption 2, they included a new fitness cost for behaving parentally: missed opportunities for extrapair copulations (EPCs). Given this cost, reduced paternity seemed to affect the evolution of parental behavior. However, Werren et al. (1980: 619) argued that "paternity differences between species cannot serve as a general explanation for the observed patterns of parental care behavior." This is because decreased average paternity implies greater opportunities for EPCs, which in turn increase the costs to males of behaving parentally instead of seeking those additional matings.

A similar outcome was presented by Knowlton and Greenwell (1984) in a model of mechanisms for the avoidance of sperm competition. Although Knowlton and Greenwell did not directly model parental behavior, they realized that paternal behavior could drive the evolution of more effective means of avoiding sperm competition, thus increasing paternity. They concluded that the resulting association between paternity and paternal care did not indicate a causal effect of paternity on parental behavior.

Recently, Winkler (1987) developed a static optimization model of parental behavior. As previous modelers had done, Winkler assumed that individuals could not assess their own parentage. Unlike the others, Winkler also assumed that the proportion of young descended from males or females varied between pairings and that behaving parentally increased mortality between breeding seasons.

Given these new assumptions, Winkler concluded that relatedness to current young does affect the optimal level of parental effort. A similar conclusion was also reached by Montgomerie and Weatherhead (1988).

Whittingham et al. (1992) obtained slightly different results in a model that substituted missed opportunities for additional matings instead of lowered survival until the next season as a cost of parental behavior. Although they also found that parental effort declined with reductions in parentage, the rate of decline depended on the shapes of the cost and benefit curves; in some circumstances reductions in parentage had a threshold effect on parental effort.

The conflicting viewpoints about the effects of parentage persist today. For example, Alcock (1989: 385) concluded in his influential textbook that "the reliability of parenthood is *not* the key factor in the evolution of parental care by one sex or the other." In contrast, Møller (1988: 996) predicted that "parental care should be negatively related to the absolute and relative number of extrapair copulations by the female mate."

Can these conflicting views be reconciled? Are some of the models incorrect, or does the effect of parentage depend on the situation? Here we develop a simple and general model to answer these questions. Our model considers a broader array of costs and benefits than has any single previous model, examines the types of decisions adults might make when allocating effort to parental care, and takes into account different patterns of parentage within and among broods. Our results duplicate those of previous models when we make the same assumptions, but novel outcomes arise when we model factors not considered previously.

### Definitions

Several key terms require definition. *Parents* are breeding adults that associate closely with and take primary care of young; this excludes helpers at the nest and other auxiliaries. We distinguish *social parents* from *genetic parents* (mothers or fathers) when it is possible and appropriate to separate social associations from genetic descent.

**Table 2**  
**Definition of variables in the optimization model**

Variable	Definition
$V$	Reproductive value, lifetime reproductive success
$PE$	Parental effort; measure of time, energy, or risk expended on parental behavior
$ME$	Mating effort; measure of time, energy, or risk expended on mating behavior
$SE$	Somatic effort; measure of time or energy expended on self-maintenance behavior
$O$	Reproduction from current breeding season
$O_c$	Reproduction from current breeding attempt
$O_m$	Reproduction from pursuit of additional matings
$R$	Reproduction from future breeding attempts
$N$	Brood size
$P_c$	Parentage to offspring in current breeding attempt
$P_m$	Parentage to offspring from additional matings
$P_f$	Parentage to offspring in future breeding attempts

*Parental behavior* is any action by a parent that increases the survival of young. Although we deal mainly with behaviors that occur after fertilization, some prefertilization behaviors can affect juvenile survival (e.g., nuptial feeding of the female: Gwynne, 1984) and may be influenced by parentage (e.g., Knowlton and Greenwell, 1984; Parker and Simmons, 1989). Following Alexander and Borgia (1979) and Low (1978), we consider an animal's reproductive effort to be the sum of three components: *parental effort* ( $PE$ ; effort expended on parental behavior), *mating effort* ( $ME$ ; effort expended in acquiring fertilizations), and *somatic effort* ( $SE$ ; effort that increases an individual's chances of survival to another breeding attempt). Although many behaviors are manifestations of more than one type of effort (e.g., Gwynne, 1984; Kurland and Gaulin, 1984; Parker and Simmons, 1989), they can be separated theoretically. For simplicity, we will assume that particular behaviors are manifestations of only one type of effort. The general logic of our model applies to behaviors involving multiple types of effort.

*Parentage* is the proportion of juveniles in a brood that are actually *offspring* of a social parent. *Reduced parentage* (i.e., reduced below 1.0) means that some young in a brood are not the offspring of at least one social parent. Previous authors (e.g., Alexander, 1979; Møller, 1988, 1991; Perrone and Zaret, 1979; Whittingham et al., 1992; Xia, 1992) have used "uncertainty" of parentage or "confidence" and "reliability" of paternity (or maternity) to describe this same circumstance. These terms imply that individuals can assess parentage and have (or lack) knowledge about their own parentage, thereby confounding the effects of parentage on the evolution of parental care with the proximal mechanisms by which adults avoid misdirecting parental care. Because these proximal mechanisms influence how parentage affects parental behavior, we advocate the more neutral term "reduced parentage."

## BASIC MODEL

We model the factors affecting the optimal level of parental effort (designated  $PE^*$ ), and treat such effort as a quantifiable variable. Unfortunately there is no consensus about how to quantify  $PE$  (Winkler and Wilkinson, 1988), largely because of the different currencies of costs. Regardless of how parental effort is quantified in any particular case, we agree with Winkler and Wilkinson (1988) that general models of relative  $PE$  can be constructed.

Natural selection should act to maximize reproductive value,  $V$  (e.g., Charnov and Krebs, 1974; Gadgil and Bossert, 1970; Williams, 1966, 1975). Reproductive value is the sum of offspring from the present season ( $O$ ) and all (expected) future offspring (i.e., residual reproductive value,  $R$ ), so  $V = O + R$ . We are interested in how much effort a parent should devote to caring for present young ( $PE$ ) versus expending effort on gaining additional matings ( $ME$ ) or conserving effort to increase the chances of survival ( $SE$ );  $ME$  expended on acquiring the mating that led to the present offspring is not part of our model. Because  $PE$ ,  $ME$ , and  $SE$  are proportions of total effort,  $(PE + ME + SE) = 1$  (see Sargent, 1985; Williams, 1966).

Our model focuses on how parentage ( $P$ ) affects the functions that translate each form of effort into the appropriate component of reproductive success. As such it is similar to previous life-history models (e.g., Nur, 1984; Schaffer, 1974; Stearns, 1976; Trivers, 1972; Williams, 1966, 1975; Winkler, 1987) and is essentially an elaboration of Hamilton's rule, with terms for benefits, costs, and relatedness. For the reader's convenience, the variables in our model are defined in Table 2.

### Benefits of parental behavior

The benefit of parental behavior is increased survival of present offspring. The number of current offspring ( $O_c$ ) is therefore a function of  $PE$ , such that

$$O_c = N_c P_c c(PE) \quad (1)$$

where  $N_c$  is the number of young in the current brood,  $P_c$  is the proportion of the brood descended from the parent, and  $c$  is the likelihood of survival per offspring as a function of parental effort ( $PE$ ). The change in  $O_c$  as  $PE$  changes is the benefit of parental behavior.

Winkler and Wilkinson (1988) reviewed data showing that  $c(PE)$  increases with increasing  $PE$ . Following their treatment, we assume that offspring survival and  $PE$  are positively correlated, but we do not assume any particular function linking them. Some parental behaviors may result in a linear increase in benefits with increasing effort, whereas others might yield a curvilinear or even a sigmoidal relationship (i.e., with diminishing returns as  $PE$  increases).

### Costs of parental behavior

Because  $PE = 1 - (ME + SE)$ , an increase in  $PE$  must be accompanied by a decrease in either  $ME$  or  $SE$ , or both. Thus the costs of behaving parentally can be measured as reductions in (1) additional offspring in the same season ( $O_m$ ) and/or (2) future

offspring ( $R$ ) (Sargent, 1985; Williams, 1966). Assuming that additional offspring cannot be gained without added mating effort,  $O_m$  as a function of  $ME$  is a cost of parental effort:

$$O_m = N_m P_m m(ME) \quad (2)$$

where  $N_m$  is the number of additional offspring gained per mating,  $P_m$  is the parentage to those offspring, and  $m$  is the number of additional matings as a function of mating effort ( $ME$ ). The shape of the function  $m$  shows an increase with increasing  $ME$ ; it could be linear, curvilinear, or sigmoidal.

Equation 2 applies to mating effort expended by either sex. When males expend  $ME$  on polygyny,  $N_m$  is the brood size,  $P_m$  is the average paternity to the new brood, and  $m(ME)$  is the number of additional pairings expected as a function of  $ME$ . When males pursue EPCs,  $N_m$  is again the brood size,  $m(ME)$  is the expected number of extrapair mates gained as a function of  $ME$ , and  $P_m$  is the average paternity to the brood of each extrapair mate. Although  $P_m$  might also be a function of  $ME$  if additional EPCs with a given female increase the number of offspring sired, for mathematical reasons we define  $P_m$  as an average paternity to the brood of an extrapair mate assuming an average number of EPCs per mate. When females expend  $ME$  on brood parasitism attempts (e.g., time and energy spent on finding host nests),  $N_m$  is the number of eggs laid per parasitism attempt,  $P_m$  must be 1.0 (females are always genetic parents of the eggs they lay), and  $m(ME)$  is the number of parasitic eggs laid successfully as a function of effort.

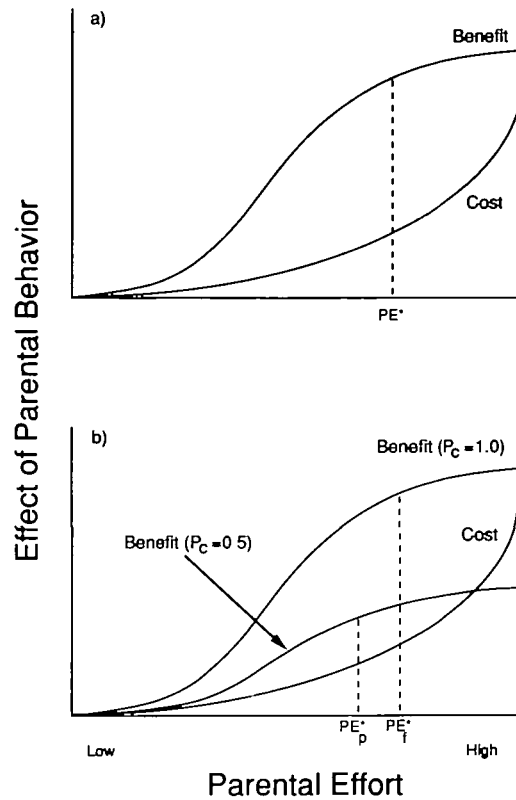
The number of offspring expected in future reproductive episodes ( $R$ ) obviously depends on parental survival. Survival, in turn, is positively related to present somatic effort ( $SE$ ), so that

$$R = N_r P_r s(SE) \quad (3)$$

where  $N_r$  is the total number of offspring expected in all future breeding attempts,  $P_r$  is the average parentage to all future broods, and  $s(SE)$  is the probability of an individual surviving to the next breeding attempt as a function of somatic effort. Mortality between the present breeding attempt and the next one affects all future reproduction, so Equation 3 can be considered a sum of effects of  $SE$  on all future attempts.

Two caveats about Equations 2 and 3 are necessary. First, we are interested primarily in a parent's decision about whether to care for the current brood. Decisions about future parental effort may affect decisions about current  $PE$ , but such interactions are beyond the scope of this paper. In Equations 2 and 3, any effects of future parental effort are buried in the functions  $m$  and  $s$ . Second, Equation 3 treats the consequences of present  $SE$  as if they occur after the current breeding attempt is over. Risks of parental behavior, such as predation during nest defense, might result in a parent dying during the current attempt and reduce the survival of the current brood. For convenience, such effects are considered part of the function  $c(PE)$  in Equation 1.

Both  $m(ME)$  and  $s(SE)$  describe the rate of fitness returns with increasing  $ME$  or  $SE$ ; this is equivalent to the rate of fitness losses as  $PE$  increases. An individual that increases  $PE$  would decrease either the number of its extra offspring ( $O_m$ ) in the current



**Figure 1**  
Graphical representation of the relationship between increasing parental effort and the benefits or costs of increasing effort. Benefits are measured in terms of survival of offspring and costs in terms of missed opportunities for additional matings and/or reduced reproduction in future attempts. (a) Optimal parental effort ( $PE^*$ , with full parentage) occurs when the difference between benefits and costs is maximal. At that point, the slope of the benefit curve (marginal rate of return) is equal to the slope of the cost curve. (b) The effect of reducing parentage to the current brood from 1.0 to 0.5 is to reduce the slope of the benefit curve. Parental effort ( $PE_p^*$ , with partial parentage) shifts down to a new optimum, reflecting the new location of the maximum net benefit (benefit minus cost).

breeding season (from EPCs, polygamy, or parasitism) or its future reproduction ( $R$ ). In most of our analyses, these costs of parental behavior are combined. With increasing  $PE$ ,  $m(ME)$  and  $s(SE)$  could decrease linearly, sigmoidally, with diminishing returns, or with more complex relationships.

### Optimal level of parental effort

We assume that  $V$  as a function of  $PE$  is at an intermediate optimum. That is, optimal  $PE$  ( $PE^*$ ) is neither 0.0 (i.e., totally absent) nor 1.0 (given to the exclusion of all other forms of effort). Any change in  $PE$  away from  $PE^*$  results in decreased  $V$ . At the optimum,  $dV/d(PE) = 0$ . Although this could conceivably occur at several points on a complex curve relating  $V$  to  $PE$ , we assume that  $V(PE)$  has only one optimum. Because

$$V = O_c + O_m + R,$$

then

$$dV/dPE = dO_c/dPE + dO_m/dME + dR/dSE. \quad (4)$$

At optimum  $V$  and because  $PE + ME + SE = 1$ ,

$$dV/dPE = P_c N_c dc/dPE - (P_m N_m dm/dPE + P_r N_r ds/dPE) = 0. \quad (5)$$

Equation 5, the heart of our model, can be visualized graphically (Figure 1a). Increasing  $PE$  is favored so long as the rate of gain exceeds the rate of loss due to decreasing  $ME$  or  $SE$ . Optimal  $PE$  occurs when those rates are equivalent—when the slopes of the benefit and cost curves in Figure 1a are equal.

We are primarily concerned with tradeoffs between  $PE$  and  $(ME + SE)$ . Presumably, trade-offs also occur between  $ME$  and  $SE$ , and we expect these

**Table 3**

**Hierarchical organization of types of behavioral responses to reductions in parentage and the predictions of specific models of parentage**

Pattern	Model	Predictions
<b>Nonfacultative response</b> (parents cannot assess their own parentage)		
Unrestricted patterns (parentage is the same for all groups of offspring)	$P_c = P_m = P_f$	No effect on <i>PE</i> *
<b>Restricted patterns</b> (parentage differs among groups of offspring)		
General	$P_c < P_m = P_f$	Reduce <i>PE</i> to present brood
EPCs or brood parasitism	$P_c < P_m$	Reduce <i>PE</i> , pursue EPCs or ISBP
<b>Age</b>		
a	$P_c < P_f$ 1st attempt, $P_c = P_f$ in later attempts	Reduce <i>PE</i> in first attempt, higher but constant <i>PE</i> in later attempts
b	$P_c > P_f$ first attempt, $P_c = P_f$ in later attempts	Higher <i>PE</i> in first attempt than in later attempts
c	Linear change with age (i.e., $P_c > P_f$ , or $P_c < P_f$ )	<i>PE</i> constant, direction of change in $P_c$ with age affects level
d	Curvilinear with age	Complex change in <i>PE</i> ,* depending on curve of $P_c$ with age
<b>Polygamy</b>		
a	$P_c = P_m$	No effect on <i>PE</i> *
b	$P_c > P_m$	Reduce polygamy, increase <i>PE</i>
c	$P_c < P_m$	Increase polygamy, reduce <i>PE</i>
<b>Offspring age</b>		
a	$P_{c1} < P_{c2}$	Feed younger juveniles
b	$P_{c1} > P_{c2}$	Feed older juveniles
<b>Facultative response</b> (parents can assess their own parentage)		
<b>Discriminant cues</b> (differences among individual young are used by adults to assess relatedness)		
Unrestricted patterns	$P_c = P_m = P_f, P_{c1} = 0, P_{c2} = 1$	<i>PE</i> directed to own offspring ( <i>k</i> )
Restricted patterns	$P_{c1} = 0, P_{c2} = 1$	<i>PE</i> directed to own offspring ( <i>k</i> )
<b>Indiscriminant cues</b> (information about likelihood of parentage is available, but not about relatedness to particular young)		
<b>Unrestricted patterns</b>		
a	$P_c = P_m = P_f$	No effect on <i>PE</i>
b	$P_c$ varies randomly	<i>PE</i> reduced when $P_c$ low
Restricted patterns	$P_c < P_m (\leq) P_f$	<i>PE</i> * reduced

*PE*, parental effort; EPCs, extrapair copulations; ISBP, intraspecific brood parasitism.

forms of effort to be optimized as well. Thus at the optimal  $V$ , the rate of return on parental, mating, and somatic effort will be equal. Although changes in *PE* will affect both *ME* and *SE* (see Sargent, 1985), the magnitude of effects on *ME* versus *SE* depends on the shapes of the functions  $m(ME)$  and  $s(SE)$ . Consideration of the factors affecting those functions (e.g., parental age and condition) is the subject of a future paper.

## RESULTS

### Effects of parentage

The impact of parentage on parental effort in our model depends on the mechanisms by which adults respond to reduced parentage within broods and the patterns of parentage among groups of young. For example, individuals might be able to assess their own parentage to the current brood and ad-

just *PE* accordingly. We call this a facultative response. Conversely, if individuals cannot assess parentage, levels of parental effort to each brood might be set through evolutionary time. We call this a nonfacultative response. Facultative responses depend on the types of cues indicating parentage. There are two general categories: discriminant cues enable adults to assess the parentage of particular young and indiscriminant cues enable adults to assess the average parentage to a group of young but not their relatedness to particular juveniles. Our model also considers two general patterns of parentage among groups of young that might affect the potential responses of adults: (1) unrestricted patterns, when parentage is the same from one group to the next (i.e.,  $P_c = P_m = P_f$ ), and (2) restricted patterns, when parentage differs among groups of young. This hierarchy of responses, cues, and patterns is summarized in Table 3, along with

the models we analyze and a synopsis of the predicted outcome.

### Nonfacultative responses

#### *Unrestricted patterns*

Suppose that parental behavior reduces survival, chances to be polygamous, or both, and that parentage is the same in each reproductive bout ( $P_c = P_m = P_f$ ). Reduced parentage modifies the costs and benefits of parental behavior equally. Parentage thus drops out of Equation 5 and has no effect on  $PE^*$ . This analysis makes the same three critical assumptions as did Maynard Smith (1978) and Grafen (1980), and the result from our model duplicates theirs.

Now assume that parental behavior reduces opportunities for extrapair matings. If changes in  $P_c$  are mirrored by changes in  $P_m$  (where  $P_m$  is the parentage to offspring of an extrapair mate), then parentage will again drop out and have no effect on optimal  $PE$ . For example, this might occur if for some reason the frequency of promiscuous matings by floating males (nonparental) increased, thereby lowering both  $P_c$  and  $P_m$  through increased sperm competition. This example illustrates the fundamental effect of parentage on the costs and benefits of parental care. Regardless of whether an adult might provide care for offspring, if parentage is the same for all matings, then it will have no effect on the evolution of parental behavior.

#### *Restricted patterns*

Suppose now that parentage differs between matings. Clearly, lowering only  $P_c$  reduces the term  $P_c N_{dc}/dPE$ , thereby reducing the slope of the benefit curve (Figure 1b). This would cause an evolutionary shift from  $PE$  to  $(ME + SE)$  to maintain the condition in Equation 5. Reducing  $P_c$  in this fashion duplicates Winkler's (1987) analysis of the effects of relatedness. This fundamental association between  $P_c$  and benefits is why Alexander and Borgia (1979), Perrone and Zaret (1979), and Ridley (1978), among others, have invoked parentage to explain patterns of parental care.

How might parentage differ among types of matings and how is parental behavior affected? We now analyze four examples of differences in parentage among matings that seem plausible given previous models and the empirical literature. In all cases we assume that parents have no information about parentage.

**Promiscuous matings.** Previously we analyzed the case of promiscuous matings as a cost of parental care assuming an unrestricted pattern of parentage; that is, changes in  $P_m$  mirrored changes in  $P_c$ . However, this might not always be the case. For example, as EPCs increase in frequency, both  $P_c$  and  $P_m$  should decline, but  $P_m$  might change relatively less. If so, then a reduction in  $P_c$  will reduce the benefits of parental effort relative to the costs, thereby favoring a shift of effort toward the pursuit of EPCs. In this sense our model duplicates the results of Werren et al. (1980), who found that when promiscuous matings were a cost of  $PE$ , parentage affected the evolution of parental behavior.

An important conclusion of Werren et al. (1980) was that parentage is unlikely to explain differences in parental behavior among species. They reasoned

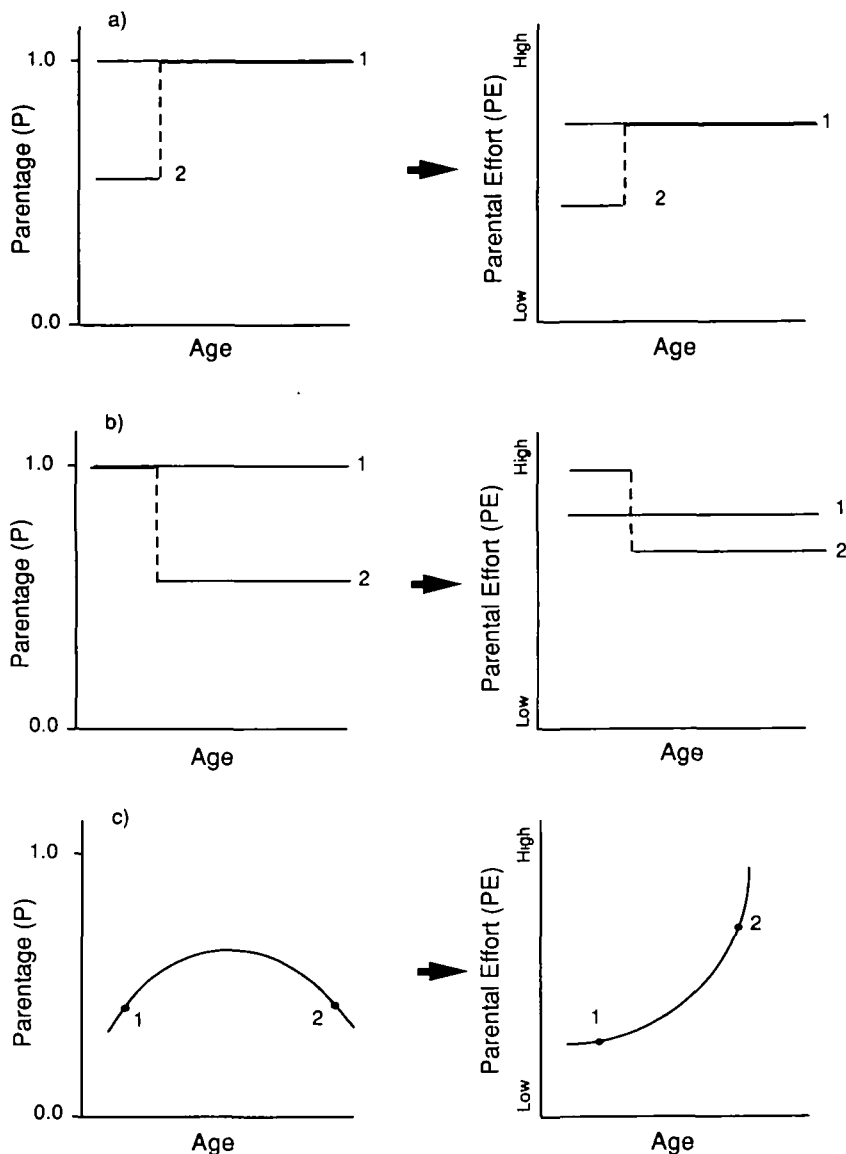
that when parentage is high, there are few opportunities for EPCs and thus little cost to parental behavior, whereas when parentage is low, there will be many opportunities for EPCs, and parental care will be costly to male fitness. Our model also yields this result. In fact, parentage may be correlated with a variety of parameters in the function for  $O_m$ . Reductions in  $P_c$  may be linked with increases in mating opportunities, a parameter in the function  $m$ . Similarly, increased mate guarding, increased number of copulations, or more effective ejaculatory plugs might increase  $P_c$  but simultaneously reduce either a parameter in  $m$  (the chances of gaining an additional mating) or in  $P_m$  (the parentage to offspring of an additional mate). All of these would cause shifts in optimal  $PE$  regardless of the effect of parentage.

Werren et al.'s (1980) basic point, that parentage correlates with other variables which also affect parental effort, is well taken. Yet this does not mean that parentage has no effect on  $PE^*$ . When reduced parentage and parameters in the function for  $O_m$  (e.g., opportunities for additional matings or parasitism) are correlated, both have effects on  $PE^*$ . This can be illustrated by supposing that we knew the parameters of the functions  $O_c$  and  $O_m$  and had accurate measures of  $ME$  and  $PE$ . Using our model, calculation of the optimal level of parental effort assuming that parentage to the current brood is 1.0 when it is actually  $< 1.0$  yields an expected value of  $PE^*$  that is higher than the observed  $PE$ , even when variables covary closely. In fact,  $(PE_{\text{expected}} - PE_{\text{observed}})$  from several populations should be correlated with the differences between a  $P_c = 1.0$  and the actual  $P_c$ .

**Age.** One of the novel predictions of our model is that different relationships between age and parentage should lead to different behavior patterns. Our models of age-related patterns are in the tradition of Schaffer's (1974) models of how age structure affects life-history strategies.

First, imagine that individuals have lower parentage in their initial breeding attempt than in any future attempts ( $P_c < P_f$ , for the first attempt only, otherwise  $P_c = P_f$ ; Figure 2a), that  $P_c = P_m$  at all ages, and that  $(SE + ME)$  is a cost of  $PE$ . During an individual's first breeding attempt, parentage modifies the slope of the benefit curve more than that of the cost curve. Therefore,  $PE^*$  should be lower for first-time parents than for experienced breeders because first-timers who defer parental care will potentially increase their chances of survival into the next season (when  $P_c$  will be higher). It is suggestive that in indigo buntings (*Passerina cyanea*) and purple martins (*Progne subis*), young males have lower parentage than older males and also provide less parental care (Morton et al., 1990; Westneat, 1988); it is unknown if reducing  $PE$  increases their chances of survival to the next season.

Second, suppose that  $P_c > P_f$ , again just for the first breeding attempt (Figure 2b). An example might be white-crowned sparrows (*Zonotrichia leucophrys*), in which parentage appears to be lower in older than in younger males (Sherman and Morton, 1988). Compared to when parentage is 1.0, the slope of the cost curve decreases more than that of the benefit curve, so  $PE^*$  shifts upward. This means that individuals with lower parentage in the



**Figure 2**

The effect of ontogenetic patterns of parentage on patterns of parental effort. In each panel, the numbers 1 and 2 distinguish different situations. (a) Parentage is low in the first breeding attempt and high in later attempts (2). Because the payoffs for future reproduction are high, adults should defer parental effort and invest in somatic effort in the first attempt. Thus, parental effort should be low for first attempt and higher later (2), compared to when parentage is always 1.0 (1). (b) When parentage is 1.0 in the first attempt but lower later (2), return on somatic effort is reduced relative to constant parentage of 1.0 (1). Thus parental effort in the first attempt should be higher than in later attempts (2) and should be higher than if parentage were always 1.0 (1). (c) Increasing and then decreasing parentage with age results in a steadily increasing level of parental effort with age. This reflects the higher value of future offspring for the first few attempts and then the higher value of present offspring for the later breeding attempts. Note that parentage at points 1 and 2 is equal, but parental effort is different, reflecting different prospects for success in future attempts and a resultant shift of somatic effort at time (1) into parental effort at time (2).

future should provide more care during their first attempt than individuals with constant parentage, even though  $P_c$  for both is 1.0. This occurs because somatic effort results in fewer future benefits when  $P_f < P_c$  and  $P_m$ , so selection will favor shifts of SE to PE and ME.

Third, imagine that parentage changes gradually with age. If  $(P_c = P_m) < P_f$  throughout an individual's lifetime, then individuals should provide a con-

stant but lower level of care through each season relative to those with a constant parentage of 1.0, even if they sacrifice some current offspring for increases in survival. If  $(P_c = P_m) > P_f$ , then individuals should provide substantial parental effort throughout their lives because they gain more from the present attempt than from surviving to the next season.

More complex (curvilinear) trajectories of parentage can lead to some unexpected patterns of parental behavior (see Figure 2c). For example, a population in which individuals have high average parentage may exhibit less parental behavior than one with low average parentage simply because the age-specific trajectories of parentage differ. Similarly, individuals of the same population might exhibit different levels of PE with similar parentage. It is the influence of parentage on future prospects that generates these results. In this sense our model expands the ideas of Clutton-Brock (1984), Stearns (1976), Williams (1966), and others that if reproductive value is low (i.e., future prospects are dim), investment in current offspring should be high.

**Breeding date.** Parentage might also differ consistently among broods within a season. For example, in wood ducks (*Aix sponsa*: Clawson et al., 1979; Haramis and Thompson, 1985), common goldeneyes (*Bucephala clangula*: Dow and Fredga, 1984), and redheads (*Aythya americana*: Sorenson, 1991), intraspecific brood parasitism is considerably higher in nests started early than in those started later on. If early and late broods do not overlap in time, then the effect of parentage parallels that of differences in parentage among age classes described above. If parentage to early broods ( $P_c$ ) is lower than to later broods ( $P_f$ ), then  $PE^*$  to early broods should be lower (see Figure 2a), but if  $P_f < P_c$ , then high  $PE^*$  to early broods should result (Figure 2b).

Differences in parentage among temporally overlapping broods will also cause new selective pressures on parental behavior and the pursuit of polygamy (either polyandry or polygyny). The critical variables are the relatedness to the first brood ( $P_c$ ) and the expected relatedness to later broods in the same season ( $P_m$ ). When  $P_c = P_m$  (and  $P_f$ ), parentage has no effect, and we have again duplicated the situation modeled by Maynard Smith (1978) and Grafen (1980). If, however,  $P_c = P_f < P_m$ , the fitness returns from additional PE are lowered more by reduced parentage than are the returns from increased ME. Adults should reduce parental behavior toward their first mate's brood and attempt to attract a second mate (polygyny or polyandry). When  $P_c > P_m$ , return on ME is reduced more than return on PE, and parental care to the present brood should increase at the expense of further mate attraction, reducing the population-wide level of polygamy.

When a parent has several mates with concurrent broods, it should invest in those broods to which it is on average most related, even if it cannot assess parentage. Thus, if  $P_c$  is consistently greater than  $P_m$ , early broods should receive more care than later broods, and vice versa when  $P_c < P_m$ . Preferential paternal assistance to primary broods is common among polygynous birds (e.g., Muldal et al., 1986; Wittenberger, 1979). The possibility that average relatedness to each brood might explain this pattern has not previously been considered.

**Within-brood patterns.** Another possible restricted response should occur if certain young are predictably less likely to be descended from their social parents. For example, if offspring are conceived sequentially rather than simultaneously, the parentage of the first and later conceptions may differ. If so, our model predicts associated changes in parental behavior. To see why, we must break the equation for  $O_c$  (Equation 1) into units for each of  $n$  offspring, such that  $P_c N_c c(PE) = \sum_{i=1}^n P_{ci} c(PE_i)$ . Individuals might then allocate effort among offspring in different ways, depending on  $P_{ci}$ . If the pattern of parentage is consistent over evolutionary time, selection would favor a bias in parental behavior toward older or younger juveniles (whichever are more closely related) even without the adult being able to assess parentage.

As a possible example, consider Stamps et al.'s (1985) study of parental care in budgerigars (*Melopsittacus undulatus*). They found that males initiated feeding bouts when youngsters begged and fed the most vigorous beggars (the first hatched and largest young) most often. Females, in contrast, fed the smallest chicks preferentially and ignored their begging rate. This might be an example of a non-facultative response to a restricted pattern of parentage if in nature male budgerigars are more likely to sire the first eggs laid by their mate than her later eggs (i.e., if mate guarding is predictably more effective at the onset of receptivity). Mate guarding appears to decline before the end of the fertilizable period in many species of birds (reviewed in Birkhead and Møller, 1992); a consequence might be lower paternity to last-laid eggs.

#### Assessment of parentage

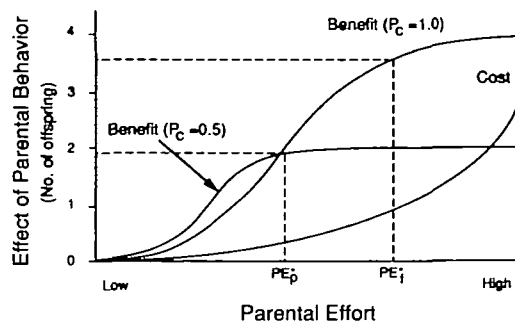
##### Discriminatory cues

Discrimination of individual young creates some interesting dynamics in our model because it enables adults to optimally apportion their parental effort, regardless of whether the pattern of parentage is restricted or unrestricted. The equation for  $O_c$  becomes a sum of equations for each juvenile, with some having  $P_{ci} = 1.0$  (i.e., the actual offspring) and the others having  $P_{ci} = 0$ . Redirection of nonshareable  $PE$  from one offspring to another changes the function  $c(PE)$ . Thus, discrimination does more than simply modify the slope of the benefit curve by a constant (e.g., as in Figure 1b); it changes the entire shape of the curve (Figure 3). Because parental effort is then divided among fewer offspring, the benefit curve becomes more extremely sigmoidal and is shifted to the left. Thus, if parental effort has diminishing effects on juvenile survival as  $PE$  increases, direct discrimination of kin will have the identical effect as reducing the brood size (e.g., Nur, 1984; Winkler, 1987). Although each offspring will receive more  $PE$ , the parent's total  $PE$  will decline as it reapportions some of that effort into  $SE$  and  $ME$ .

##### Indiscriminatory cues

**Unrestricted patterns of parentage.** If parentage is the same from one mating to the next (i.e.,  $P_c = P_m = P_f$ ) and there is no variation in parentage, then parentage will have no effect on  $PE$  even if parents can assess parentage. Again, this duplicates the models of Maynard Smith (1978) and Grafen (1980).

Parentage, however, is unlikely to be invariant.



**Figure 3**

Effect of discrimination among offspring on the benefit of parental behavior (brood size = 4). When some juveniles are offspring of the potential parent and that adult can reallocate parental effort to those offspring, the function relating  $PE$  to survival of offspring shows a higher rate of return at low levels of  $PE$ . Thus the benefit curve when  $P_c = 0.5$  is altered beyond a linear modification of the slope as shown in Figure 1b. Optimal  $PE$  for the benefit curve when  $P_c = 0.5$  ( $PE_p^*$ ) is lower than when  $P_c = 1.0$  ( $PE_i^*$ ), but the effect of  $PE$  per offspring is greater (shown by horizontal dashed lines).

When there is variation, then even if average parentage is the same from one mating to the next, when a parent can assess parentage it should adjust  $PE$  accordingly. Suppose that variation in parentage is stochastic. If a male sees his mate copulate with a neighbor or a female sees a potential parasite at her nest, then each might do better to reduce  $PE$  and expend the extra effort on finding a new mate (males) or building a new nest (females) because parentage to the new brood likely would be higher by chance alone. This result is similar to that found by Xia (1992), but differs in mechanism: Here individuals can assess parentage, whereas in Xia's model a nonfacultative response is selected through reduced variation in fitness.

**Restricted patterns of parentage.** Adults with a low likelihood of parentage to an entire brood should reduce  $PE$  and increase either  $ME$  or  $SE$  if their future prospects are better than their present circumstances (e.g., if  $P_m$  or  $P_f$  will be higher than  $P_c$ ). Situations in which parents might know that  $P_m$  and/or  $P_f > P_c$  can occur in several ways. First, they might be able to assess circumstances that change between breeding attempts. For example, breeding density and synchrony, availability of fertilizable females and unguarded nests, and the age or experience of breeders could all affect parentage (e.g., Westneat et al., 1990) and change over time. These factors could select for either facultative or nonfacultative restricted responses. Second, polygamous individuals might witness the events leading to reduced parentage or be able to assess conditions associated with reduced parentage and allocate care among broods or litters accordingly.

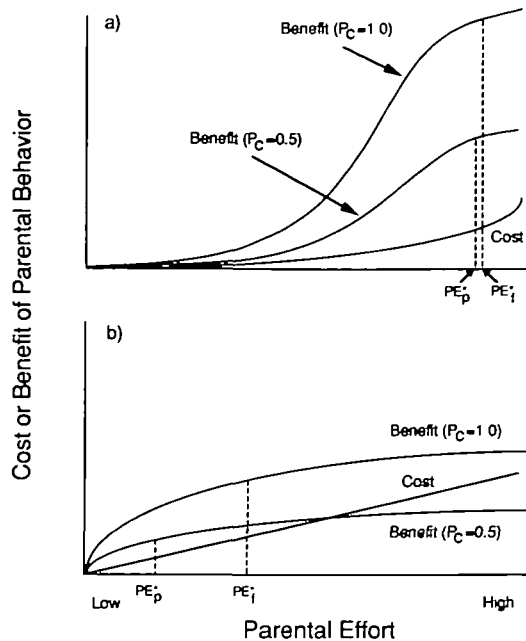
Interestingly, even when parents have information about reduced parentage they might not benefit from reducing parental effort. For example, suppose a female has been the victim of conspecific nest parasitism because she was an ineffective nest guarder (perhaps because she was in poor condition). Although it may be clear that she has been parasitized, she might nevertheless provide parental care if she is in no condition to try parasitism herself and is unlikely to be able to improve survival to the next year by reducing  $PE$ .

##### Influence of relative costs and benefits

In all of our models, the relative shapes of the benefit and cost curves will influence how much reduced parentage affects parental behavior. Reduced parentage will have little effect when there are large differences between the benefit curve and the cost curve at certain values of  $PE$  (e.g., Figure 4a). Conversely, reduced parentage will have a dramatic effect when the difference between the benefit curve and the cost curve is slight at all values



**Figure 4**  
The effect of the relative shape of cost and benefit curves on the influence of reduced parentage on  $PE$ . (a) Increasing  $PE$  has a dramatic effect on offspring survival, with a minimal effect on the costs. Because optimal  $PE$  is at the top of a steep part of the benefit curve, reducing parentage to 0.5 has only a slight effect on  $PE^*$  ( $PE_p^*$  versus  $PE_i^*$ ). (b) Increasing  $PE$  has minimal effects on offspring survival but substantial effects on the costs.  $PE^*$  is low even when parentage is 1.0 ( $PE_i^*$ ), but because the rate of return on  $PE$  is so slight, reducing parentage to 0.5 causes  $PE^*$  ( $PE_p^*$ ) to decline by two-thirds.



of  $PE$  (e.g., Figure 4b). Thus, reduced parentage is more likely to have an effect in some species than in others due just to the relative costs and benefits of parental behavior.

Whittingham et al. (1992) have independently reached similar conclusions based on a model of a specific case. They modeled a situation that we would classify as a restricted pattern of parentage with facultative responses to indiscriminant cues. They found that  $PE$  declines at different rates with reductions in parentage depending on the shapes of the cost and benefit curves. This result suggests that reduced parentage might have different effects on different types of parental behavior in the same population. This could happen if different parental behaviors have different parameters in the functions  $c$ ,  $m$ , or  $s$ , thereby creating variously shaped benefit and cost curves. Reductions in  $P_c$  would have similar effects on the slope of these curves, but because optimal parental effort depends on the benefits relative to the costs,  $P_c$  could have different effects on  $PE^*$  for each type of care (e.g., Figure 4).

The types of care most affected will also be influenced by how animals assess parentage. For example, nonshareable care (e.g., feeding young) and shareable care (e.g., nest defense) will be equally affected by parentage if adults do not recognize their own offspring. If adults can recognize individual offspring, nonshareable effort will be affected more than shareable effort because the parent can reallocate the former to individual offspring.

## DISCUSSION

Controversies over the role of parentage in the evolution of parental behavior have focused on three questions: (1) Does parentage have any effect on the evolution of parental behavior? (2) Why do parental species predominate in some taxa but not in others? and (3) Why does one sex provide more care than the other? Our analyses offer some perspective on these issues.

First, our model reveals many situations in which parentage does affect the evolution of parental behavior, and some in which it does not. Our results duplicate those of Maynard Smith (1978), Grafen (1980), Werren et al. (1980), and others when we make the same assumptions they did. However, some of our conclusions differ considerably from theirs. This is because we have expanded on these previous approaches and included in our model a greater array of costs of parental behavior (e.g., both promiscuous matings and survival to the next breeding season). These differences lead to the different outcomes of our model, and, we believe, lend generality and realism to the discussion. Our model indicates that attempts to understand the effects of parentage on parental behavior must consider (1) the possibility that parentage can vary systematically with age, (2) whether additional matings are EPCs or polygynous, and (3) whether individuals can assess their own parentage.

Although our model considers parentage primarily within populations, it is useful in exploring broader taxonomic patterns. For example, populations with similar average parentage might show different levels of parental behavior because of different patterns of parentage with age (e.g., Figure 2). The overall or species-typical pattern will depend on the proportion of the population with different ontogenetic trajectories of parentage. Similarly, our analysis of nonfacultative responses and restricted patterns of parentage indicates that parentage affects parental behavior when some matings are promiscuous, in agreement with Werren et al. (1980). Thus, absolute differences in parentage among species may help explain absolute differences in parental behavior.

The often noted correlation between external fertilization and paternal care in fishes (e.g., Blumer, 1979; Ridley, 1978) and frogs (Gross and Shine, 1981) is consistent with our model if we follow Alexander (1974) in assuming that external fertilization is associated with higher male parentage. However, parentage is probably not the sole or even the most important correlate of frog and fish parental behavior patterns (e.g., Clutton-Brock, 1991). As Williams (1975) noted (see Gross and Sargent, 1985; Sargent and Gross, 1986), male association with embryos may instead provide the key selective circumstance. Male fish that maintain territories where females lay their eggs can easily provide care to eggs or young without sacrificing mating effort. This is not to say that parentage has no effect, but rather that it might not be the most important selective factor in this case.

Our model can also be used to analyze differences in parental behavior between the sexes. Many authors (e.g., Alexander, 1974; Kurland and Gaulin 1984; Ridley, 1978) have argued that the skew toward uniparental care by females among internally fertilized organisms is due to the fact that females have higher parentage than males. Others (e.g., Werren et al., 1980) have emphasized that because individuals compete only with members of their own sex for reproductive success, whether one sex is selected to behave parentally does not depend directly on the costs and benefits of care to the other sex. Perhaps this disagreement is more semantic than substantive. Although the costs and benefits of parental behavior for males do not affect

the optimal behavior of females, they will affect the probability that males evolve parental behavior. If parental care is required for rearing young but differences between the sexes in parentage mean that males are less likely to evolve care than females, then we expect more species to evolve female care than male care.

### Predictions about parentage

Our model shows that the effect of parentage on parental behavior depends on the type of response by the parent (facultative versus nonfacultative), the types of cues (discriminant versus indiscriminant), and the patterns of parentage among broods (restricted versus unrestricted). Predictions based on our analyses of these variables are summarized in Table 3. However, to predict how specific species or groups of species might behave, we need information about the patterns of parentage across species, the costs and benefits of parental behavior, the behavioral alternatives to parental behavior, and the mechanisms for assessing parentage and their accuracy. As was recently emphasized by Clutton-Brock (1991), for most creatures we know precious little about these aspects of breeding biology. Nonetheless, some general predictions can be made.

Selection for direct discrimination of descendants should be strongest when parentage is reduced frequently or drastically, e.g., when females routinely copulate with multiple males or when intraspecific brood parasitism is rampant (Sherman, 1991). The evolution of kin recognition abilities implies that there are fitness costs associated with assisting nonrelatives and benefits for correct discriminations. Both are likely when parents provide nonshareable care, such as food to individual young, so recognition of individual offspring is favored when parental behavior is nonshareable. If the main form of parental behavior is shareable (e.g., defense of the entire brood), offspring recognition is not favored because it provides no additional benefits.

At present there is no evidence that parents can discriminate related and unrelated offspring within broods (see Alexander, 1990; Beecher, 1991). This may or may not be significant. The frequency of extrapair fertilizations and brood parasitism in species with extensive paternal care (e.g., birds) is only now becoming clear (e.g., Birkhead, 1987; Birkhead and Møller, 1992; Rohwer and Freeman, 1989; Westneat et al., 1990). Whether males in such species routinely discriminate offspring from nonkin in mixed broods is currently unstudied.

One interesting datum does exist, and it suggests a lack of direct paternal discrimination. In dunlocks (*Prunella modularis*), paternity is quite variable, and males provide substantial assistance to chicks (Davies, 1985). Burke et al. (1989) reported that males fed broods of mixed parentage so long as they had spent time alone with (i.e., copulated with) the mother of the brood when she was sexually receptive. Thus, males sometimes fed broods that contained none of their offspring, and among broods of mixed paternity there was no evidence that males could distinguish their own chicks.

Indiscriminant mechanisms for facultatively responding to reduced parentage ought to be com-

mon. Such responses require only that reduced parentage (EPCs and brood parasitism) be reliably associated with environmental cues (e.g., mate or nest-guarding abilities, breeding synchrony). However, whether information about low parentage will affect parental behavior depends on why an individual had low parentage. If the same factors that led to reduced parentage affect the alternatives to providing care, then no changes in *PE* are expected (e.g., Westneat, 1988).

Evidence of indiscriminant mechanisms exists. Many North American songbirds abandon their nests if they have been interspecifically parasitized (e.g., by cowbirds; Rothstein, 1975), and heavy intraspecific parasitism leads to nest abandonment in several ducks (Andersson, 1984; Andersson and Eriksson, 1982; Semel et al., 1988). Møller (1988) reported that male barn swallows (*Hirundo rustica*) fed nestlings in roughly inverse proportion to the number of extrapair copulations by their social mate. Finally, Koenig (1990) temporarily removed male acorn woodpeckers (*Melanerpes formicivorus*) during the mating period and observed increased rates of nest destruction and lower rates of paternal care as a result.

In some mammals infanticide by males is apparently mediated by associational cues that indicate parentage rather than by direct discrimination of phenotypically similar young. If eliminating dependent juveniles reduces the time until a female is receptive again, infanticide by males is appropriately seen as an extreme form of mating effort (e.g., Hausfater et al., 1982). Our model is applicable to infanticide if sparing offspring is costly because it delays remating, and  $P_c$  is low and can be assessed by the male. Infanticide in some felids (e.g., lions), primates (langurs), and rodents (house mice) occurs when an offspring is born soon after a new male ousts the former resident and takes over a group of females (e.g., Brooks, 1984; Hrdy, 1974; Leland et al., 1984; Packer and Pusey, 1984). In these cases males do not appear to directly recognize their offspring; however, the timing and circumstances of the association between the male and the females is an indicator of paternity. For example, a male mouse will not kill pups if he associated with their dam long enough, even if he was not the sire; conversely, if he only associated with a female briefly, he may kill offspring that he actually did sire (vom Saal, 1984; vom Saal and Howard, 1982).

Our model suggests that nonfacultative responses may be common, but identifying them will be much more difficult than recognizing facultative responses. This is because nonfacultative responses are often correlated with opportunities for additional matings. For example, male indigo buntings are frequently cuckolded and rarely provide food for nestlings (Westneat, 1988). It is not clear whether low paternal effort is an evolutionary result of selection caused by the high rates of cuckoldry or the frequent opportunities for extrapair matings, or both, as is predicted by our model.

Restricted nonfacultative responses may also be correlated with other factors that affect parental behavior, such as age. If parental behavior is nonfacultative, experiments in which parentage is manipulated will not be very helpful. Comparative analyses across phylogenetic groups and studies that precisely measure the fitness costs and benefits of

parental behavior within species will be necessary to understand such responses.

In summary, opposing viewpoints about the influence of parentage on parental behavior can be reconciled. Our intent was to see if and when parentage affected selection, not to assess the importance of parentage relative to all other factors affecting the evolution of parental behavior. Our static optimization model is simple but general. It reveals that parentage and the evolution of parental care are intimately linked, but that their interrelationship is complex. Our model's outcomes agree with those of previous models, but offer some novel conclusions as well. In particular: (1) different age-related patterns of paternity or maternity can have surprising effects on age-related patterns of parental behavior, (2) the ability of parents to assess parentage and differences in the amount and type of information parents have about parentage will affect parental behavior, and (3) both factors 1 and 2 can create differences within and among species in patterns of parental behavior that can be explained in part by parentage. Several aspects of our model accord with field observations, but unambiguous tests of many of our predictions await the collection of the relevant data. We hope the ideas presented here will help stimulate and guide such research.

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