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Review

An evolutionary theory of the family

(ecological constraints/kin selection/reproductive skew/step-parent/incest avoidance)

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ABSTRACT **An evolutionary framework for viewing the formation, the stability, the organizational structure, and the social dynamics of biological families is developed. This framework is based upon three conceptual pillars: ecological constraints theory, inclusive fitness theory, and reproductive skew theory. I offer a set of 15 predictions pertaining to living within family groups. The logic of each is discussed, and empirical evidence from family-living vertebrates is summarized. I argue that knowledge of four basic parameters, (*i*) genetic relatedness, (*ii*) social dominance, (*iii*) the benefits of group living, and (*iv*) the probable success of independent reproduction, can explain many aspects of family life in birds and mammals. I suggest that this evolutionary perspective will provide insights into understanding human family systems as well.**

Two decades ago, in the introduction to his treatise, *Sociobiology: The New Synthesis*, E. O. Wilson (1) stated that "... sociology and the other social sciences ... are the last branches of biology waiting to be included in the Modern Synthesis." He was referring to the untapped potential of darwinian thinking to provide a conceptual framework for better understanding many aspects of human behavior. In the intervening years, a small but growing number of evolutionary anthropologists and psychologists has begun making inroads into "darwinizing" the social sciences. But their progress has been slow and has often been met with resistance.

Two often-cited reasons for such resistance are (*i*) a belief that the tremendous plasticity that exists in the expression of social behaviors renders applicability of biological (genetic) principles unlikely and (*ii*) the view that culture, rather than genes, is of overriding importance in mediating such behaviors in our own species. The first seemingly contradicts the idea of a heritable basis for social behaviors (an assumption of sociobiology), while the second argues that, even if present, heritable aspects of social behavior will be of minor importance.

Both criticisms can be easily dispelled. The condition-dependent expression of many social behaviors in no way precludes them from genetic influence. The work of researchers such as Maynard-Smith (2) and Parker (3) has clarified the relationship between conditionality and the evolution of behavior. Indeed, the last decade has seen a marked shift toward viewing organisms as "decision makers," selected to accurately assess the consequences of different behavioral options available to them and to express those behavioral variants that maximize their fitnesses (e.g., refs. 4 and 5). Depending upon social circumstances, the optimal choice of behaviors may vary. But, providing that heritable variation exists in the assessment algorithms underlying the choices, natural selection can fine-tune the decision rules and thereby bring them into the realm of darwinian predictability.

The second criticism pertains to the use of evolutionary models to predict the social behaviors of higher primates, particularly our own species. The obvious importance of cultural influences on our behavior does not negate the probability that we humans also possess a set of biologically based predispositions for interacting with one another. It is these predispositions that one attempts to predict from evolutionary models of behavior.

Progress in "darwinizing" the social sciences has also been slowed by the absence of a general evolutionary theory of the family. The seminal contributions, for example, of Trivers (6) on parent–offspring conflict, of Trivers and Willard (7) on differential investment in sons and daughters by parents, of Alexander (8) on paternity and nepotism, and of Daly and Wilson (9, 10) on the effects of genetic relatedness on child abuse, represent important steps in this direction.

Building on these and other studies, I develop a general evolutionary framework for understanding biological families. This framework is based upon the integration of three overlapping conceptual areas of behavioral ecology:

(*i*) Ecological constraints theory (11–16)—which examines factors affecting dispersal options of sexually maturing offspring. It specifies the conditions for delayed dispersal and, hence, the formation of family social units.

(*ii*) Kin selection theory (6, 17, 18)—which helps identify the types and contexts of social interactions expected among family members (most of whom are genetic relatives).

(*iii*) Reproductive skew theory (19–24)—which incorporates and expands on areas *i* and *ii* to predict when conflict over reproduction is expected within families and when such conflict will result in reproductive sharing. Such sharing creates extended family structures.

A set of 15 evolutionary predictions pertinent to family living is presented below in *Family Formation and Stability, Family Dynamics*, and *Family Structure.* I discuss the logic of each prediction and provide a synopsis of the relevant literature from family-dwelling vertebrates. Predictions and data are summarized in Table 1. Additionally, I discuss why these predictions should generalize across taxa, to all species that live in family groups, including humans.

Definition of Family

There is no strict consensus among social scientists as to what constitutes a family. Sociologists typically stress functional aspects of the child rearing unit: families are groups of coresident adults responsible for the production, socialization, and education of offspring (e.g., refs. 72–74). Anthropologists stress kinship and intergenerational aspects of families: families are kin groups through which descent lines are traced and which consist, at a minimum, of parent(s) and unmarried offspring (75, 76).

In humans, preferential interactions occur between offspring and their parents even after offspring have established households of their own. To ease the task of seeking parallels between human and nonhuman species, I restrict the definition of animal families to those cases where offspring also continue to interact regularly, into adulthood, with their parents

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Table 1. Biological families: Evolutionary predictions and empirical evidence

No.	Abbreviated prediction	Evidence
	Family formation: The importance of delayed dispersal	
1	Family groupings will be unstable, disintegrating when acceptable reproductive opportunities materialize elsewhere.	**Supportive**: avian, *Melanerpes formicivorus* (25), *Picoides borealis* (26), *Phoeniculus purpureus* (27), *Malurus cyaneus* (28), *Aphelocoma coerulescens* (29), *Nesomimus parvulus* (30), and *Acrocephalus sechellensis* (31); mammalian, *Peromyscus leucopus* (32) and *Dipodomys spectabilis* (33)
2	Family stability will be greatest in those groups controlling high quality resources. Dynasties may form.	**Supportive**: avian, *Melanerpes formicivorus* (34, 35), *Aphelocoma ultramarina* (36), *Aphelocoma coerulescens* (37), *Campylorhynchus nuchallis* (38), and *Acrocephalus sechellensis* (31)
	Family dynamics: Kinship and cooperation	
3	Help with rearing offspring will be the norm.	**Supportive**: 107 avian species* and 57 mammalian species* **Counter**: 5 avian species* and 6 mammalian species*
4	Help will be expressed to the greatest extent between closest genetic relatives.	**Supportive**: avian, *Merops bullockoides* (39), *Manorina melanophrys* (40, 41), *Manorina melanocephala* (42), *Nesomimus parvulus* (43), and *Gymnorhinus cyanocephalus* (44); mammalian, *Hyaena brunnea* (45), *Helogale parvula* (46), and *Panthera leo* (47) **Counter**: avian, *Aphelocoma ultramarina* (36)
5	Sexually related aggression will be reduced because incestuous matings will be avoided. Pairings will be exogamous.	**Supportive**: 18 avian species* and 17 mammalian species* **Counter**: 1 avian species* and 3 mammalian species*
6	Breeding males will invest less in offspring as their certainty of paternity decreases.	**Supportive**: avian, *Melanerpes formicivorus* (48) (Many additional studies, some supportive, others counter, have been conducted on nonfamilial species.)
	Family dynamics: Disruption after breeder loss or replacement	
7	Family conflict will surface over filling the reproductive vacancy created by the loss of a breeder.	**Supportive**: avian, *Melanerpes formicivorus* (34), *Picoides borealis* (49), *Eopsaltria georgiana* (50), *Campylorhynchus nuchallis* (38), *Acrocephalus sechellensis*†, and *Turdoides squamiceps* (51)
8	Sexually related aggression will increase because incest restrictions do not apply to replacement mates. Offspring may mate with a step-parent.	**Supportive**: avian, *Melanerpes formicivorus* (34, 52), and *Merops bullockoides*‡, *Campylorhynchus nuchalis* (53), and *Turdoides squamiceps* (51)
9	Replacement mates (step-parents) will invest less in existing offspring than will biological parents. Infanticide may occur.	**Supportive**: avian, *Melanerpes formicivorus* (48, 54, 55) and *Nesomimus parvulus* (56); mammalian, for summaries of mammalian data, see Hrdy (57) and Hausfater and Hrdy (58)
10	Family members will reduce their investment in future offspring after the repairing of a parent.	**Supportive**: avian, *Aphelocoma coerulescens* (59) and *Acrocephalus sechellensis* (60) **Counter**: avian, *Picoides borealis* (49) and *Campylorhynchus nuchallis* (102)
11	Step-families will be less stable than biologically intact families.	(No data currently available)
	Family structure: Reproductive sharing leads to extended families	
12	Decreasing ecological constraints will lead to increased sharing of reproduction.	**Supportive**: avian, *Merops bullockoides* (14) and *Nesomimus parvulus* (62)
13	Decreasing asymmetry in dominance will lead to increased sharing of reproduction.	**Supportive**: avian, *Malurus splendens* (61) and *Turdoides squamiceps* (51); mammalian, *Helogale parvula* (69, 70)
14	Increasing symmetry of kinship will lead to increased sharing of reproduction.	**Supportive**: avian, *Melanerpes formicivorus* (63), *Merops bullockoides* (64), *Aphelocoma ultramarina* (36), and *Turdoides squamiceps* (51)
15	Decreasing genetic relatedness will lead to increased sharing of reproduction. Reproductive suppression will be greatest among closest kin.	**Supportive**: avian, *Poryhyrio poryhyrio* (65), *Buteo galapagoensis* (66), *Merops bullockoides* (64, 67), *Crotophaga sulcirostris* (68) and *Prunella modularis* (107); mammalian, *Helogale parvula* (69, 70) and *Panthera leo* (71)

Species listed are those for which available data allow testing of the prediction in question. Numbers in parentheses refer to references.

*S.T.E. and N. J. Demong, unpublished compilation.

†J. Komdeur, personal communication.

‡S.T.E., P. H. Wrege, and N. J. Demong, unpublished data.

(16). Typically, this occurs when offspring delay dispersal and continue to reside with one or both parents past the age of sexual maturity. I distinguish between simple families (single parent or conjugal pair), in which only a single female breeds, and extended families, in which two or more relatives of the same sex reproduce. The presence of a breeding male is not essential to the definition of a family. Rather the presence or absence of reproductive males forms the basis of a second partitioning into biparental, vs. matrilineal, families. It is useful to further differentiate between intact families, those where the original breeders are still the reproductives, and replacement families where, because of death, divorce, or departure, a breeder has been replaced. For simplicity, I exclude large assemblages in which parents and mature offspring reside but have no spatial territory of their own (e.g., many troop-living primates and ungulates) although many of the predictions should also apply to them.

Family Formation and Stability

The key to understanding the evolution of families is understanding the causes of delayed dispersal. One probable reason why families are so rare in nature (only 3% of bird and mammal species are known to be familial) is that delayed dispersal entails an automatic fitness cost. In intact simple families, offspring do not reproduce and in extended families their reproduction is frequently suppressed. Thus the cost of delayed dispersal is the forfeiture of fitness associated with missed reproductive opportunities. Families develop only when offspring that remain with their parents and forego early breeding opportunities somehow compensate for this cost (16).

Two seemingly opposing schools of thought have emerged to explain delayed dispersal. Ecological constraints models (11–16) emphasize the scarcity of acceptable reproductive vacancies available to maturing offspring, as well as the low success often associated with early, or unaided, breeding attempts by such individuals. The automatic cost is low because the fitness benefit associated with leaving home is low. The "missed reproductive opportunities" are nonexistent or of poor quality.

In contrast, benefits-of-philopatry models (35, 77–79) emphasize the fitness benefit gained by staying with one's parents on the natal territory. Benefits may include enhanced survivorship while waiting for outside reproductive opportunities to arise, improved abilities to compete when they materialize, and the possibility of sharing or inheriting the natal breeding position itself. Also included are any indirect benefits gained by helping parents or other kin while staying home.

I have argued elsewhere (refs. 14 and 16; see also refs. 15 and 80) that these two models represent two sides of a semantic coin. Both assume that maturing offspring assess the profitabilities of two options: dispersing early and attempting to breed independently (B) vs. delaying dispersal and staying at home (S). Both further assume that offspring remain with their parent(s) only when the expected inclusive fitness benefit of doing so exceeds that expected by leaving (i.e., when $S - B > 0$). And both emphasize similar interrelated variables: having poor options for independent breeding is an integral part of what makes for a good situation at home, and vice versa.

Consequently, I propose a generalized economic model of family formation (14, 16) that incorporates aspects of both arguments above. It can be stated as follows: (*i*) Delayed breeding occurs when the production of mature offspring exceeds the availability of acceptable opportunities for their independent reproduction. (*ii*) Under such circumstances, some offspring must wait until acceptable reproductive vacancies arise and then compete to fill them. (*iii*) Families form when such waiting is best done at home, when remaining on the natal territory and/or associating with one's family somehow augments the offspring's inclusive fitness. Family formation thus can be viewed as a "solution" to the temporary problem of a shortage of acceptable reproductive opportunities. This leads directly to my first prediction.

Prediction 1. *Family groupings will be inherently unstable. They will form and expand when there is a shortage of acceptable reproductive opportunities for mature offspring, and they will diminish in size or dissolve (break up) as acceptable opportunities become available.*

Evidence in support of *Prediction 1* comes from a number of long-term observational studies and from field experiments in which breeding vacancies were artificially manipulated. Data from five avian (25, 27, 29–31) and two mammalian (32, 33) species provide especially convincing evidence that families form only when acceptable breeding opportunities are limited. Experimental verification of this causal link has been obtained in three bird species (26, 28, 31). For each, breeding vacancies were created where none previously existed. The effects on family stability were striking. In each case, mature offspring living within their parents' territories left home to fill the vacancies, causing the dissolution of family groups.

Prediction 2. *Families that control high quality resources will be more stable than those with lower quality resources. Some resource-rich areas will support dynasties in which one genetic lineage continuously occupies the same area over many successive generations.*

Prediction 2 follows from the realization that what constitutes an acceptable reproductive opportunity for one individual may be quite unacceptable to another. When the fitness associated with staying at home varies with the quality of the natal territory or the composition of the family group, the quality of the reproductive opportunity that will be sufficient to favor dispersal also will vary. Specifically, offspring from high quality natal situations will be more choosy in their dispersal decisions (15, 16, 77). A smaller fraction of available breeding vacancies will be acceptable to such individuals, and competition to fill these vacancies will be more intense. The result will be prolonged philopatry and greater temporal stability of family units controlling high-quality resources.

Six avian studies allow testing of *Prediction 2*; each provides supportive results (31, 34–38).

Inheritance of the parental breeding position represents a common route to achieving breeding status among many species of family-dwelling birds and mammals (see refs. 13, 25, and 81–83). The greater the quality of the resources controlled by the family, the greater will be the incentive to remain at home to inherit them (see *Prediction 7*). Few studies have proceeded long enough to test this portion of *Prediction 2.* But work on Florida scrub jays, *Aphelocoma coerulescens*, has documented the continuous occupancy of high quality territories by familial lineages over several generations (G. Woolfenden, personal communication). I expect family dynasties will prove common as long-term monitoring studies continue.

Family Dynamics: Kinship and Cooperation

Family dynamics, the social interactions that occur among family members, are expected to differ from the dynamics of other types of social groupings because families are largely composed of genetic relatives. Hamilton's theory of kin selection (17) revolutionized evolutionary thinking about social behavior by stressing that individuals contribute genetically to future generations both directly, through the production of their own offspring, and indirectly, through their positive effects upon the reproduction of relatives. The sum of these two effects constitutes an individual's inclusive fitness. By virtue of common descent, both one's offspring and the offspring of relatives have predictable probabilities of carrying alleles that are identical to one's own. The closer the genetic relationship, the greater the frequency of such shared alleles.

Kinship is thus predicted to influence the types of behaviors exhibited within families. *Predictions 3* and *4* derive directly from kin selection theory.

Prediction 3. *Assistance in rearing offspring (cooperative breeding) will be more prevalent in family groups than in otherwise comparable groups composed of nonrelatives.*

Cooperative breeding occurs when an adult member of a social group provides regular care to offspring that are not genetically its own. It typically involves provisioning and defending such offspring for a prolonged period of time.

A survey of the literature provides strong support for *Prediction 3.* More than 90% of both family-living birds and mammals (excluding primates) exhibit cooperative breeding (Table 1). Cooperative breeding also occurs in familial species of both eusocial insects (84, 85) and social spiders (86, 87). Assistance in the rearing of young appears to be the norm within family-structured societies.

In contrast, such assistance is rare in nonfamilial species. Of all the birds and mammals known to exhibit cooperative breeding, fully 88 and 95% of those for which social organization is known live in family groups (107 of 121 and 57 of 60 species, respectively; S.T.E. and N. J. Demong, unpublished compilation). Cooperative breeding as a reproductive system thus is largely restricted to familial societies.

Prediction 4. *Assistance in rearing offspring (cooperative breeding) will be expressed to the greatest extent between those family members that are the closest genetic relatives.*

The clearest tests of *Prediction 4* come from cooperatively breeding species that live in extended families, those in which multiple individuals (or pairs) are breeders. This situation provides potential alloparents with choices, making it possible to ask whether they preferentially aid their closest kin. In studies conducted to date, five of six bird species (39–44) and three of three mammals (45–47) show the predicted preferential allocation of aid.

Prediction 5. *Sexually related aggression will be less prevalent in family groups than in otherwise comparable groups composed of nonrelatives. This is because opposite-sex close genetic relatives will avoid incestuously mating with one another.*

Prediction 5 derives from the fact that incestuous matings between close relatives often have deleterious genetic consequences in normally outbred populations. Inbreeding causes an increased frequency of homozygosity that results in the phenotypic expression of recessive alleles whose negative effects are otherwise masked. Deleterious effects of inbreeding have been documented in many (but not all) vertebrate species examined (e.g., refs. 88–92).

Natural selection is thus expected to foster the evolution of inbreeding avoidance mechanisms. These mechanisms will lead to decreased tendencies to pair with, or to show sexual interest in, close genetic relatives of the opposite sex. Consequently, sons will rarely compete with their father and daughters will rarely compete with their mother for sexual access to the parent of the opposite sex. Neither will siblings compete for sexual access to one another. The result will be a reduced incidence of mate guarding and other forms of sexually related harassment and aggression within family groups.

A literature survey (S.T.E. and N. J. Demong, unpublished compilation) indicates that, despite frequent opportunities to interact sexually with other family members, incestuous matings are exceedingly rare. Fully 18 of 19 avian, and 17 of 20 mammalian, family species for which data are available show strong tendencies to pair exogamously (Table 1).

Incest avoidance is not universal among vertebrates, however (see refs. 93 and 94). Neither is *Prediction 5* an absolute. As ecological constraints on the option of independent breeding become increasingly severe, a point may be reached where it is better to breed incestuously than to risk not breeding at all. These conditions have been modeled by Bengtsson (95) and Waser *et al.* (96).

Prediction 6. *Breeding males will invest less in offspring as their certainty of paternity decreases.*

This prediction is not restricted to familial species but will apply to any situation where males provide care for dependent young. Parental care is a form of kin assistance. Offspring share half their genes with each parent, providing that the social parent is actually a biological parent. When a breeder has been cuckolded, however, its relatedness to the offspring is zero, and the fitness benefit accrued by caring for such offspring largely disappears.

For most vertebrate species, parental uncertainty is primarily a male problem. We thus should expect males to be sensitive to their risk of cuckoldry and to adjust their behaviors accordingly (97). Recent models (e.g., ref. 98) suggest that cuckolded males should reduce or terminate their investment in current young when continued care is costly and when there is a sufficiently high probability of their achieving greater assurance of paternity in future breedings.

Only one study of a familial species has tested *Prediction 6.* By varying the timing of temporary removal experiments, Koenig (48) showed that breeding male Acorn woodpeckers, *Melanerpes formicivorus*, indeed vary their nurturing behaviors according to their probability of siring offspring.

Family Dynamics: Disruption After Breeder Loss or Replacement

The death, divorce, or departure of a breeding parent, and its replacement from outside the group, will alter the basic genetic structure of the family unit. Such loss of a parent is expected to profoundly alter the social dynamics of the family group and, potentially, its stability as well. *Predictions 7–11* pertain to these changes. These predictions are phrased in terms of biparental families, but all except *Prediction 8* are applicable, with slight modifications, to matrilineal families as well.

Prediction 7. *The loss of a breeder will result in family conflict over the filling of the resulting reproductive vacancy. In the specific case of simple conjugal families, the surviving parent and its mature opposite-sex offspring will now compete for breeder status. The conflict will be especially severe when offspring are of the dominant sex and when resources controlled by the family are of high quality.*

If family formation is a "solution" to the problem of a shortage of acceptable breeding vacancies and if one route to becoming a breeder is to inherit the natal breeding position, then the loss of a parent creates an excellent opportunity for an offspring (or another subordinate kin in the case of extended families) to ascend to breeding status on its home territory. The higher the quality of the family resources, the more intense the expected competition to fill the breeding vacancy.

Offspring of most species, however, will not pair with a parent (*Prediction 5*). Consequently, an offspring can only secure the breeding vacancy for itself if it obtains an unrelated mate from outside the group. In simple families (in which only one female breeds), the offspring must also prevent continued reproduction by its surviving parent. Such prevention can include resisting the settlement of a replacement mate, behaviorally suppressing breeding by the surviving parent, or physically evicting the parent from the group. Without such action, the surviving parent will recruit a new mate of its own and continue as sole breeder.

In most vertebrate species, dominance is influenced by gender and age. Males typically are dominant over females, and older individuals are dominant over younger ones. Thus when a breeding female dies, a surviving daughter will rarely challenge her father for breeder status. However, challenges are expected between sons and mothers (and sons and potential step-fathers) after the loss of a father.

Note that an offspring will be less related to future young produced by a surviving parent and step-parent (its half-siblings) than to its own future offspring should it become a breeder. This provides an additional evolutionary "incentive" for attempting to usurp the breeding position after the disappearance of a parent (see also *Prediction 10*).

The literature is full of vivid accounts of within-family power struggles for breeding status after a parental loss (e.g., refs. 34, 38, 50, and 51). And in simple conjugal family species, sons replace their deceased fathers as breeders much more often than daughters replace their deceased mothers (see refs. 13 and 82). To cite one example, in Red-cockaded woodpeckers, *Picoides borealis*, in each of 23 instances after the death of a father, sons assumed breeder status and mothers dispersed (49).

Prediction 8. *Sexually related aggression will increase after the re-pairing of a parent. In the specific case of simple conjugal families, the surviving parent and its mature same-sex offspring will now compete for sexual access to the replacement mate (step-parent). This conflict will be especially severe when the asymmetry in dominance between the surviving breeder and its same-sex offspring is small.*

If a divorced, widowed, or abandoned parent takes a new mate, the replacement is almost invariably from outside the family group (*Prediction 5*). Parental re-pairing thus provides a mating opportunity that is exempt from incest restrictions for mature offspring of the same sex as the remaining parent. This opens an avenue for such offspring to gain direct fitness by reproducing with the new unrelated breeder.

Shared reproduction, however, typically will have detrimental fitness consequences for the surviving parent. Thus while the appearance of sexual behavior in previously nonsexual offspring is expected after the re-pairing of a parent, so too is an accompanying increase in sexual conflict (e.g., mate guarding, intrasexual aggression, and attempted reproductive suppression) between family members.

In one of the few studies to examine *Prediction 8*, Piper and Slater (53) contrasted behavior in intact vs. replacement families of Stripe-backed wrens, *Campylorhynchus nuchalis.* Sons displayed no sexual interest in their mothers, but they frequently courted their step-mothers. Paternity data showed that while sons never sired offspring with their biological mothers, they did so with their step-mothers. Replacement families also showed marked increases in father–son aggression. Analogous results are reported in three other avian studies (34, 51, 52).

Prediction 9. *Replacement breeders (step-parents) will invest less in existing offspring than will biological parents. They may infanticidally kill current young when such action speeds the occurrence, or otherwise increases the success, of their own reproduction. This will be more likely when the replacement mate is of the dominant sex.*

This prediction builds on *Prediction 6.* Because replacement mates typically will be unrelated to current family members, they will gain no clear fitness benefit from helping to rear dependent offspring from previous breedings. Such help is not expected unless the replacement mate benefits in some other way from its actions.

In circumstances where the continued care of extant offspring delays reproduction by the replacement mate, conflict is expected. The abandonment, eviction, or infanticidal destruction of such offspring may result. Given the typical dominance asymmetries between the sexes, such forcible actions will occur more frequently with male, than with female, replacement mates.

The hypothesis of adaptive sexually selected infanticide was first proposed by Hrdy (57) and has received support from numerous studies of rodents, carnivores, and primates (for review, see ref. 58). Among birds, there is a growing literature documenting cases of rejection or destruction of eggs and young by avian step-parents (e.g., refs. 48, 54–56, and 99–101). These trade-offs are discussed more fully by Rohwer (100) who examines the conditions under which an incoming mate is expected to adopt, ignore, or destroy any current dependent young.

Prediction 10. *Nonreproductive family members will reduce their investment in future offspring after the replacement of a closely related breeder by a more distantly or unrelated individual.*

This prediction follows directly from kin selection theory. Natal family members will be only one-half as related to future offspring produced by a parent and an unrelated replacement mate as to former offspring produced by both biological parents. The indirect benefit realized by helping to rear such future offspring will be correspondingly decreased.

Surprisingly few vertebrate studies have tested this prediction. Two avian reports (49, 102) provide contrary evidence (nonbreeders provisioned full- and half-siblings equally), whereas two others (59, 60) demonstrate support (the proportion of family members assisting in rearing young decreased significantly when a step-parent assumed a breeding role and dropped to near zero when both parents were replaced).

Prediction 11. *Replacement (step-) families will be inherently less stable than biologically intact families. This will be especially true when offspring from the originally intact family are of the same sex as the step-parent.*

I have argued that the replacement of a parent by an unrelated breeder will have negative consequences on the fitness of offspring that continue to reside with their replacement families. Offspring of both sexes suffer a reduction in future indirect benefits available from helping rear young of the new breeding pair (*Prediction 10*), and all risk possible reduction in investment in them by the replacement breeder (*Prediction 9*). These factors are predicted to make replacement families less stable than intact families because a reduction in the fitness associated with staying at home lowers the quality of the outside reproductive opportunity sufficient to favor offspring dispersal (which leads to family dissolution).

In biparental families, these negative consequences may be offset for a mature offspring of the same sex as the surviving biological parent. With incest inhibitions lifted, such an offspring might reproduce with the replacement mate (*Prediction 8*). If this occurs, the offspring will gain direct fitness through personal reproduction. Should the surviving biological parent die, the offspring is well-positioned to inherit the primary breeding spot because it already has a suitable mate. The stability of the new family unit will depend, in part, upon the specifics of these fitness trade-offs.

Neither of these potential benefits is available to offspring of the same sex as the step-parent, who are, therefore, predicted to be more likely to leave the family unit after a parental replacement.

Prediction 11 has yet to be tested rigorously. However, in three avian species offspring of the same sex as the step-parent are more likely to leave their family group after the re-pairing of a parent than are their opposite-sex siblings (34, 103, 104).

Family Structure: Reproductive Sharing Leads to Extended Families

Much of the previous discussion has dealt with simple families (single parents or conjugal pairs and their grown offspring) in which reproduction is monopolized by the single dominant female. Sometimes, however, two or more relatives of the same sex breed, giving rise to extended family structures. In vertebrates, this most typically occurs when offspring reproduce concurrently with their parent(s). Extended families may be matrilineal or biparental. They generate assemblages of relatives that may include grandparents, aunts, uncles, cousins, and in-laws, in addition to simply parents and offspring.

The fundamental challenge in explaining the diversity of family structures lies in identifying the conditions under which reproduction becomes shared. Several models, collectively known as reproductive skew theory, have addressed this question (19–24). Reproductive skew refers to the distribution of direct reproduction among same-sex members of a group and can vary from a value of 1 (when reproduction is totally monopolized by a single individual) to 0 (when reproduction is distributed equitably among all mature individuals) (20, 21). All models assume that dominant individuals control the reproduction of subordinates. All further assume that, all else being equal, dominant individuals will maximize their own fitness by monopolizing breeding themselves.

The central idea of skew theory is that when dominants in the group benefit from the continued presence of subordinates, dominants may, under certain circumstances, share reproduction in order to induce the subordinates to remain. Alexander (18) and Emlen (19) call such inducements "fitness forfeiting"; Reeve and Ratnieks (23) call them "staying incentives." Provided that the dominant, while sharing reproduction, still realizes a higher inclusive fitness than it would in the absence of the subordinate, the result can be a "win–win" situation for both participants. The sequence of decisions leading to various types of family structures is shown in Fig. 1.

Skew models identify four parameters that specify the conditions under which reproductive sharing should occur and the amount of sharing expected. These are (*i*) the magnitude of any benefit realized by the dominant if the subordinate should stay, (*ii*) the expected success of the subordinate if it should leave, (*iii*) the relative asymmetry in

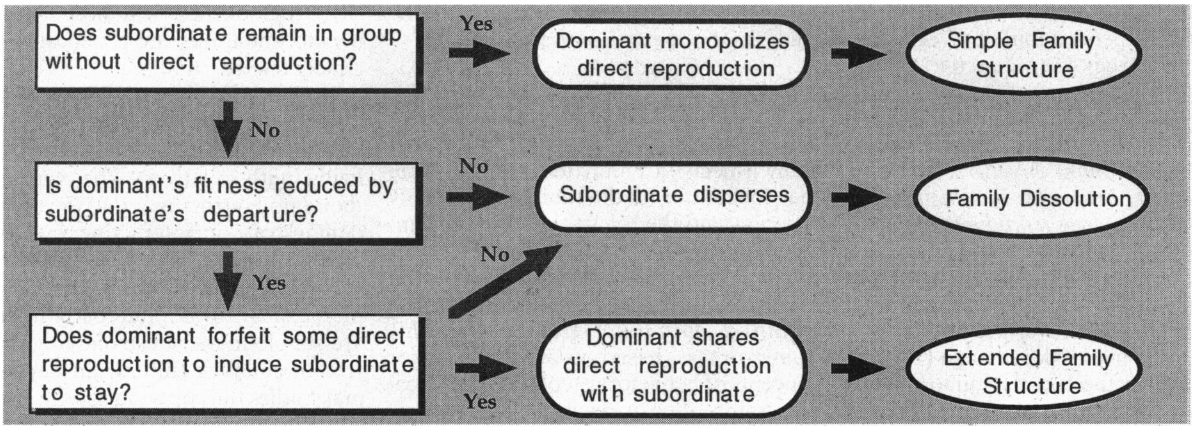

FIG. 1. Reproductive skew theory depicts the formation of extended family structures as the compromise resolution to family conflict over the dispersal decisions of subordinates. Shared reproduction is predicted when the dominant benefits from the continued retention of the subordinate within the family group, but the subordinate, in the absence of any direct reproduction, would realize greater fitness by leaving. Extended families are more reproductively egalitarian than simple families (patterned after figure 3.1 of ref. 23).

dominance between the potential cobreeders (the dominant and subordinate), and (*iv*) the genetic relatedness between them (19–24). Each parameter influences the relative payoffs of staying vs. leaving for the different participants. Collectively, they determine the leverage that the dominant has in "withholding," and the subordinate has in "demanding," (anthropomorphically speaking) a share of reproduction.

The interaction of these four factors determines the outcome of reproductive competition within the family. A necessary precondition for reproductive sharing is that the dominant must benefit from its continued association with the subordinate; only then will extended family structures develop. The remaining three parameters form the bases for the final four predictions.

Prediction 12. *Reproduction within a family will become increasingly shared as the severity of ecological constraints decreases, that is, as the expected profitability of the subordinate's option of dispersal and independent reproduction increases.*

The leverage that a subordinate can wield depends both on the profitability of its dispersal option and on the magnitude of the benefit to the dominant of continuing its association with the subordinate. The profitability of the subordinate's dispersal option, in turn, depends on the number and quality of available breeding vacancies, as well as the expected success of unaided breeding attempts. These are the same factors that define the severity of the ecological constraints on independent breeding (12–14).

Interestingly, if conditions become too benign (e.g., if the advantages of large group size, or cooperative rearing of offspring, decrease sufficiently), the importance of subordinates to the inclusive fitness of the dominant may cease. When this occurs, subordinate dispersal will be in the best interest of all parties, and families will dissolve (*Prediction 1*).

Reproductive sharing thus is expected primarily at intermediate levels of severity of ecological constraints, when conditions afford viable reproductive opportunities for subordinates, but are not so benign that the benefits of continued group living for dominants disappear altogether.

Familial species that exhibit variable levels of reproductive skew are ideal subjects for testing *Prediction 12.* In both White-fronted bee-eaters, *Merops bullockoides*, and Galapagos mockingbirds, *Nesomimus parvulus* (the only two vertebrate species for which requisite data are available), the frequency of shared breeding was greatest in seasons when ecological constraints were most benign (12, 62).

Prediction 13. *Reproduction within a family will become increasingly shared as the asymmetry in social dominance between potential cobreeders decreases.*

A subordinate always has the option of directly challenging the dominant for reproductive rights within the group. A successful challenge can result in the dominant's overthrow and the subordinate's assumption of breeder status. The costs can be high for both participants. Fights may lead to injury, eviction, or even death.

All else being equal, the benefits of such challenges for a subordinate, as well as the risks for a dominant, will be greatest when the disparity in their fighting abilities is least (23). It may then be advantageous for the dominant to share reproduction. Such sharing will increase the profitability for the subordinate of staying and continuing to cooperate, thereby reducing the magnitude of any gain to be realized by challenging the dominant. Reeve and Ratnieks (23) call such fitness forfeiting a "peace incentive."

Several studies provide suggestive support for *Prediction 13.* For example, in Splendid fairy-wrens, *Malurus splendens* (61), Arabian babblers, *Turdoides squamiceps* (51), and Dwarf mongooses, *Helogale parvula* (69, 70), family members close to the dominant in age (and thus in dominance) are more likely to become cobreeders than are individuals more dissimilar in age.

Prediction 14. *Reproduction within a family will be shared more equitably when the potential cobreeders consist of siblings than when they consist of parent(s) and grown offspring.*

In some extended families, same-sex siblings will be potential cobreeders. When this occurs, the genetic relatedness between each sibling and the offspring of the other is symmetrical ($r = 0.25$ for each). All else being equal, under conditions where reproductive sharing is favored by one sibling, it will also be favored by the other.

In contrast, mothers and daughters (or fathers and sons) typically are asymmetrically (unequally) related to one another's future offspring. Assuming mate fidelity on the part of the parents, an offspring will be more closely related to its parents' future offspring (its full siblings, $r = 0.5$) than the parents will be to the offspring's offspring (their grand-offspring, $r = 0.25$). The parent thus has more to gain from withholding shared reproduction than the offspring does from demanding it. This will lead to greater reproductive skew in parent–offspring, compared with sibling–sibling, associations (105). This will only be true, however, provided that no parental mate-change or extra-pair fertilization has occurred. Reeve and Keller (105), who recently modeled this comparison, cite several species that breed in extended families of variable composition and show the predicted shift in reproductive skew (36, 51, 63). I would add one more (64).

Prediction 14 will be difficult to test definitively because two additional factors, the age-related dominance asymmetry typical between parents and offspring (*Prediction 13*) and the avoidance of incestuous matings between parent and offspring (*Prediction 5*), yield the same expectation of greater reproductive skew in matrifilial/patrifilial groupings than in sibling–sibling associations. Teasing apart the relative contributions of these three factors will depend upon close examination of the degree of reproductive skew in different types of familial associations.

Prediction 15. *Reproduction will be shared most with those family members to whom the dominant breeders are least closely related. In species in which dominants actively suppress reproduction by subordinates, such suppression will be greatest in those subordinates to whom the dominant is most closely related.*

This counterintuitive prediction was first proposed over a decade ago (19–22). It follows from the fact that subordinates differ in the magnitude of the indirect benefits that they obtain by remaining and helping in their family groups. All else being equal, these benefits are proportional to the subordinates' degree of genetic relatedness to the breeders. Subordinates to whom the dominant pair is most closely related receive the largest amount of indirect benefit from helping (*Prediction 4*). They therefore are predicted to require the smallest "staying incentives" to keep them in the family group. In contrast, distantly or nonrelated subordinates gain little or no indirect benefits from staying and helping and, thus, require a greater amount of personal reproduction to be induced to remain.

Several recent studies provide clear tests of *Prediction 15.* Both pukekos, *Porphyrio porphyrio* (an Australasian gallinule), and lions, *Panthera leo*, form extended families in which the group males may or may not be closely related to one another. Copulation and paternity data confirm that reproduction is shared quite equitably among males when the groups are composed of unrelated individuals, but dominants monopolize reproduction when the potential mate-sharing groups are composed of close male relatives (65, 71).

Reproductive competition often takes the form of disruption or suppression of the breeding attempts of subordinates. In the extended families of White-fronted bee-eaters, dominant breeders preferentially disrupt the breedings of their closest kin (64, 67), often inducing the latter to become helpers at their nests.

In families of Dwarf mongooses, the dominant male and female typically suppress the reproduction of subordinates. In keeping with *Predictions 13* and *15*, those subordinates that do reproduce are the oldest and those least closely related to the dominant breeders (69, 70).

Only three other cases of egalitarian breeding have been reported among highly social cooperatively breeding vertebrates (66, 68, 107). In each, the multiple breeders have proven to be nonrelatives.

Although the predictions for reproductive sharing within kin groups are univariate, the four parameters of reproductive skew theory interact with each other. The full value of the theory can only be tested by considering all four together in the analysis of any particular society.

Conclusions

I have attempted to demonstrate that many aspects of family life, ranging from the formation and stability of family groupings, to the roles that different family members adopt in their interactions with one another, to the structural form of the family unit itself, can be understood within a darwinian framework. This framework is based upon three major concepts of behavioral ecology: ecological constraints theory, inclusive fitness theory, and reproductive skew theory. Each assumes that individual behaviors are based, at least partially, on adaptive decision rules shaped by natural selection.

From these basic tenets of evolutionary biology, I have distilled a set of 15 predictions that provide an integrated framework for considering the workings of the family and other kin associations. Abbreviated versions of the predictions appear in Table 1, along with relevant nonhuman examples from the vertebrate literature.

Predictions 1 and *2* forecast the conditions under which families originate and discuss how stable these families are likely to be. Stability depends on the trade-offs between the fitness benefits available from staying home vs. those available from dispersing to attempt reproducing elsewhere.

Predictions 3–5 discuss the extent to which reproductive cooperation (helping behavior and reduced sexual competition) can be expected among family members. *Prediction 6* introduces family conflict, in the form of reduced paternal investment by males that may have been cuckolded.

Predictions 7–11 pertain to the disruptive effects on family dynamics that result from the disappearance of a biological parent and its subsequent replacement by a step-parent. The death of a father in a simple conjugal family, for example, will lead to conflict between a mother and her eldest mature son over her retention, vs. his assumption, of breeder status. Mothers will often lose their breeding positions to their dominant sons at these times.

The arrival of a replacement breeder is predicted to cause further disruptions. There will be reduced incentive for current offspring to remain at home or for step-parents to invest heavily in these offspring. Step-families thus are forecasted to be less stable than biologically intact families.

Delayed dispersal, coupled with the sharing of direct reproduction by dominants with subordinates, gives rise to a diversity of extended, as opposed to simple family structures. The final four predictions describe conditions under which extended families are expected to form, and specify which family members will become cobreeders. *Prediction 15* offers the counterintuitive argument that dominants will be most likely to share reproduction with those family members to whom they are genetically the least closely related.

Social vertebrates, and particularly birds, are excellent subjects for generating and testing darwinian hypotheses about living with relatives. The variations in their family structures, and the tactics they demonstrate in interacting with one another, often have direct parallels in human society. Their social behaviors, while complex enough to be inherently interesting, are simple in the sense of being relatively free of complex cultural influences. Animal studies thus provide us with a valuable window through which we can more easily view the fundamental biological rules that govern social interactions within family groups. By looking within this window, we can gain insights into noncultural factors that affect our own social behaviors.

Human behavior, while highly flexible, is not infinitely malleable. While agreeing that human behavior is strongly shaped by the cultural environment, I argue that humans also possess a set of biologically based predispositions for interacting with relatives, a biological heritage based on flexible decision rules that were adaptive during our long evolutionary history of living in extended family groups. It is these predispositions that I attempt to predict in this paper.

This view of family systems is very different from that adopted by many social scientists. The adaptive framework presented here in no way contradicts, but rather supplements, studies of the proximal and developmental mechanisms that influence the behavior of human family members. The adaptive and mechanistic viewpoints are not mutually exclusive. Rather they constitute paradigms reflecting different levels of analysis (106, 108). Each stands to benefit by incorporating elements of the other into its approach.

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