PARENTAL TREATMENT AND OFFSPRING DIFFERENTIATION: AN EVOLUTIONARY ANALYSIS

BY
JENNIFER NERISSA DAVIS, B.A.

A Thesis
Submitted to the School of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree
Doctor of Philosophy

McMaster University

Parental Treatment and Offspring Differentiation

DOCTOR OF PHILOSOPHY (1996)
(Psychology)

McMaster University
Hamilton, Ontario

TITLE: Parental Treatment And Offspring Differentiation:
An Evolutionary Analysis

AUTHOR: Jennifer Nerissa Davis, B.A. (Cornell University)

SUPERVISOR: Professor Martin Daly

NUMBER OF PAGES: x, 189

ABSTRACT

This thesis presents research on the nature of human kinship interactions, with special emphasis on birth order and its relationship to discriminative parental treatment of offspring and the development of within family differences. These issues are looked at through the lens of evolutionary psychology, a brief explanation of which is given in chapter 1. Chapter 2 is a theoretical and empirical critique of the applicability of a recent theoretical analysis of family relations in the animal kingdom in general to the specific case of human family relations. Chapters 3 and 4 focus specifically on birth order and parent-offspring relations, and their potential relationship to important life decisions, such as the age at which children leave home, and the amount of education they receive, among other things. Chapter 5 presents work on birth order, or rather, hatch order, and parent-offspring and sibling-sibling relations in a non-human animal, the herring gull, and serves to highlight the close integration of theory that exists between evolutionary psychology and animal behavior. The human and herring gull work represented here are both predicated on the same theoretical groundwork. The different ways in which these influences are played out is a function of the different ecology of these two species.

ACKNOWLEDGEMENTS

Thanks to all my committee members - to Rolphe for taking someone with a serious math phobia and teaching her not just how to do statistics, but to actually enjoy it, to Jim for allowing me to do my own thing with the herring gulls, and to Lisle for always being available when I needed you. Special thanks to Martin for always believing in me, even when I couldn't believe in myself. I actually made it! Thanks for all the support, for the patience and understanding, and for putting up with me all these years.

There are so many others to whom I am in debt - to Margo for always being willing to listen to my ideas and offer feedback and encouragement, to Erie, to everyone in the ever increasing Daly/Wilson lab, especially Joanna, to Steve for more than I could ever fit in this small space.

Most of all I wish to thank my father for having the good sense to raise me in the zoo. Not many parents would have been so enlightened. When I sought knowledge, you taught me; when I craved responsibility, you gave it to me; and when I was bored you handed me a clipboard, a pencil, and a watch. You taught me how to question things, and to always look for answers. This is for you.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Introduction

What is evolutionary psychology?

Evolutionary psychology is the study of behavioral adaptations, and the search for the hypothesized mental mechanisms that underlie them. The field of evolutionary psychology has arisen fairly recently, and draws heavily from the fields of animal behavior and behavioral ecology, which have achieved great success in increasing our understanding of the behavior of non-human animals. The basic tenet of all of these disciplines is that the mechanisms and processes that generate behavior have evolved by natural selection. This does not mean that everything an individual does has been selected for, or that even if a particular trait has been selected for, that the current expression of that trait confers some advantage on the individual expressing it. What it does mean, however, is that the behaviors expressed by individuals are expected to be a result of the interaction between their evolved psychologies and the environment in which they live. Environments may fluctuate, but mental mechanisms are likely, for the most part, to be species typical. Students of evolutionary psychology attempt to map these mechanisms and they may do so both by examining the universality of aspects of behavior across environments and by examining the ways in which a given behavior varies across them as well.

A consideration of human nature as the product of evolution provides a theoretical basis from which to make predictions about the nature of human psychology. To the extent to which we can know the probable selective forces that shaped the evolution of our species, we can also make predictions about the ways in which these forces are likely to have shaped our psychology. Such informed hypotheses have proven fruitful in increasing our understanding of, for example, human cognition, mate choice and mate competition tactics, linguistic variation, and criminology (e.g. see Betzig et al., Barkow et al).

This thesis focuses on the area of kin interactions, on the ways in which current theory and knowledge concerning the evolution of family systems in the animal kingdom can further our knowledge of human kinship relations in general, and parent-offspring relations in particular. To that end, a brief description of basic theories behind the evolution of kin relations and parent-offspring interactions is perhaps warranted.

Kinship and Inclusive Fitness

Inclusive fitness theory was developed by W. D. Hamilton (1964) to explain the evolution of altruism. One of the greatest puzzles in the study of animal behavior had been how the evolution of seemingly altruistic behavior, that is, behavior that seems detrimental to an individual's own ability to produce offspring while instead aiding others, could be maintained in a population. From the standpoint of selectionist thinking, altruism should not have been able to evolve. What Hamilton showed was that such behavior could evolve if the beneficiaries of these altruistic acts were relatives. As relatives of a given degree they would have a specifiable probability of carrying the gene or gene complement coding for that altruistic behavior, and by assisting such relatives to survive an individual would enhance the chances that this helping gene would be passed on to future generations. Altruistic behavior is therefore predicted to be selected for as long as the cost (in terms of lost personal reproduction) to the altruist is less than the benefit to the individual being helped (in terms of increased reproduction) times the altruist's genetic relatedness to that individual. The total benefit to an individual or the "fitness" of the sum of its behaviors across its lifespan can be measured in terms of both the number of offspring that individual produces, and the number of offspring it helps its relatives to rear. This is known as inclusive fitness.

Individuals, then, may increase their fitness by helping their relatives, even if they incur some cost in doing so. Hamilton's inclusive fitness theory opened the door to studies of the existence of acts whose adaptive function resides in the benefit they bestow on relatives of the actor, and of further theoretical work regarding the parameters that affect when they will and will not be seen. Some of this work is presented and reviewed in chapter 2, which is an empirically and theoretically driven critique of an attempted application of these theories to the study of human family relations.

Parental investment theory and parent-offspring conflict.

Hamilton's inclusive fitness theory provides a guideline for studies of kinship relations in general. The remaining chapters of this thesis focus on one particular relationship: that of parents and offspring. There are additional theories particularly relevant to studies of this relationship. These are parental investment theory and parent-offspring conflict theory, both originally proposed by Robert Trivers (1972, 1974).

Parental investment can be defined as anything parents give to their offspring, i.e. time, energy, or resources, which benefit offspring at some cost to parents. It is, by definition, a limited resource. Within this finite resource pool, parents may be further limited in the ways in which they can divide it up. For example, food given to one child cannot be fed to another. Because of this constraint, parents are expected to have evolved ways of optimizing the distribution of their investment. In the case of humans, this involves decisions about the age at which to bear the first child, the length of subsequent interbirth intervals, and the number of children to have, as well as the amount and distribution of investment in each child. These decisions are not expected to be conscious, the use of the word decision is merely meant to imply that there exists some evolved algorithm or decision rule that affects the organism's, or in this case the parent's, behavior.

The variation in these factors between parents, and the relevant ecological parameters governing these parental decisions are poorly understood. This is unsurprising as parental investment is a notoriously difficult thing to measure. Still, work has been carried out on certain aspects of investment decisions, especially on the ways in which available investment is divided up among existing children. Previous research on step-parental treatment of children, differential treatment of children by sex of the child, and by birth order of the child is reviewed in chapters 2, 3, and 4.

Chapters 3 and 4 present empirical work on the relationship between birth order, sibship size and a variety of major life events based on a large national probability sample of Canadians surveyed by Statistics Canada in 1990 (Statistics Canada 1991). The results of this work are consistent with previously published studies that show that oldest children live at home longer, stay in school longer, and generally seem to follow a life course consistent with the hypothesis that they are striving for higher status. The analyses also show that sibship size is less relevant to the outcome of oldest children on these measures than it is to youngest children. The analyses are framed in the context of parental investment theory. Admittedly, while this theory has guided the research, the observed patterns of results are still consistent with other hypotheses that are not hinged on variations in parental investment between offspring. Further empirical work will be required to determine the most likely causes of these effects.

Part of their explanation is likely to lie in the fact that offspring are not merely passive recipients of the investment parents choose to give them. Offspring are expected, according to Trivers's parent-offspring conflict theory, to have their own agendas when it comes to the division of parental resources. Because parents are equally related to all their offspring, while children are more related to themselves than to their siblings, these two parties are expected, from an evolutionary perspective, to be somewhat at odds (Trivers 1974). Specifically, offspring should be selected to try to obtain more investment for themselves than parents are selected to want to give them. This difference leads to conflict between parents and offspring over the distribution of investment. The choices children make are as likely to be a result of their own optimal strategies and of the outcome of parent-offspring conflict as they are to be a result purely of parental decisions.

Chapter 5 presents analyses of the relationship between birth, or rather hatch order, and parental interactions and sibling interactions in the herring gull, a species in which parents have been shown to discriminate between offspring on the basis of laying order, prior to hatching. In herring gulls, the assumption has been made that once the eggs hatch, parents continue to discriminate against the last hatched chick (usually from the last laid egg). These assumptions have been based primarily on measures of mortality and growth of chicks. Little behavioral observation of parent-chick and chick-chick interactions has been carried out. Chapter 5 presents field data collected on these interactions which suggests that parental behavioral biases are not as extreme as has been assumed. Contrary to these assumptions, parents were not found to discriminate against the youngest chick, and this chick was in fact found to be more aggressive than its siblings. Inclusion of work on herring gulls serves to emphasize the continuity of this approach to psychology with the field of animal behavior. The same theories relevant to the explanation of birth order differences in human behavior are expected to be relevant to hatch order differences in the behavior of gulls as well.

References

Barkow, J., L. Cosmides, and J. Tooby. 1992. *The Adapted Mind.* Oxford University Press, Oxford.

Betzig, L., M, Borgerhoff Mulder, and P. Turke. 1988. *Human Reproductive Behavior.* Cambridge University Press, Cambridge.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. *J. Theoret. Biol.,* 7:1-52.

Statistics Canada. 1991. The 1990 general social survey cycle 5: family and friends. Public use microdata file, documentation, and user's guide

Trivers, R. L. 1972. Parental investment and sexual selection. In B Campbell (ed.), *Sexual Selection and the Descent of Man 1871-1971,* pp. 136-179. Aldine, Chicago.

Trivers, R. L. 1974. Parent-offspring conflict. *Amer. Zool.,* 14:249-264.

Women, power, reciprocity, and an evolutionary theory of the human family

submitted to the Quarterly Review of Biology

Jennifer Nerissa Davis
Martin Daly
Department of Psychology
McMaster University
Hamilton, Ontario, Canada

Abstract

Emlen's recent paper "An evolutionary theory of the family" provides an invaluable summary of existing theories about the nature of family systems and the reasons why they have evolved in certain animal species. Emlen's theoretical account leads him to propose 15 predictions about how family systems function cross-species, and he reviews evidence in their favor. While he suggests that these predictions should be applicable to the human case, he himself does not attempt to do so. The present paper extends Emlen's 15 predictions to the study of human family systems. Several aspects of the life history and ecology of *Homo sapiens* require changes to the predictions in order to make them applicable to humans. These considerations are 1) the complex nature of exchange and reciprocity in human society, 2) the theoretical implications of having dominant, post-reproductive helpers, and 3) the potential existence of status striving as a particularly powerful human drive. While some predictions require revision, we wish to emphasize that this does not constitute a refutation of the more basic theories from which they are derived. A revised set of predictions is presented.

Human social dynamics are exceedingly complex, governed by intricate systems of nepotism and reciprocal exchange. Many fields of inquiry, such as sociology, demography, anthropology, psychology, and economics, have made it their mandate to explain various aspects of these dynamics. Recent advances in the field of evolutionary biology offer the opportunity to gain additional insight into some of the forces governing human social systems.

The application of evolutionary theory to the study of human behavior is not new, and has already yielded novel information about the nature of the human animal in a variety of domains (e.g. see Betzig et al., 1988; Barkow et al. 1992). Recent theoretical and empirical research on the factors governing the stability of family systems, or systems in which multiple individuals cooperate in the rearing of young provides another source of information with the potential to further elucidate the mechanisms governing human family dynamics. This research is based on a cost-benefit analysis of alternative choices available to an individual at a given time, as measured in units of inclusive fitness.

Both ecological constraints theory and reproductive skew theory, depend on Hamilton's inclusive fitness theory as a starting point to explain 1) when individuals are expected to stay and help rather than disperse and attempt independent reproduction, and 2) the degree of conflict that should be exhibited over the division of reproduction between members of a group. Basically, an individual is expected to stay put and assist in the rearing of others' offspring when the inclusive fitness gains of such a strategy outweigh the gains to be had by attempting to disperse. Such a situation is most likely to arise when there are severe ecological constraints on an individual's ability to survive alone, or to find a suitable habitat in which to breed, thus lowering the expected number of offspring produced by dispersers to a very low level. This is known as ecological constraints or benefits of philopatry (e.g. Emlen, 1982 a and b; Emlen, 1991; Stacey and Ligon, 1991; Koenig et al., 1992).

Skew theory concerns the division of reproduction within an established group (e.g., Emlen and Vehrencamp, 1983; Vehrencamp, 1983 a and b; Reeve and Ratnieks, 1993; Keller and Reeve, 1994). Dominant members of a group may share reproduction with subordinates if doing so will either prevent the subordinates from dispersing or reduce the competition between the dominant and subordinate for reproductive status. Again, the existence of this sharing and the degree to which it occurs are governed by the inclusive fitness payoffs to the dominant of giving up more or less reproduction, which in turn are governed by the strategies of subordinates. These strategies are in turn governed by the fitness payoffs to the subordinate of staying versus dispersing versus fighting for reproductive rights.

Inasmuch as these theories represent attempts to model general selection pressures governing the cohesion of social groups, they provide an obvious starting point for attempts to understand the evolution of family systems, including those of humans. The basics of this approach have already been articulated in "An evolutionary theory of the family" (Emlen, 1995) as a "general evolutionary framework for understanding biological families." This conceptual framework is built on ecological constraints theory, inclusive fitness theory, and reproductive skew theory, from which Emlen (1995) derives 15 predictions (see Table 1) about family living which he claims "should generalize across all taxa, to all species that live in family groups, including humans " (p. 8092).

Although Emlen proposed that his theory should apply to the human animal, he did not, himself, test his predictions against human data. The present study represents an attempt to do so. In the case of humans, certain aspects of their life history and ecology at least potentially affect the applicability of these predictions in their stated form. As our goal is to apply them specifically to *Homo sapiens*, it is important to consider known aspects of the natural history of the human animal in evaluating the evidence. Even if the specific predictions are not upheld, an examination of the ways in which the evidence deviates from them and how these deviations relate back to the theories underlying the conceptual framework upon which the predictions are built may suggest ways in which those predictions can be reformulated to better fit the human case. The evidence reviewed below suggests that while many of the predictions made regarding aspects of family dynamics and structure are upheld at least in part, the human case does deviate significantly from the predicted pattern of family formation.

Stephen Emlen, with a distinguished career in the study of the behavioral ecology of birds, draws most of his examples from avian systems. Among cooperatively breeding birds, males are generally the more philopatric sex, and thus more likely to be helpers (Emlen et al., 1986). Evidence about human social and family systems, however, indicates that in *Homo sapiens*, females, not males, assume greater responsibility for the maintenance of social ties and the provisioning of social support both within the family and with friends. This is true in the modern West (Oliveri and Reiss, 1987; House et al., 1988; Salmon and Daly, in press), where actual exchange of support is more likely to flow between families related through females than through male lines (Mutran, 1985; Chatters et al., 1986; Hogan and Eggebeen, 1995), as well as in hunter-gatherer societies (van den Berghe 1979). Hunter-gatherers, who live in conditions closest to those that existed during much of our evolutionary past, appear to be bilineal with stronger matrilineal ties. Therefore, in considering the evidence pertaining to the application of Emlen's predictions to humans, we shall place special emphasis on the potential role of women as helpers. Of course this does not mean that men never fulfill this role. Rather than ignore the potential of males as helpers, we have attempted to include data about family relations for both sexes where possible.

The evidence we present about the nature of human families is drawn from a wide variety of sources, from detailed ethnographic accounts of particular societies to cross-cultural analyses of patterns of behavior to demographic data from modern Western cultures. Each of these sources of evidence has its place, in turn, in the analysis of the evolved nature of human family relations. Ethnographic accounts and cross-cultural data serve primarily to provide us with some idea about the flexibility of human behavioral strategies across different ecological and social contexts. Such comparisons may be made between individuals within a culture, or between cultures. In the case of cross-cultural analyses it is important to keep in mind that the organism under study is a single species, and therefore the range of variation seen in behavior represents the flexibility of the adaptations governing it. It does not represent separate adaptations. Studies of modern Western human behavior can also provide insights about the nature of behavioral adaptations. Even when such behavior is divorced from predictions based on fitness calculations, the ways in which the behavior departs from theoretical expectations can prove valuable in elucidating the selective processes underlying the alleged adaptations. In truth this distinction is no different from the way behavioral ecologists study many non-human animals (e.g. see Semel et al., 1988).

A search for the forces governing family relations is a search for the psychological adaptations underlying these behaviors. These adaptations evolved over time in an environment very different from the one in which we live today. Studies of modern day hunter gatherers are likely to yield insight into the way human adaptations functioned in ancestral environments, but present day tribal societies are highly variable and generally live in marginal habitats. Studies of people in more technologically complex societies in general, and in the modern West in particular, must consider the possibility that social relations are significantly different from the environments of selection.

Even if we have gained the technical expertise to recreate our environments to suit our desires, the environment we create for ourselves is still the product of our evolved psychology, of the things we have been selected over time to crave, to strive for, and to enjoy. Knowledge of how things break down and what aspects of environment are related to the function of these psychological mechanisms can be quite useful in discovering the nature of an adaptation. Studies of modern human behavior, therefore, can be illuminative in the search to understand our adapted psychology.

Definition of a Family

Any theory of the family must start with a definition. Emlen (1995) defines a family as an assemblage of relatives who interact regularly but do not necessarily co-reside (although they typically do so). The possible absence of co-residency or spatial boundaries in defining families means that for humans, regular family interaction might include all forms of communication including letters, phone calls, email and faxes as well as face to face contact. To avoid possible confusion we have considered data from both perspectives wherever possible, that is with families defined by co-residence and by simple maintenance of contact.

Emlen's discussion and most of his predictions deal specifically with situations in which offspring who are old enough to reproduce remain celibate on their parents' territory and assist in rearing siblings. This is a common scenario in non-human species with helpers, but it is not the only type of family found. Emlen's predictions can easily be extended to other degrees of relatives, and he certainly means them to be extendible in this manner. Similarly, in humans parent offspring relationships are not the only family ties, though they are certainly central to family interaction. Wherever data on extended family relations are available we have attempted to include them in our discussion of the predictions. In practice, however, it is the data on parent-offspring interaction that are the most numerous. We wish to be clear that this bias in the data we present is a function of the relative availability of information, not of a lack of interest in extended family relations and we certainly do not wish to give the impression that extended families are irrelevant or unimportant to the development of this line of research.

Co-residency among relatives

Since families have been defined as groups of individuals that either co-reside or remain in contact, it is important to know what sorts of opportunities exist for the maintenance of such contact in humans. In a cross-cultural analysis of adolescence, Schlegel and Barry (1991) have quantified relevant data about the general nature of human co-residency patterns, at least with reference to the parent-offspring relationship. Their analyses show that in many cultures children continue to reside with their parents after puberty, but this pattern is far from universal. For girls, at least, there is typically a 2 year period of adolescent subfertility after menarche. Therefore, unless marriage (used as a proxy for the start of reproduction) is delayed for at least 3 years, women residing at home after puberty are not necessarily capable of reproduction. In 112 of 178 societies (63%), women typically married within 2 years of reaching puberty, and in most of the remainder they married within 5. Thus, families in which offspring linger on parental property beyond the age of maturity are infrequent or even absent in the majority of human societies, at least as regards daughters, and is particularly absent in pre-industrial, face-to-face societies like those in which the human psyche evolved and to which it is presumably adapted. The residency patterns of pubescent boys are more variable and whether a boy remains at home or disperses before marriage is more dependent on the mating system of a culture. The trend seems to be towards slightly longer co-residence with parents, though the difference is not great (Schlegel and Barry, 1991; Davis, in prep.).

Traditional societies with early marriage are usually either matrilocal or patrilocal, however, so even if marriage means the beginning of a reproductive career, it does not necessarily imply emigration from the parental community. By the criterion of regular interaction into adulthood, human beings in all societies seem to be intensely familial. Still, we wish to emphasize that continued residence in the parental community does not typically mean continued residence in the parental home. The modern Western practice of prolonged pre-marital residence in the parental home is certainly not species-typical.

Nor does continued residence in the parental community, even in matrilocal societies, imply reproductive competition between mother and daughter. Indeed, human cooperative ingenuity is such that the reproduction of both mother and daughter is likely to be facilitated by their continuing proximity. Staying with kin does not necessarily mean fewer resources and reduced reproductive opportunity per capita. Quite the contrary, kin alliances may well enhance an individual's power and material and social success. The possibility that reproductive opportunity might increase acceleratingly as group size increases has been considered in birds (Koenig et al., 1992), and may play a significant role in human family dynamics.

Dominance and care-giving

Another point bearing on the relevance of Emlen's predictions to the human case concerns the direction of care-giving within a family. Human females are unusual, perhaps unique among mammals, in that they undergo reproductive senescence (menopause) well in advance of other body systems. Even in traditional societies a woman's reproductive career ends by the time she is 45, yet she may continue to survive for an additional 15 or 25 years (Hill & Hurtado, 1991). There is an extended period of time in which mothers are incapable of continuing their own reproduction and may have no option but to assume the role of helper themselves, should they continue to take on a family role. In fact, the predominant theory of the function of menopause is based on the assumption that post-menopausal women become helpers (e.g. Williams, 1957; Hamilton, 1966; Alexander, 1974), though there are others (Hill & Hurtado, 1991).

Emlen's 15 predictions are based on comparative evidence from non-human species and several of them follow from assumptions that 1) breeders are dominant to helpers, and 2) helpers have the option of breeding independently, even if their likelihood of success is very small. If it is assumed that parents remain socially dominant to their offspring throughout life, the first assumption is violated when post-menopausal women provide care to the families of their adult children. The second assumption does not apply to this situation either, as post-menopausal women do not have the option of independent reproduction.

These considerations may have a substantial effect on the cost-benefit structure of dispersal and competition within family groups, as will be explained later. While it might be argued that these things are relevant only to discussions of human parent-offspring relationships, we do not believe this to be the case. If parents do act as helpers to their reproductively mature offspring, the existence of such a helper will affect the cost-benefit analyses of both providing help to and receiving help from other relatives. Specifically, it may lower the benefits of receiving help from additional family members in the domains in which help is received from parents. The decision rules governing helping behaviors are not expected to change, but the threshold for helping, and thus the variability of helping responses seen, may well be altered.

This is not to say that the helper-breeder role in human families always exhibits this reversal from the typical non-human case. In some human societies pre-reproductive children contribute significantly to family subsistence or assist in caring for younger siblings (Weisner, 1982; Turke, 1988; Schlegel and Barry, 1991; Seginer, 1992), and may even suffer a decrease in their personal reproduction because of it (Turke 1988). This does not seem to hold for modern Western society, however (Spitze and Ward, 1995). Although children who serve as helpers to parents are subordinate to them (Schlegel and Barry, 1991), this situation fails to fit the assumptions of the theories on which Emlen bases his predictions because the pre-pubertal and circum-pubertal children who help do not have the option of independent reproduction. One implicit assumption of the proposed general model of family systems is that the dependent life stage in which one consumes rather than produces familial resources is followed immediately by a lifestage of reproductive maturity, or in other words that personal reproduction and nepotistic assistance of reproducing relatives become available as alternatives at one and the same life stage, as in seasonally breeding birds who might either help or reproduce at one year of age. Nepotistic investment in younger siblings is an option that is available to human beings well before sexual maturity, however, and this is not unique to humans. A similar situation has been demonstrated in some cooperatively breeding fish (Taborsky, 1994).

Of course, human males are capable of continued reproduction throughout life, though their fertility does decline somewhat with advanced age. As previously noted, however, men do not seem to engage in as much familial support or provide such assistance to nearly the same degree as do women. So while the possibility that some predictions may hold more for men than for women exists, we think it unlikely. In any case, if this is truly a general model, the predictions should hold for both sexes. Although we focus primarily on helping and reproduction on the part of women, whenever possible we have included data about both male and female family relationships. For the most part, except where differences have explicitly been predicted by Emlen, we have found no sex differences.

The Predictions

With these things in mind, discussion will now turn to the individual predictions. The evidence for each will be considered in turn, followed by a general discussion of the relevance of the predictions, as stated, to human family systems. The order of the predictions will be the same as Emlen's. He broke them down into three sections: family formation and stability, family dynamics, and family structure.

Family Formation and Stability

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.

This prediction stems from Emlen's view of family formation as a "'solution to the temporary problem of a shortage of acceptable reproductive opportunities." This view, in turn, is derived from the ecological constraints and benefits of philopatry theories of delayed dispersal (see: Emlen, 1982 a and b; Emlen, 1991; Stacey and Ligon, 1991; Koenig et al., 1992). Although it is not obvious from the prediction itself, these models place strong emphasis on the effect of environmental factors on breeding opportunities. The relevant factors that have been identified in non-human animals are availability of appropriate breeding territories and food supply. Are these factors related to delayed dispersal in humans as well?

Although it is not a direct answer to this question, Low's (1989) analysis of the effects of a variety of ecological factors on group size suggests that such factors are not important determinants of cross-cultural variation in familial cohesion and dispersal. Group density increases with average moisture and decreases with extremely cold climate, but Low found no significant relationships between group size and extremes of heat, cold, dryness, wetness, range of variation in temperature, or predictability, constancy, contingency, or coefficient of variation of rainfall. In other words, there was no correlation between group size and any of the ecological variables she measured, nor was there any correlation between pathogen pressure, starvation risk or protein deficiency and group size.

Low's (1989) conclusion from this analysis is that humans, with their complex network of direct and indirect reciprocity and sophisticated ways of modifying environmental conditions, appear not to be limited by the extremes of environmental variation in the same way as other species. This suggests the possibility that traditionally studied ecological parameters (i.e. territory and food availability) are less relevant to the reasons for aggregation and familial cohesion in humans than in other species. Alexander (e.g. 1990) has developed this argument more fully. He argues that social environmental factors have been of greater selective relevance in the evolution of human sociality than physical factors, and that the evolution of the complex human social system was a response to between group competition leading to increasing levels of family and clan group solidarity. The potential effect of social factors on human group size at least warrants further study. Why is this relevant to the prediction? If Alexander is correct, and humans have been the predominant environmental force acting on their own evolution, then it is unlikely that ecological constraints are ever such as to truly favor dispersal. Familial affiliation or cooperation may be a human universal, not a result of temporary shortages. The opportunities for breeding within one's familial group or dispersing to another group may or may not be limited, but the degree of reproductive skew within a group is addressed in later predictions. Prediction 1 is specifically concerned with whether or not these groups exist. Our point is merely that it is possible, even likely, that humans are obligately, not facultatively, familial.

Regardless of whether this suggestion is correct, Emlen's first prediction is that families are inherently unstable, dependent on the available reproductive opportunities for mature offspring. This is what we will consider. How is the applicability of this claim to the human case affected by the two earlier observations that a) helpers may not always be capable of independent breeding, and b) helpers may not always be subordinate to breeders?

Obviously, helpers who are not capable of independent reproduction should not cease to help simply because a breeding vacancy arises. Yes, they are likely to face decisions about whether or not to help and how much, but these considerations do not necessarily lead to the prediction that family groupings will be inherently unstable. An individual incapable of reproduction ought to benefit by helping to rear relatives regardless of the number of available breeding vacancies. Where this proposition might be violated, however, and Emlen's expectation of a helping response that is inverse to the perceived availability of breeding opportunities might be upheld, is if the prepubertal potential helper's chance of attaining breeding status were diminished in proportion to the amount of help presently provided. There is some evidence that in humans this may be the case, at least in some circumstances (Turke 1988). In the case of post-reproductive helpers, like menopausal women, who have no future personal reproduction, consideration of future breeding opportunities is meaningless, and they ought to provide help regardless of ecological conditions. Again, this strengthens the notion that humans are likely to be an obligately familial species.

The fact that a non-reproductive human helper is not necessarily subordinate is less damaging to this prediction. In fact, it should not affect the prediction at all. Helpers, be they dominant or subordinate, may still be less likely to help as the number of acceptable breeding opportunities increases. However, insofar as dominant helpers are mature women whose own fertility is declining, the previous point applies: reproductive opportunities are of scant and fleeting value, and hence of little appeal.

Thus far, we have been considering potential reasons to doubt that Emlen's first prediction can be applied straightforwardly to the human case. But what is the empirical fact of the matter? Does human behavior conform to the prediction? The General Social Survey by Statistics Canada contains a number of questions about respondents' relations with family members, and we have analyzed people's responses with respect to this question.

Emlen's prediction is that families, defined mainly by the persistence of regular interaction among related adults such as parents and adult offspring, will form when available breeding opportunities are scarce and dissolve as acceptable ones become available. Using Canada's General Social Survey, we can examine the relationship between marital status and the frequency of contact (by letter, phone, and actual visits) between respondents and their parents, grandparents, and siblings. Following Emlen's prediction, married respondents, i.e. those who have found and moved into a potential "breeding vacancy," should maintain less contact with their natal families than same-age respondents who remain unmarried. As Emlen's definition of the family was ambiguous as to whether it refers to continued contact or only co-residence, we have also performed analyses of the residence patterns of married and unmarried respondents. If a family is defined by co-residence, then married respondents should be less likely to live with their parents than un-married respondents.

Of course, the rationale for these analyses assumes that offspring are the helpers in these relationships, which, as we have previously noted, is not necessarily the case.

Methods

The General Social Survey (GSS) cycle 5 on Family and Friends was a telephone survey carried out in 1990 (Statistics Canada 1991). It was conducted on a stratified random sample of all persons 15 years or older living in Canada except for residents of the Yukon and Northwest Territories and full-time residents of institutions. The survey also had a supplementary sample of the elderly and Ontario residents. The survey had a 75% response rate, and data were obtained from 13,495 households. Further details about the content of and sampling procedure used in the survey are available from Statistics Canada (1991).

For the present analyses respondents were divided into the following six age and sex categories: men age 15 to 24, 25 to 34, and 35 to 44, women age 15 to 24, 25 to 34, and 35 to 44. Thus each analysis was performed six times, once for each group.

χ^2 tests were performed to determine whether a relationship existed between marital status (never married vs. married or common-law) and frequency of contact with relatives. Formerly married but currently single respondents were not included in the analyses. Two different measures of contact were used: frequency with which that relative was actually seen and frequency of contact by letter or phone. Three different types of relatives were considered: parents (or mother if parents did not live together), grandparents, and siblings. Frequency of contact was coded into five levels: daily, at least once a week, at least once a month, less than once a month, and never. When an analysis reached significance, the χ^2 table was partitioned to determine where the significance actually lay.

Analyses of the frequency of contact were confined to respondents who had living relatives in the category under consideration, but did not currently reside with the relative in question. A second set of χ^2 tests was performed to examine the relationship between marital status and place of residence of the respondent (with mother vs. without mother).

Results/Discussion

If one defines a family group as co-residing individuals, then these groups do seem to break up in modern Canada as "breeding opportunities" become available. The analysis of the relationship between marital status and residence patterns was significant for all age groups for both men and women (N ranges from 746 to 1470, χ^2 ranges from 82.09 to 369.71, for all $df=1$ and $p<0.00001$). In all cases married respondents were significantly less likely to live with their parents than single respondents.

For the vast majority of respondents, however, contact with family members did not end with the cessation of co-residence. Among those not living at home, there was no clear relationship between maintenance of parental contact and marital status. In fact, the analyses suggest that for men, being married is associated with more frequent contact with parents (Fig. 1).

---Figure 1 about here---

There was no significant difference in amount of contact with parents on either measure for women of any age group. Married men age 15-24 and 25-34 visited with their parents significantly *more* often than single men (N=444, χ^2=25.54, df=4, $p< 0.00004$ and N=1108, χ^2=13.58, df=4, $p< 0.009$ respectively). There was also a significant difference between married and single men age 25-34 in the amount of contact they had with their parents by letter or phone; however, partitioning revealed no consistent trend of greater contact for one group or the other. There was no difference between married and single men age 35-44 for either measure of contact with their parents.

Of course, it is possible that single individuals living away from home had a specific reason for doing so. Perhaps they left because they didn't get along with their parents. There is a positive relationship between parent-child affection and both frequency of association and coresidence in the U.S. (Aquilino and Supple, 1991; Bengtson and Roberts, 1991). This, however, is an inappropriate argument to salvage the original prediction. Why didn't they get along with their parents? One might expect that family discord would be associated with the activation of the evolved psychological mechanisms that function to bring about family dissolution and that harmonious affect would be associated with the activation of those functioning to maintain cohesion. Such a possibility must be tested.

In contrast to the case of contact with parents, both single men and women, at least when younger, seem to have more contact with their grandparents than same-age married persons, although the results were not consistent across all analyses (Fig. 2). This is consistent with prediction 1. Presumably this contact does not represent pre-reproductive helping of senior kin who are still reproducing, however. On the contrary, this is evidence for the predicted role of grandparents as post-reproductive helpers.

---Figure 2 about here---

Single men kept in more frequent contact with their grandparents by both measures (15-25: visiting N=833, χ^2=18.53, df=4, $p<0.001$, letter/phone N=833, χ^2=14.68, df=4, $p<0.005$, 25-34: visiting N=590, χ^2= 13.17, df=4, $p<0.01$, letter/phone N=589, χ^2=13.11, df=4, $p<0.01$). However, in the case of contact by letter or phone for men between 25-34, single men were also more likely than married men not to be in contact at all (χ^2=5.948, df=1, $p<0.05$). The same pattern appeared for men age 15-24 in the frequency with which they visited grandparents (χ^2=4.59, df=1, $p<0.05$). Single women age 15-24 visited with their grandparents more and kept in more frequent contact with them by letter or phone than did married women (N=975 and 974, χ^2=29.22 and 29.57 respectively, df=1 and $p<0.00001$ for both). There was no difference between single and married women age 25-34 with respect to either type of contact. There were not enough respondents in the sample between the ages of 35 and 44 with living grandparents to carry out analyses for this group.

There seems to be no relationship between marital status and frequency of contact with siblings. Again, this is inconsistent with Emlen's prediction. With two exceptions, there were no significant differences between married and single men or women in the amount of contact they had with siblings. The first exception occurred for men age 15-24. Married men in this age group had more contact with their siblings than single men (N=697, χ^2=7.72, df=1, p<0.05) The second exception was for women age 25-34. Married women in this group had less contact with their siblings than single women (N=1554, χ^2=18.87, df=4, p<0.0008).

These results are consistent with previous work on patterns of giving. Eggebeen and Hogan (1990) looked at patterns of exchange in American families, and found, after partialling out effects of such variables as income and presence of children, that married persons exchanged goods and labor with their parents neither more nor less than single, separated, divorced, and widowed persons. Persons with young children, however, were much more involved in exchange with their parents, and were, as a group, the recipients of the largest amount of aid from them. This increase was primarily accounted for by child care. This suggests that the slight tendency we observed towards increase in contact with relatives for "mated" respondents might be even greater if we had limited our analyses to couples with children and not included childless married respondents.

Thus, some of the GSS analyses were consistent with prediction 1, but most were not. At best, this prediction only holds for some demographic groups with some types of relatives. These results, together with Eggebeen and Hogan's (1990) study of intergenerational giving, call into question the applicability of this prediction to at least modern Western society. There is no indication that mature offspring only remain in contact with parents and siblings until or unless they can assume reproductive status. On the contrary, the results reported by Eggebeen and Hogan (1990) support our notion of parents as post-reproductive helpers of their children, behavior which should be non-contingent on ecological circumstances. Of course, the relationship between ecological constraints and family stability in pre-technological cultures is still unknown. Still, on the basis of the theoretical arguments we have presented we suspect that this relationship will not hold within them either, that is, we are likely to be an obligately familial species.

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.

According to ecological constraints and benefit of philopatry models, an available breeding vacancy should only be acceptable if its expected payoff is at least as high as the payoff an individual expects to receive by remaining at home. Emlen argues that those reared in high quality environments should therefore be more choosy than those from low quality natal environments. For humans, then, we would expect to find that wealthy and powerful families are more stable than impoverished ones.

If a helper is not capable of independent breeding, there is little reason to expect it to make its help contingent on the economic circumstances of its natal family. Unless helping influences the likelihood of acquiring a breeding opportunity, a helper ought to benefit by helping to rear relatives regardless of the quality of the available breeding vacancies. In the case of post-reproductive helpers, help should once again not be influenced by ecological circumstances.

Appropriate consideration of the applicability of prediction 2 to humans hinges on what exactly is meant by a stable family, whether helpers on resource rich territories have an increased chance of being able to bud off a piece of it for themselves, and if so, whether the resulting circumstance of several groups of related individuals breeding in the same area, but on separate territories, would still be called a family. If stable families are considered to only be those that are co-resident, i.e. on the same territory, then available evidence indicates that the prediction is not borne out.

In a review of parent-offspring co-residence, White (1994) reports that children in families with more resources are less likely to live at home, and less likely to return once they have left. Schlegel and Barry (1991) also present evidence bearing on this question. In their cross-cultural study of adolescence they include an analysis of the factors affecting age at marriage. For lack of a more precise available measure we will use marriage as a rough indicator of the cessation of co-residence. Across cultures, marriage is often under the control of kin. Males are described as free to make their own decisions about whom to marry in only 18% of 141 cultures surveyed, and females in only 13% of 131.

Early marriage of daughters was found to be most common in societies with bride service or bridewealth. This pattern is to the advantage of parents of daughters as it brings goods or labor into the household. In dowry giving societies, on the other hand, marriage tends to be late. There are several exceptions to this rule, however, and it is Schlegel and Barry's (1991) analysis of these exceptions that provides the strongest evidence against prediction 2.

In India, ancient Rome, and pre-industrial Europe, all dowry giving societies, age at marriage varied according to parental status. High status families married off their daughters at an early age, while low status families married them off late, an opposite pattern to that which Emlen predicts. Schlegel and Barry (1991) argue that from an economic standpoint it is to the advantage of a family of limited means to delay the marriage of a daughter in dowry giving societies. With her marriage the family will lose not only part of its wealth but also her labor. In a wealthy family, on the other hand, female domestic labor is augmented by that of slaves and servants. The family has adequate resources for a dowry, and furthermore can use those resources to 'buy' a son-in-law that improves the family's own social position. When daughters can function as social capital there is no advantage to delaying marriage. Schlegel and Barry (1991) focus on marriage as a form of economic exchange which is manipulated to the benefit of the people (usually parents) who arrange it.

Schlegel and Barry's (1991) account suggests that in societies where children provide labor and/or where it is expensive to marry them off, their dispersal could affect the "territory quality" of their parents. If marriage transactions are manipulated to improve social standing this would also have an effect on prediction 2. Instead of high status children leaving later because they have higher standards for what constitutes a suitable opportunity, low status children may wind up marrying later because their departure significantly decreases the resource capital of their parents.

The available evidence is more in line with Emlen's prediction if stable families are instead defined as families in which individuals maintain contact with each other in adulthood. Studies of the relationship between socioeconomic status (SES) and various measures of family relations in modern Western cultures show a consistent pattern of stronger ties in high SES families. Taylor (1986) found, in a study of black Americans, that those with lower incomes were less likely to receive support from their families. Evidence also exists that people with lower education and family income are less likely to receive social support from their adult siblings (White and Reidmann, 1992). Similarly, Eggebeen and Hogan (1990) found that high SES is associated with greater intergenerational exchange within families in the U.S.

All of these studies, however, simply measure the existence of support or exchange. None provide evidence about the frequency of it, but again we can use data from Canada's General Social Survey to test the hypothesis that the frequency (not merely the existence) of contact with kin is greater in wealthier families.

Method

These analyses used the same data set used to test prediction 1, and each analysis was conducted separately for the same six age and sex combinations of respondents as before. Frequency of contact was coded as before. Analyses were run on the relationship between the respondent's total annual household income and frequency of face to face contact and contact by letter or phone with parents, grand-parents, and siblings respectively. Total annual household income was divided into four groups: $0 to $19,999, $20,000 to $39,999, $40,000 to $59,999, and $60,000 and up. All analyses were χ^2.

Each analysis yielded a 4x5 contingency table, so when one reached significance it was necessary to partition it to determine where the significant differences lay and whether they were along dimensions relevant to the hypothesis being tested. Each significant analysis was partitioned in the following manner: Income groups were combined to yield two groups, those that earned less than $40,000 a year, and those that earned $40,000 or more. This allowed us to see if the existing trend was consistent with our prediction and be certain that, for example, the observed significance was not due to the wealthiest and poorest families both engaging in more contact than middle income families. The next partitioning tested whether they kept in any contact with relatives at all. The final partitioning looked only at those respondents who kept in at least some contact with the relevant family member and tested whether respondents in one of the two income groups were more likely to maintain daily contact than the other.

Results/Discussion

Although not all analyses and partitions were significant, all showed the same pattern. All trends showed that wealthy respondents were more likely to maintain some sort of contact than poor respondents, a result consistent with previous studies on familial social ties and exchange. However, among those who did maintain contact with their families, poor respondents were in more frequent contact with family members than wealthy ones. So, while respondents with low household incomes did seem to be more likely not to maintain contact with their families, they were also more likely to be in frequent contact than those with high incomes (Fig. 3).

—Figure 3 about here—

For male respondents between the ages of 15 and 24, there was no significant relationship between income and frequency of face to face contact with parents, grandparents, or siblings, nor was there any effect of income on frequency of contact with parents by letter or phone . There was a significant relationship between income and frequency of contact by letter or phone with grandparents (N=541, χ^2=40.63, df=12, p<0.00006) and with siblings (N=438, χ^2=27.30, df=12, p<0.007) for this group. Although respondents in the low income group were more likely not to be in contact with their grandparents at all (χ^2=14.85, df=1, p<0.05), this was not true for siblings. Among respondents who maintained at least *some* contact, those in the low income group were significantly more likely to be in *daily* contact while those in the high income group were significantly more likely to be in less frequent contact (grandparents: χ^2=6.98, df=1, p<0.05; siblings: χ^2=9.15, df=1, p<0.05). There were no significant relationships between income and frequency of contact for any of the analyses carried out for female respondents between the ages of 15 and 24.

For males age 25-34 there was no effect of income group on the frequency of contact by letter or phone with parents or the frequency of face to face contact with grandparents. There was a significant relationship between income and frequency of face to face contact with parents (N=987, χ^2=23.48, df=12, $p<0.02$), contact by letter or phone with grandparents (N=570, χ^2=30.51, df=12, $p<0.002$), and both types of contact with siblings (visits: N=1131, χ^2=37.11, df=12, $p<0.0002$; letter and phone: N=1131, χ^2=39.35, df=12, $p<0.00009$). There was no significant difference between income groups in the likelihood of maintaining at least some contact in any of these four analyses. In all cases, however, the trend was for respondents in the low income group to be less likely to maintain contact. For three of the four analyses, face to face contact with parents and both types of contact with siblings, respondents in the low income group were more likely to be in *daily* contact with their relatives (parents: χ^2=9.11, df=1, $p<0.05$; visits with siblings: χ^2=14.00, df=1, $p<0.05$; letter/phone with siblings: χ^2=8.60, df=1, $p<0.05$). The grandparental contact analysis, while failing to reach significance, showed the same trend.

Analyses of frequency of contact data for females age 25-34 showed a pattern similar to the male results. The analyses of frequency of contact with grandparents failed to reach significance. The relationship between income and frequency of contact was significant for parents and siblings for both types of contact (visits with parents: N=1236, χ^2=32.85, df=12, $p<0.001$; letter/phone with parents: N=1234, χ^2=30.24, df=12, $p<0.003$; visits with siblings: N=1344, χ^2=44.51, df=12, $p<0.00001$; letter/phone with siblings: N=1343, χ^2=35.95, df=12, $p<0.0003$). Respondents in the high income group were significantly more likely to maintain at least some contact with their parents by letter or phone than low income respondents ($\chi^2=8.46$, df=1, $p<0.05$), and analyses for sibling and grandparental contact were in a similar direction but nonsignificant. All four analyses showed that respondents in the low income group were significantly more likely to be in *daily* contact with their relatives than high income respondents (visits with parents: $\chi^2=10.17$, df=1, $p<0.05$; letter/phone with parents: $\chi^2=5.82$, df=1, $p<0.05$; visits with siblings: $\chi^2=6.13$, df=1, $p<0.05$; letter/phone with siblings: $\chi^2=10.31$, df=1, $p<0.05$).

Analyses of male respondents between the ages of 35 and 44 showed a significant relationship between income and frequency of face to face contact with parents and siblings (parents: N=708, $\chi^2=38.03$, df=12, $p<0.0002$; siblings: N=850, $\chi^2=25.80$, df=1, $p<0.01$). Analyses of female respondents revealed a significant relationship between income and frequency of contact with parents by letter or phone and face to face contact with siblings (parents: N=677, $\chi^2=27.80$, df=12, $p<0.006$; siblings: N=812, $\chi^2=51.56$, df=12, $p<0.00001$). Analyses of frequency of contact with grandparents were not run on male or female respondents between the ages of 35 and 44 due to small sample sizes. Once again, for two of these significant analyses, wealthier respondents were more likely to keep in at least some contact with family than poorer respondents (parents for males: $\chi^2=4.92$, df=1, $p<0.05$; siblings for females: $\chi^2=10.11$, df=1, $p<0.05$). The remaining two showed the same trend. Once again all four also showed that poorer respondents were significantly more likely than wealthier respondents to be in *daily* contact with family (parents for males: $\chi^2=9.60$, df=1, $p<0.05$; siblings for males: $\chi^2=6.49$, df=1, $p<0.05$; parents for females: $\chi^2=3.78$, df=1, $p<0.05$; siblings for females: $\chi^2=21.71$, df=1, $p<0.05$).

What does this mean for the prediction that wealthy families should be more stable? Certainly, the available evidence indicates that wealthy families are more likely to maintain social ties at some level and to engage in exchange, but the present analyses also suggest that the strength of those ties may be weaker. Prediction 2 did not make an explicit distinction between these two outcomes, but it seems plausible that the strength, not just the existence of family ties would be an important determinant of family stability. It is thus still interesting to ask what could account for the observed relationship between income and frequency of contact.

One factor overlooked in the present analyses is the availability of support from family members. Individuals with low incomes may require more support, thus the greater frequency of contact among those who maintain contact. Since they are poorer, however, they may not always have family members with the capacity to provide support, thus the greater likelihood of not maintaining any contact. Individuals with high incomes, on the other hand, may be more likely to have family members capable of providing support, hence the greater likelihood of maintaining at least some contact, but those who need support may not need as much of it and so may maintain a lower frequency of contact.

To the extent that parental resources can finance dispersal, high resource holdings could make it easier for offspring to disperse, and disperse at an earlier age. Thus in its general form this prediction should perhaps be restricted to systems with non-partable resources.

To the extent that familial resources are non-partable in a given human society, then, prediction 2 may be expected to hold. That is, when offspring can take resources with them upon dispersal, then a high level of parental resources could lead to earlier dispersal than a low level, because families with more resources may be better able to finance dispersal.

Family Dynamics: Kinship and Cooperation

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

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

These predictions will be considered together. Both are derived from Hamilton's inclusive fitness theory (1964). Hamilton pointed out that individuals can contribute genetically to future generations by producing offspring of their own (direct fitness), and by assisting their relatives to do so (indirect fitness). Thus, because the fitness return is greater per unit of assistance, helpers are expected to preferentially help relatives over non-relatives, and close relatives over distant ones.

If a family is defined as a group composed of related individuals of widely varying ages who live together or maintain close contact over a long period of time, it is hard to think of what a 'comparable group of non-relatives' would be in this situation. We interpret the sheer difficulty of contemplating such a system as support for these predictions.

If, on the other hand, such comparable groups are broadly defined as individuals that interact with each other on a regular basis, even if all are in the same age category, then the opportunity for reciprocal exchange poses some potential problems for these predictions. Friendships and the existence of reciprocal alliances between unrelated individuals could affect the relationship between relatedness and assistance rearing offspring and render these predictions, as currently stated, false.

We can again use the Canadian GSS data to perform a preliminary test of the prediction that assistance in rearing offspring will always be more prominent in family groups against the hypothesis that assistance in rearing offspring will be dependent on the opportunity for reciprocal exchange. One of the questions in the survey was specifically concerned with the allocation of child care. We performed a χ^2 test using respondents living with children under the age of 13 versus respondents with no children living in their household who provided child care to either family or friends to test the question: when respondents provide child care, to whom are they more likely to provide it, family or friends?

Analysis revealed that respondents without children in their home are significantly more likely to provide child care to family, while respondents with children 12 and under in their home are more likely to provide it to friends (χ^2=339.57, df=1, n=3085, p<0.00001). Of course, this effect could be due to age differences between respondents and their relatives. Older respondents are less likely to have children of their own and less likely to have friends (who are presumably in the same age class) with children. Thus when they help they may have little option but to help relatives. To attempt to correct for this we also performed an analysis of the likelihood of providing child care to siblings (who are more likely to be close to the respondent in age) versus friends versus other relatives for respondents 40 years old or younger. Although the overall number of respondents who helped friends versus relatives was very evenly split (49.2% helped friends, 50.8% helped relatives), respondents without children were more likely to help siblings and other relatives than expected, and respondents with children were more likely to help friends ($\chi^2=61.82$, df=2, n=2193, p<0.00001, See Fig. 4). This provides good support for the notion of child care as a popular form of reciprocal exchange between friends, and potentially non-reciprocal exchange between relatives.

—Figure 4 about here—

Because the GSS only gathered data on child care about relatives related by r=0.5 (parents, children, and siblings), it is not possible to test the prediction about relatedness and assistance rearing offspring with this data set.

Predictions 3 and 4 seem reasonably robust with respect to human family systems, but given the intricate nature of exchange relationships between humans they could be rendered more accurate if they specified that assistance be non-reciprocal, or rather, that the amount of aid given without expecting compensation will be higher when the recipient is a relative, and higher still the more closely related that relative is. In practice this may be difficult to test given the complexity of reciprocity in human social systems (Trivers, 1971), although there is some evidence that men will permit unpaid labor reciprocity debts to build up more with brothers than with friends (Hames, 1988).

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.

It appears from Emlen's discussion that he intends the term "sexually related aggression" to refer primarily to competitive interactions between same-sex rivals and lesserly to violent or coercive heterosexual transactions. Although incest avoidance is not an absolute, in many species there exists a lack of sexual interest in opposite sex close relatives. This incest avoidance is thought to have evolved due to an increase in the frequency of homozygously deleterious recessive alleles that occurs when close relatives pair in normally outbreeding populations.

Again, it is difficult to envisage a comparable group of non-relatives, and again this may be considered support for Emlen's hypothesis. Of course, however, if the helper in such a system is not capable of reproduction then there should not be sexually related aggression regardless of the degree of relatedness between family members.

Emlen argues that inbreeding avoidance will result in "a reduced incidence of mate guarding and other forms of sexually related harassment and aggression within family groups." While we agree that aggression over sexual access to relatives is low, and that this prediction appears to be accurate with respect to humans, it should be pointed out that parental attempts to control the sexual behavior of children are not rare in humans. In a cross cultural analysis of adolescence, Schlegel and Barry (1991) found that the expected degree of subordination (obedience and deference) of both girls and boys to their parents was significantly positively related to both the ability of children to choose their own mates and the existence of economic marriage transactions (e.g. bridewealth, dowry). Parents in societies in which children did not choose their own mates and in which goods were exchanged at the time of marriage expected a significantly higher degree of subordination from adolescents. Although this pattern of control hardly counts as a failure to manifest incest avoidance, it is still noteworthy in that it underscores the notion that sexually related aggression of a different type does seem to exist in human societies.

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

The terms certainty of paternity and confidence of paternity have been used interchangeably in the sociobiological literature, with both terms encompassing two closely related concepts whose distinct meanings are obscured. One referent of these terms is a population parameter, which might better be called the probability of paternity (i.e. 1.0 minus the proportionate incidence of extrapair paternity). This parameter is invoked in modeling the evolution of species-typical male reproductive effort allocations, and in particular in addressing the evolutionary stability or instability of paternal care. The appropriate tests of prediction 6 under this interpretation are comparative, with paternal investment expected to be present or substantial in those species or populations in which paternal probability is high, and absent or relatively slight where it is lower. The second meaning of certainty of paternity is more literal: a psychological parameter varying between individuals within populations according to available cues of the paternity of particular young.

Evolution-minded students of human behavior have long been cognizant of the grounds for prediction 6, and it has inspired a number of cross-cultural analyses. The main issue of interest has been whether avuncular inheritance, the practice of passing a man's resources to his sister's sons or other matrilineal relatives rather than to his putative offspring, is associated with and motivated by paternity doubt. The idea antedates Darwin. Alexander (1974) rediscovered this hypothesis in a modern context, and subsequent studies have both strongly confirmed the association between the avunculate and threats to paternity and lent some support to the proposed mediation through male reluctance to invest in unrelated children (Kurland, 1979; Gaulin & Schlegel 1980; Flinn, 1981; Hartung, 1985).

At the level of modulated parental investment within a society, prediction 6 remains largely untested. A putative father has two principle sources of information about his likelihood of paternity: the phenotype of his putative offspring plus whatever sort of information he may have that bears on the probable fidelity of his mate. There is evidence that males of various species use mate fidelity cues as paternity cues, but there is apparently no evidence that any non-human animal uses offspring phenotype in this context. People, however, are clearly capable of this feat, and although systematic studies remain to be done, there is an abundance of anecdotal, ethnographic and folkloric evidence of phenotypic resemblance affecting human male investment decisions (Daly and Wilson, 1987).

Moreover, people exhibit strong patrilineal bias in their interest and claims about the familial resemblances of newborn babies, and the details of this bias are readily interpreted as indicating that people are concerned both to improve their own estimates of the likelihood that a putative father is correctly identified and to manipulate the beliefs of the father and other interested persons (Daly and Wilson, 1982; Regalski and Gaulin, 1993). Presumably this implies that paternity confidence or doubt is consequential.

Daly and Wilson (1987) suggested that paternal affection may have evolved to be more strongly influenced by resemblance to self than maternal affection because of paternal "uncertainty," and that this influence may still be manifest in adoptive parenthood despite the social father's knowing full well that he is not the child's genitor, but this hypothesis awaits a good test. Similarly, it is at least plausible that cues of paternity affect paternal affection in men who sincerely profess complete certainty that the children in question are their own. There is a venerable anthropological controversy about whether any recent human society had yet to discover the link between sex and reproduction, but there is no question that there are societies in which ideology and professed belief deny paternal descent. Interestingly, one of these societies, namely the Trobriand Islanders, provides one of the most intriguing suggestions of modulated patrilineal investment in relation to paternity cues. Although the Trobriand people explicitly denied patrilineal descent and ostensibly practiced strictly matrilineal inheritance, material goods were also bestowed on patrilateral relatives in ways apparently contingent on phenotypic resemblance (Daly and Wilson, 1987).

Although paternity certainty is not necessarily synonymous with consciously accessible beliefs, it is not necessarily independent thereof either. A sudden revelation of non-paternity, provided by the evolutionarily novel information source of genetic testing, can at least occasionally demolish paternal affection in one fell swoop (Daly and Wilson, 1987). How verbally transmitted and other sorts of more direct information are integrated with motives and emotions in this sphere is a challenging question for the future. Nevertheless, the currently available evidence strongly supports the relevance of this prediction for humans.

Family Dynamics: Disruption after breeder loss or replacement

Prediction7. 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.

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.

In some polygynous societies sons indeed compete with fathers for sexual access to the fathers' junior wives (LeVine, 1961), but this has nothing in particular to do with mate replacement. A father's decision to take a young wife can enforce postponement of his son's marital prospects, especially in polygynous bride-price societies (e.g., LeVine, 1961), and such conflicts can indeed be severe, even lethal (Daly and

Wilson, 1988). In contradiction to the situation envisaged above, however, such competitive conflict is likely to be exacerbated by *scarce* familial resources rather than by their high quality, and more importantly, the "loss of a breeder" is not the precipitating circumstance. Once again we are reminded that the potential to use resources to finance offspring dispersal or reproduction may be an additional and important parameter beyond the sheer resource availability.

Nor is such competition sexually symmetrical. According to the widely accepted theory developed by Bateman (1948), Williams (1966), and Trivers (1972), sexual access to females is indeed a scarce resource limiting male fitness in animals where females make greater parental investment (or at least greater obligate parental investment) than males, but female fitness is not importantly constrained by sexual access to males. In light of this generalization, we interpret sexual access in these predictions as another way of again alluding to access to scarce "reproductive vacancies," and insofar as the latter concept is inapplicable to human family dynamics, so again are these predictions. In any event, the available evidence does not support these predictions in this case: mother-daughter competition for sexual access to the latter's stepfather is apparently rare and aberrant. A far more frequent scenario is the stepfather's imposition of unwanted sexual attention on the stepdaughter (e.g., Russell, 1984; Gordon, 1989).

In the human animal, one's entire reproductive career is affected to an unusual degree by mating decisions and reproduction in early adulthood, especially for women, and that may be one reason why predictions 7 and 8 do not quite seem to fit. A woman's early sexual and reproductive behavior can have crucial consequences for her capacity to make and maintain a good marriage later, and it is partly for this reason that it may seldom be to her advantage to "compete" for reproductive status with a still fertile mother while still residing with her. The degree to which such reputational and marital career constraints are evolutionary novelties versus longtime elements of human sociality will require consideration in any attempt to construct a fuller cost-benefit model of optimal sexual and reproductive decision making at different life stages.

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.

The first part of this prediction seems clearly applicable to the human case. Step-parental investment is indeed bestowed more reluctantly and in lesser amount than genetic parental investment, according to a wide range of direct and indirect evidence, and this difference is apparently cross-culturally universal (see Daly and Wilson, 1996).

It is also true that people murder stepchildren at very much higher rates than their genetic children (Daly and Wilson, 1988, 1994). However, it is unlikely that this represents a specifically infanticidal adaptation in the human case. Such homicide is nowhere typical. It is carried out too inefficiently to meet conventional criteria of an adaptation, often following from prolonged non-lethal abuse that actually raises the investment costs for the abuser. It has too high a cost in potential retribution (although it is admittedly difficult to assess what this cost might be in pre-modern non-state societies), and, contrary to the predominant adaptationist explanation for infanticide in other species as a sexually selected adaptation (e.g., Hausfater and Hrdy, 1984), it is more likely to end the homicidal stepfather's relationship with the mother than to hasten the next birth. Daly and Wilson (1995) argue that such homicides are rare nonadaptive byproducts of discriminative motivational mechanisms that for the most part function adaptively to keep step-parental affection and investment restrained.

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.

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.

The proposition that human stepfamilies will be relatively unstable appears to be true. Human stepchildren indeed leave the parental home at earlier ages than genetic children. Our own analysis, again using Canadian GSS data, of the age at which step-children versus genetic children leave home also supports this notion. We also agree that the conflicts leading to departure are ultimately founded in genetic self-interests and the various parties' opportunities for nepotism (Daly and Wilson, 1996). However, our own analyses did not support the prediction that boys with step-fathers leave significantly earlier than girls, and girls with step-mothers leave earlier than boys. In fact, step-sons leave earlier than step-daughters regardless of the sex of their step-parent (Fig. 5).

---Figure 5 about here---

Analysis was carried out on the age at which children left the respondent's home for respondents who had either step or genetic children, but not both. Only the oldest child from each family was included in the analysis. The independent variables included in the analysis were sex of the child, sex of the respondent, and parental status of the respondent. Results of a 3-way ANOVA showed significant main effects for all three variables (N=4287; parental status: F=34.203, p<0.001; sex of the child: F=17.864, p<0.001; sex of the parent: F=68.843, p<0.001), and a significant interaction effect between parental status and sex of the child (F=4.619, p<0.032). None of the other interaction effects were significant. Overall, step children left earlier than genetic children, but step-sons left earlier than step-daughters while genetic sons left later than genetic daughters. This pattern was the same regardless of sex of the responding parent.

This difference in the age of emigration for genetic versus stepchildren could reflect the child's own decreased inclination to be a helper, as Emlen seems to suggest, but it could also be the result of anticipated or actual diminution of received investment from stepparents. An additional GSS analysis showed no difference in the age at which step-children left home regardless of whether their younger siblings were half or full siblings. This analysis was run for step-children who were the oldest children in their family and who had either full or half siblings, but not both. Results of a two-way ANOVA on the age at which they left by sex of the step-child and type of sibling showed no significant effects (N=261, sex of child: F=1.934, p<0.166; type of sibling: F=0.938, p<0.334; interaction: F=1.218, p<0.271).

Human stepfamilies are also unstable in that the marriage partners themselves (the "established breeders" of Emlen's terminology) are relatively likely to separate, and whereas the marital duration specific likelihood of American divorce has been found to decrease with each additional child of the union (at least for the first few), and it increases with each child of former unions (Becker et al., 1977; White and Booth, 1985).

Family Structure: Reproductive sharing leads to extended families

Whereas the previous predictions focus on families in which only one pair bred, the final four deal with situations where there may be more than one pair of breeders. Of course, the line between what is relevant for simple versus extended families can be fuzzy, as the preceding predictions are still consistent with situations in which more than one couple within a family breeds. The following predictions are meant to deal explicitly with that situation, however. They are derived from reproductive skew theory (e.g., Emlen and Vehrencamp, 1983; Vehrencamp, 1983 a and b; Reeve and Ratnieks, 1993; Keller and Reeve, 1994). Emlen (1995, pp. 8096-8097) provides a concise and insightful summary of the theory and its assumptions:

> 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...
>
> 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 dominance between the potential cobreeders (the dominant and subordinate), and (iv) the genetic relatedness between them. 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," a share of reproduction.

It is in considering the application of the predictions based on reproductive skew theory to human family groups that the issues of helper dominance and the helper's capacity to reproduce become most important. If it is assumed that parents remain dominant to their children at least through late middle age, then the potential exists for post-menopausal women to act as non-reproductive, dominant helpers to their children. While this situation should have little if any impact on reproductive skew theory, it does have a significant effect on Emlen's predictions because as currently worded they assume, as do general discussions of skew theory, that dominants are reproductive.

Discussion of the remaining predictions is primarily theoretical, as we were unable to find many previous studies that bear on these predictions, and the GSS contains insufficient information to conduct novel analyses of them.

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.

Of course if dominants are *incapable* of independent reproduction, then it would be impossible for them to *share* their reproduction with anyone. Dominant non-breeders could, however, still exert control over the reproductive decisions of subordinates. As previously discussed, available evidence indicates that this is widespread across human societies. The extent to which dominants are able to exert such control may very well be determined by the subordinates' dispersal options. Although we could find no pre-existing analyses of this phenomenon, we suggest that a cross cultural analysis of the relationship between the potential for successful 'dispersal' (i.e. survival outside the family sphere) and who controls marriages would be one way to test this hypothesis.

Skew theory predicts that reproductive sharing occurs primarily at some intermediate level of severity of ecological constraints (Reeve and Ratnieks, 1993). If conditions are very good, and therefore the advantages of group living decrease greatly, the importance of subordinates to the inclusive fitness of dominants may disappear and dominants may favor the dispersal of subordinates. Again, this rationale assumes that dominants are capable of reproduction. As long as the reproductive control of dominants over subordinates is in the inclusive fitness interests of the non-breeding dominant, dispersal should not occur. However, the degree of control exerted should still decrease dramatically as the subordinate's options for dispersal increase. If there is the potential for multiple breeding pairs (e.g., if the dominant has several potentially reproductive offspring), the fitness interests of the dominant and subordinate may diverge, thus engendering conflict.

In the case of relationships within extended family systems between two or more individuals capable of reproduction this prediction should still hold as stated.

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

Once again assume that a family is composed of parents and grown offspring, particularly mothers and grown offspring. Even allowing for the possibility that asymmetry in dominance decreases as children age, it is unlikely that reproduction will become increasingly shared as mothers reach menopause. Again, however, maternal control over the reproductive decisions of children may decline as their dominance increases relative to their mother's.

An effect of dominance on increasingly shared reproduction has been found in at least one case with respect to sibling cobreeders. Polyandrously mated oldest brothers in Tibet share sexual access to their wife more equitably with their younger brothers when they are close in age (Crook and Crook, 1988).

In the case of relationships within extended family systems between two or more individuals capable of reproduction this prediction should still hold as stated.

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.

This prediction is based on the idea that because siblings are symmetrically related to each other's children (r=0.25) and parents and offspring are not, parents have more to gain by refusing to share reproduction than their offspring do in demanding it be shared (parents are related by r=0.25 to children's children while children are related by r=0.5 to their parents' children).

In the human case, reproduction probably is more equitably shared between siblings than between parents and offspring, but lesser sharing with parents is more likely to be due to the cessation of parental reproduction, not the suppression of offspring reproduction. That is, to the degree that there is parent-offspring reproductive competition in humans, children should garner a disproportionate share of reproduction, not parents.

Of course, in some societies where fathers continue to marry new wives and reproduce well into old age, this sort of reproductive competition could take place between them and their grown offspring. Some ethnographic evidence exists indicating that it does (LeVine, 1961; see also the discussion of predictions 7 and 8).

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.

Although it may seem counterintuitive, this prediction is based on the idea that the inclusive fitness benefits obtained by helpers will vary with the degree of genetic relatedness to the breeder. More distantly related helpers should require greater "staying incentives" in order to remain and assist.

Non-reproductive helpers, especially post-reproductive helpers, should not help unless they gain at least some inclusive fitness benefits, and then they should pattern their assistance so as to maximize those benefits. Reproduction would not be shared, and the provision of help would be greatest to those breeders to whom the helper is most closely related.

In the case of relationships within extended family systems between two or more individuals capable of reproduction this prediction should still hold as stated.

General Discussion

There are two possible intentions one could have regarding the application of these predictions to humans. These are two separate issues, though they frequently are confused. Extensions of Emlen's analysis to the human case could either be intended to predict current choices between reproductive and nepotistic investments or to explain why the human animal has evolved its particular life history in which, for example, nepotistic investment becomes an option before personal reproduction. The questions of why a behavior occurs now and why it evolved are different, separable levels of analysis (Emlen et al., 1990). The following discussion will assume that the predictions refer to expected patterns of current behavior, as this is what we are most interested in. Insofar as Emlen's intention was only to reconstruct aspects of the evolution of family systems, much of the following critique is admittedly less relevant. For example: the existence of pre-pubescent helpers could have evolved secondarily to initial conditions of solely post-reproductive aged helpers. Similarly, the assumption that the potential for successful dispersal exists and that reproductive opportunity decreases as group size increases would be valid in a discussion of possible origins of helping in humans, but not necessarily in a discussion of the current nature of family systems.

Available evidence and additional theoretical considerations render aspects of some of these predictions, as currently worded, inaccurate with respect to human family systems. We do not mean to imply they are not still useful, and certainly do not mean to imply that the theories from which the predictions were derived have been disconfirmed by these analyses. On the contrary, the theories upon which Emlen bases his predictions are invaluable to the understanding of this issue and we expect that the application of these theories to the peculiar circumstances of the human situation will increase our understanding of the factors governing human family relations. Moreover, the 15 predictions provide a useful and much needed starting point for those undertaking a study of the evolution of human family systems. They could be rendered more applicable, however, were they reformulated to take into account certain peculiar aspects of the human animal. Careful consideration of these features will not only make it easier to uncover relevant aspects of the social organization of non-human animals for the study of human behavior, but an understanding of human behavior will also help to refine our ability to apply the basic theories on which Emlen's predictions are built.

Some of the lack of fit between the available data and predictions is likely to be due to the complexity of reciprocal exchanges in human society. Certainly, predictions that specify greater assistance between relatives than non-relatives (3, 4) would be rendered more accurate if reformulated to specify greater degrees of non-reciprocated assistance instead of focusing on assistance in general.

The existence of menopause and the possibility that mothers who are no longer capable of reproduction act as helpers have obvious effects on the predictions about reproductive sharing (12 through 15). Dominant family members incapable of independent reproduction obviously cannot share it with others. This issue also has a more subtle effect on the predictions pertaining to family formation and stability (1 and 2). If helpers are dominant and incapable of reproduction, they are unlikely to be tempted to disperse, regardless of ecological conditions, as long as they can gain inclusive fitness benefits by helping. Subordinate breeders should remain as well, as long as the actions of the helper provide a net benefit to them. Of course dominant helpers, by virtue of being dominant, will have more latitude in the degree of help they provide than would subordinate helpers. The ideal amount of help for the helper may not be the breeder's ideal amount, but as long as it is better than nothing the family grouping should remain stable, regardless of whether there are acceptable reproductive opportunities elsewhere and regardless of the resource situation of the family. An increase in acceptable independent breeding opportunities will change the degree of influence the dominant helper has over the breeder, but it should have little effect on the stability of the family. In other words, the existence of post-reproductive family members as helpers should provide an unusually strong incentive not to disperse.

A detailed study of parent-adolescent conflict could be an interesting avenue for further exploration of intra-familial dominance relationships. When parents and adolescents argue, their conflict typically revolves around the adolescent's resistance to parental attempts to control his or her life (Montemeyor, 1983; Ellis-Schwabe and Thornburg, 1986). This is not as true for younger children. According to Turiel (1975, 1977), early adolescents consider certain social conventions to be largely arbitrary. They may defer to a conventional rule when it is convenient for them to do so, but still deny its legitimacy. While younger children agree that parents have the right to establish rules, by the age of 12 or 13 they begin to question the legitimacy of parental rule-making. Furthermore, the temporal pattern of this conflict has been shown to follow a distinct U-shaped pattern (Montemayor, 1983; Steinberg, 1989). Conflict increases with the onset of puberty and reaches a zenith at the apex of pubertal growth before declining. This holds at least for modern Western society, as marked parent-offspring conflict does not appear to be cross-culturally universal (Schlegel and Barry, 1991). Together these findings suggest that the onset of adolescence is a trigger for changes in dominance relations with parents. An increased understanding of these dominance relations and the factors leading to differences in cross-cultural expression of parent-adolescent conflict would be invaluable to a thorough understanding of the nature of human family systems.

So far the discussion has taken it for granted that mothers of adult offspring are post-reproductive. Why don't mothers share reproduction? Why do they undergo such early menopause? There is no definitive answer yet, although there are a few theories. One of the most common explanations is that by ceasing reproduction early and spending her remaining years assisting her existing offspring, a woman gains greater overall fitness benefits than she would if she were to keep reproducing. Hill and Hurtado (1991) have tested this hypothesis with data gathered from Ache hunter-gatherers, and found negligible support for it. Still, there is little support for any competing hypotheses they outline, and they suggest in their conclusion that the answer may well be a combination of factors. Leaving the adaptive significance of menopause as a still unanswered question, just because post-menopausal mothers are not reproducing doesn't mean they can't benefit by influencing the reproductive lives of their existing children.

Remember that parents are related to all their children equally (r=0.5), while each child is more closely related to itself (r=1.0) than to any non-identical full sibling (r=0.5) or half-sibling (r=0.25). It stands to reason that parents could increase their own net reproductive success by influencing that of their children, in the same way parents can gain by equalizing investment across all offspring (Trivers, 1974).

The major twist added by menopause, however, is a change in the dispersal probability of children. A post-reproductive mother, though she may not have the best interest of a *particular* child in mind, still has only one available means of increasing her reproductive success: increasing that of her existing relatives. Assuming she has the ability to do this, those relatives that stand to benefit, e.g. her children, ought to maintain ties with her throughout their lives. Thus, while predictions 12 - 15 can merely be slightly reworded, predictions 1 and 2, which deal with family stability, need to be reconsidered, and may be inapplicable to the human case as far as parent-offspring relations are concerned.

The lack of fit between expected and observed data for other predictions, and other aspects of these predictions (2, 7, 8, 12), is not so simple. There is, however, a noticeable pattern: the deviations by and large seem to be related to status, i.e. attempts to improve status or prevent loss of status. The idea that status striving is an evolved mechanism that helps to maximize the reproductive success (RS) of individuals in social species is not new. In general, the correlation between status and RS in non-human animals is good, though not perfect (Dewsbury, 1982). High ranking individuals tend to achieve greater copulatory success and leave more offspring (see Dewsbury, 1982; Fedigan, 1983 for reviews). The problem, and a source of much debate among those who study the evolution of human behavior, is that this relationship doesn't always hold for humans (see *Ethology and Sociobiology* 1990, num. 4/5).

The explanation for this dissociation may lie in the reasonable assumption that people (or other species) are unlikely to achieve maximal RS by consciously trying to do so. Instead such ends are achieved through the development of adaptations that track more easily determined things that have been reliably correlated with high RS. Status seeking is a good candidate for such an adaptation. Both non-human and some human evidence suggest that status seeking is likely to have been a good proximate mechanism for achieving high RS in the past (Dewsbury, 1982; Fedigan, 1983; Betzig, 1986; Pérusse, 1993). The universality with which high status is assumed to be a good thing, to such a degree that the existence of a desire for increasing it is often taken for granted, is perhaps the most convincing argument that it is an adaptation for something.

The benefits of high status may have remained through much of recorded history, at least for men. Betzig (1986, 1994) has reviewed historical and cross-cultural evidence from Roman times until the present and has found the clear pattern that wealthy and powerful men obtain sexual access to the greatest number of women. While most sire only a few legitimate offspring, they may sire many illegitimate children. This trend breaks down with the advent of modern democracy. It does not, however, disappear. It has been shown in modern Quebec that mens' sexual opportunities (and hence presumably their fertility, were it not for contraception) are positively correlated with social status (Pérusse, 1993), and we expect that this association is widespread.

The relationship between status and RS in women seems to be much less clear. It appears that in societies where women gain prestige through motherhood the expected correlation exists, but it seems to break down when women can gain status by other means, e.g. labor or education, or when high fertility can lead to a reduction of status for offspring (Kasarda et al., 1986). Similarly, the number of legitimate offspring sired by wealthy or powerful men also seems to decline when large numbers lead to overpartitioning of resources and decreased familial status. Obviously more work needs to be done on this topic.

Status seeking seems to be governed by such a strong drive that it interferes with rather than increases RS in certain environments. It is fine to claim that status, therefore, is correlated with RS but for the effects of modern culture, but the real question is why has it broken down this way. The most frequently blamed culprit for this disassociation is birth control (Pérusse, 1993). However, it is a misconception that effective birth control did not exist until the later half of the 20th century. In fact, attempts to limit fertility, through contraceptive techniques, abortion, or infanticide, are so ubiquitous as to be considered a human universal (Himes, 1936; McLaren, 1990). The ancient Greeks and Romans, for example, possessed remarkably effective contraceptives and abortifacients. These were derived from various plants which recent research has shown do, in fact, serve their desired purpose. The demand for effective birth control in the ancient world was so great that the most popular remedy, a plant called sylphium, from the genus *Ferula*, was rendered extinct by the 4th century A.D. (Riddle 1992). Nor is classical civilization unique in this knowledge. Plants possessing known contraceptive abilities are harvested even today by women in places as diverse as India, Latin America, and the Appalachian Mountains of the United States (Riddle 1992). Moreover, the mere availability of modern birth control methods and knowledge of how to use them properly does not guarantee their use. Such knowledge and availability have been ineffective in reducing fertility in overpopulated third world countries (McLaren, 1990; Kasarda et al., 1986), where women tend to use modern methods in place of their traditional birth control techniques to regulate birth intervals, but not to limit family size (McLaren, 1990).

The real question, then, is why do people so frequently try to limit fertility? We hypothesize that such behavior, which is primarily engaged in by women, is somehow linked to attempts to either increase or prevent a decrease in status. When having children drains resources and can lower status, women may seek to have fewer children. In an attempt to find a means to control the intractably high birth rates seen in developing countries, Kasarda et al. (1986) argue, based on a review of the available literature on the relationship between social mobility and fertility, that the status of women is critical to the shaping of reproductive behavior. Their fundamental conclusion is that in order to limit fertility, it is necessary to shift the determination of a woman's status from predominantly male-dependent to a female-oriented, self-determined focus. They discuss three variables that have been shown to be the most successful in limiting family size: increasing the amount of education women receive, increasing women's participation in the labor force (but only if the job held provides the opportunity for advancement and cannot be combined with child care), and decreasing the value of children as net wage or labor producers in the household.

Certainly all of these conditions are met in modern industrial society, which also exhibits remarkably low fertility. Just as effective contraception is not as novel as widely believed, the modern world is not the only one to experience decreased fertility. The Roman Empire is known to have suffered population decline between A.D. 1 and 500 (Riddle 1992). Writers of the time decried the phenomenon, and laws were passed to encourage increased family size (McLaren, 1990). Women are also known to have held an unusual amount of power in Roman society. They could inherit, own, and bequeath property. A Roman woman could obtain a divorce from her husband, and upon separation her dowry was returned to her, not her natal family (Leftowitz and Fant, 1992).

In answer to the puzzle of the relationship between status and reproductive success in humans, given the available evidence we think it a reasonable hypothesis that status seeking itself interferes with the relationship between status seeking and RS (for a similar argument see Donaldson, 1991). Why this would be so is an as yet unanswered question.

How does this relate to Emlen's predictions? If it is in fact true that people are more directly concerned with status than with maximizing their direct and indirect fitness when making reproductive decisions, then the behavioral link between these decisions and actual maximization of net RS in many recent human societies could be severed. In other words, while many of Emlen's predictions may have been borne out in ancestral environments, at least some of them do not appear to hold in modern times. Certainly, that is what the available evidence seems to indicate.

The data reported by Schlegel and Barry (1991) on marriage transactions imply that when parents are in control, the timing of marriage is based on status concerns. Flinn (1988), in a study of daughter guarding in a Caribbean village, presents evidence that even in societies where parents do not choose their childrens' mates, they still attempt to control their reproductive decisions. Evidence that kin can have a powerful interest on an individual's marriage choices has perhaps been most compellingly demonstrated by Chagnon (1979) in his analyses of mate competition and marriage transactions in the Yanomamö.

The concept that status concerns affect reproductive decisions is evident in some of Emlen's predictions. However, based on the evidence presented about the relationship between reproduction and status striving, and the demonstrated nature of the lack of fit of some predictions with the evidence, this concept needs to be elaborated and taken into greater account. Parents sometimes control children to further their own personal interests. If a given behavior can lead to increased status, then humans are likely to engage in it, regardless of its fitness payoff. Since Emlen's predictions are predicated on an implicit analysis of this payoff, they may not always hold.

One final topic that bears addressing is the issue of the appropriate level at which to define a human group or family. Humans are highly social and can live in extremely large groups composed of many, many different families who may or may not interact extensively with each other. Much of the theory behind these predictions may also be appropriately applied to analyses of human behavior in these larger social units. Research has already been carried out in this area by Betzig (1994), who has successfully used skew theory to understand the existence of despotism versus democracy in human societies through history.

In conclusion, although much of this commentary may be in contradiction to Emlen's predictions, the value of his laying out these issues and putting them in a domain where they can be discussed and refined cannot be overemphasized. Refining the predictions to take into account: 1) the complex nature of exchange and reciprocity in human society, 2) the effect of having dominant, post-reproductive helpers, and 3) status striving as a particularly powerful drive, will provide a solid base from which to explore the detailed nature of human family systems. We have made a first attempt at such a refinement, based on the points presented in this paper (see Table 1).

Of course, further exploration of the evolved psychology of human family relations should not be limited to the scope of these predictions. Inclusive fitness theory, ecological constraints theory, and skew theory provide a wealth of ideas about the expected outcomes of family dynamics. Their basic logic or insights will have to be part of any truly comprehensive theory of human familial affiliation and stability.

Rather than focusing effort exclusively on the determination of universal organizing principles, we suggest that the additional strategy of examining the tremendous variability that can exist even within one species such as humans, the degree to which this variability can be usefully interpreted in light of these theories, and an understanding of the psychological adaptations that govern family relations will prove just as valuable in the search to understand our families and ourselves.

Acknowledgments

We thank S. Braude, S. Emlen, J. Quinn, and M. Wilson for helpful comments on this manuscript. Thanks also to M. Wilson and P. Robinson for procurement of the SPSS data file. Special thanks to S. Emlen for his openness and willingness to discuss these issues. This research derived financial support from a Natural Sciences and Engineering Research Council of Canada grant awarded to M. Daly.

References

Alexander, R. D. 1974.The evolution of social behavior. *Annu. Rev. Ecol. Syst.*, 5:325-383.

Alexander, R. D. 1990. How did humans evolve? *Museum of Zoology, the University of Michigan Special Publication No. 1.*

Aquilino, W. S. and K. R. Supple. 1991. Parent-child relations and parent's satisfaction with living arrangements when adult children leave home. *J. Mar. Fam.*, 53:13-27.

Barkow, J., L. Cosmides, and J. Tooby. 1992. *The Adapted Mind.* Oxford University Press, New York.

Bateman, A. J. 1948. Intra-sexual selection in *Drosophila. Hered.*, 2:349-368.

Becker, G. S., E. M. Landes, and R. T. Michael. 1977. An economic analysis of marital instability. *J. Pol. Econ.*, 85:1141-1187.

Bengtson, V. L. and R. E. L. Roberts. 1991. Intergenerational solidarity in aging families: an example of formal theory construction. *J. Mar. Fam.*, 53:856-870.

Betzig, L. L. 1986. *Despotism and Differential Reproduction: A Darwinian View of History*. Aldine, New York.

Betzig, L. 1994. The point of politics. *Anal. Krit.*, 16:20-37.

Betzig, L., M, Borgerhoff Mulder, and P. Turke. 1988. *Human Reproductive Behavior.* Cambridge University Press, Cambridge.

Chagnon, N. A. 1979. Mate competition, favoring close kin, and village fissioning among the Yanomamö Indians. In N. A. Chagnon and W. Irons (eds.), *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, pp. 86-131. Duxbury Press, North Scituate MA.

Chatters, L. M., R. J. Taylor, and J. S. Jackson. 1986. Aged blacks' choices for an informal helper network. *J. Gerontol.*, 41:94-100.

Crook, J. H. and S. J. Crook. 1988. Tibetan polyandry: problems of adaptation and fitness. In, L Betzig, M, Borgerhoff Mulder, and P. Turke (eds.), *Human Reproductive Behavior*, pp. 97-114. Cambridge University Press, Cambridge.

Daly, M., and M. I. Wilson. 1982. Whom are newborn babies said to resemble? *Ethol. Sociobiol.*, 3:69-78.

Daly, M., and M. I. Wilson. 1987. The Darwinian psychology of discriminative parental solicitude. *Nebraska Symposium on Motivation.*, 35:91-144.

Daly, M., and M. I. Wilson. 1988. *Homicide*. Aldine deGruyter, New York.

Daly, M., and M. I. Wilson. 1990. Is parent-offspring conflict sex-linked? Freudian and Darwinian models. *J. Personal.*, 58:163-189.

Daly, M., and M. I. Wilson. 1994. Some differential attributes of lethal assaults on small children by stepfathers versus genetic fathers. *Ethol. Sociobiol.*, 15:207-217.

Daly, M., and M. I. Wilson. 1995a. Discriminative parental solicitude and the relevance of evolutionary models to the analysis of motivational systems. In M. Gazzaniga (ed.), *The Cognitive Neurosciences*, pp. 1269-1286. MIT Press, Cambridge MA.

Daly, M., and M. I. Wilson. 1995b. Stepparenthood and the evolved psychology of discriminative parental solicitude. In S. Parmigiani and F. vomSaal (eds.), *Infanticide and Parental Care*, pp. 121-134. Harwood Press, London.

Daly, M., and M. I. Wilson. 1996. Violence against stepchildren. *Current Directions in Psychological Science.*, in press.

Davis, J. N. In prep. Birth order and age of dispersal in modern Canada.

Dewsbury, D. A. 1982. Dominance rank, copulatory behavior, and differential reproduction. *Q. Rev. Biol.*, 57:135-158.

Donaldson, L. 1991. *Fertility Transition*. Basil Blackwell, Cambridge MA.

Eggebeen, D. J and D. P. Hogan. 1990. Giving between generations in American families. *Hum. Nat.*, 1:211-232.

Ellis-Schwabe, M. E., and H. D. Thornburg. 1986. Conflict areas between parents and their adolescents. *J. Psychol.*, 120:59-68.

Emlen, S. T. 1982a. The evolution of helping I. an ecologicl constraints model. *Am. Nat.*, 119:9-39.

Emlen, S. T. 1982b. The evolution of helping II. the role of behavioral conflict. *Am. Nat.*, 119:40-53.

Emlen, S. T. 1991. In J. Krebs and N. B. Davies (eds.), *Behavioral Ecology: An Evolutionary Approach*, PP. 301-337. Blackwell Scientific, Oxford.

Emlen, S. T. 1995. An evolutionary theory of the family. *Proc. Natl. Acad. Sci.*, 92:8092-8099.

Emlen, S. T., and S. L. Vehrencamp. 1983. Cooperative breeding strategies among birds. In A. H. Brush and J. G. A. Clark (eds.), *Perspectives in Ornithology*, pp. 93-133. Oxford University Press, Oxford.

Emlen, S. T., H. K. Reeve, P. W. Sherman, P. H. Wrege, F. L. W. Ratnieks, and J. Shellman-Reeve. 1990. Adaptive versus non-adaptive explanations of behavior: the case of alloparental helping. *Am. Nat.*, 138:259-270.

Ethology and Sociobiology 1990. 11(4/5).

Fedigan, L. M. 1983. Dominance and reproductive success in primates. *Yearb. Phys. Anthropol*, 26:91-129.

Flinn, M.V. 1981. Uterine vs. agnatic kinship variability and associated cousin marriage preferences: an evolutionary biological analysis. In R. D. Alexander and D. W. Tinkle (eds.), *Natural Selection and Social Behavior*, pp 439-475. Chiron Press, New York.

Flinn, M. V. 1988. Step-and genetic parent/offspring relations in a Caribbean village. *Ethol. Sociobiol.*, 9:335-369.

Gaulin, S. J. C. and A. Schlegel. 1980. Paternal confidence and paternal investment: a cross-cultural test of a sociobiological hypothesis. *Ethol. Sociobiol.*, 1:301-309.

Gordon, M. 1989. The family environment of sexual abuse: a comparison of natal and stepfather abuse. *Child Abuse and Neglect*, 13:121-130.

Hames, R. 1988. Relatedness and garden labor exchange among the Ye'kwana. *Ethol. Sociobiol.*, 8:354-392.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. *J. Theoret. Biol.*, 7:1-52.

Hamilton, W. D. 1966. The moulding of senescence by natural selection. *J. Theoret. Biol.*, 12:12-45.

Hartung, J. 1985. Matrilineal inheritence: new theory and analysis. *Behav. Brain Sci.*, 8:661-688.

Hill, K., and M. Hurtado. 1991. The evolution of premature reproductive senescence and menopause in human females: an evaluation of the "grandmother hypothesis." *Hum. Nat.*, 2:313-350.

Himes, N. E. 1936. *Medical History of Contraception.* Williams and Wilkins, Baltimore.

Hogan, D. P., and D. J. Eggebeen. 1995. Sources of emergency help and routine assistance in old age. *Soc. Forces.*, 73:917-936.

House, J. S., D. Umberson, and K. R. Landis. 1988. Structure and processes of social support. *Ann. Rev. Sociol.*, 14:293-318.

Kasarda, J. D., J. O. G. Billy, and K. West. 1986. *Status Enhancement and Fertility.* Academic Press, Orlando FL.

Keller, L., and H. K. Reeve. 1994. Partitioning of reproduction in animal societies. *Trends Ecol. Evol.*, 9:98-102.

Koenig, W. D., F. A. Pitelka, W. J. Carmen, R. L. Mumme, and M. T. Stanback. 1992. The evolution of delayed dispersal in cooperative breeders. *Q. Rev. Biol.*, 67:111-150.

Kurland, J. A. 1979. Paternity, mother's brother, and human sociality. In N. A. Chagnon and W. Irons (eds.), *Evolutionary Biology and Human Social Behavior: an Anthropological Perspective*, pp. 145-180. Duxbury Press, North Scituate MA.

Leftowitz, M. R. and M. B. Fant. 1992. *Women's Life in Greece and Rome*. Duckworth, London.

LeVine, R. A. 1961. Intergenerational tensions and extended family structures in Africa. In E. Shanas and G. F. Streib (eds.), *Social Structure and the Family: Generational Relations*, pp. 188-204. Prentice-Hall, Englewood Cliffs NJ.

Low, B. S. 1989. Human responses to environmental extremeness and uncertainty: a cross-cultural perspective. In E. Cashdan (ed.), *Risk and Uncertainty in Tribal and Peasant Economies*, pp. 229-255. Westview Press, Boulder CO.

McLaren, A. 1990. *A History of Conception*. Basil Blackwell, Cambridge, MA.

Montemayor, R. 1983. Parents and adolescents in conflict: all families some of the time and some families most of the time. *Journal of Early Adolescence*, 3:83-103.

Mutran, E. 1985. Intergenerational support among blacks and whites: response to cultural or socioeconomic differences. *J. Gerontol.*, 40:382-389.

Oliveri, M. E., and D. Reiss. 1987. Social networks of family members: distinctive roles of mothers and fathers. *Sex Roles*, 17:719-736.

Pérusse, D. 1993. Cultural and reproductive success in industrial societies: testing the relationship at proximate and ultimate levels. *Behav. Brain Sci.*, 16:267-322.

Reeve, H. K. and L. W. Ratneiks. 1993. Queen-queen conflicts in polygynous societies: mutual tolerance and reproductive skew. In L Keller (ed.), *Queen Number and Sociality in Insects*, Oxford University Press, Oxford.

Regalski, J. M. and S. J. C. Gaulin. 1993. Whom are Mexican infants said to resemble? Monitoring and fostering paternal confidence in the Yucatan. *Ethol. Sociobiol.*, 14:97-113.

Riddle, J. M. 1992. *Contraception and Abortion from the Ancient World to the Renaissance.* Harvard University Press, Cambridge MA.

Russell , D. E. H. 1984. The prevalence and seriousness of incestuous abuse: stepfathers versus biological fathers. *Child Abuse and Neglect*, 8:15-22.

Salmon, C. and M. Daly. (in press). On the importance of kin relations to Canadian women and men. *Ethol. Sociobiol.*

Schlegel, A., and H. Barry. 1991. *Adolescence: an Anthropological Inquiry.* The Free Press, New York.

Seginer, R. 1992. Sibling relationships in early adolescence: a study of Israeli Arab sisters. *Journal of Early Adolescence*, 12:96-110.

Semel, B., P. W. Sherman, and S. M. Beyers 1988. Effects of brood parasitism and nest-box placement on wood duck breeding ecology. *The Condor*, 90:920-930.

Spitze, G. and R. Ward. 1995. Household labor in intergenerational households. *J. Mar. Fam.*, 57:355-361.

Stacey, P. B., and J. D. Ligon. 1991. Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat saturation model of cooperative breeding. *Am. Nat.*, 137:831-846.

Statistics Canada. 1991. The 1990 general social survey cycle 5: family and friends. Public use microdata file, documentation, and user's guide

Steinberg, L. Pubertal maturation and parent-adolescent distance: an evolutionaryperspective. In G. R. Adams, R. Montemayor, and T. Gullotta (eds.), *Biology of Adolescent Behavior and Development*, Sage, pp. 71-97. Newbury Park CA.

Taborsky, M. 1994. Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior*, 23:1-101.

Taylor, R. J. 1986. Receipt of support from family among black Americans: demographic and familial differences. *J. Mar. Fam.*, 48:647-77.

Trivers, R. L. 1972. Parental investment and sexual selection. In B Campbell (ed.), *Sexual Selection and the Descent of Man 1871-1971*, pp. 136-179. Aldine, Chicago.

Trivers, R. L. 1974. Parent-offspring conflict. *Amer. Zool.*, 14:249-264.

Trivers, R. L. 1985. *Social Evolution*. Benjamin/Cummings, Menlo Park CA.

Turiel, E. 1975. The development of social concepts. In D. DePalma and J. Foley (eds.), *Moral Development* . Erlbaum, Hillsdale NJ.

Turiel, E. 1977. The development of concepts of social structure. In J. Glick and A. Clark-Stewart (eds.), *Personality and Social Development (Vol. 1)*. Gardner Press, New York.

Turke, P. 1988. Helpers at the nest: childcare networks on Ifaluk. In, L Betzig, M, Borgerhoff Mulder, and P. Turke (eds.), pp. 173-188. *Human Reproductive Behavior*. Cambridge University Press, Cambridge.

Vehrencamp, S. L. 1983a. A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.*, 31:667-682.

Vehrencamp, S. L. 1983b. Optimal degree of skew in cooperative societies. *Amer. Zool.*, 23:327-335.

Weisner , T. S. 1982. Sibling interdependence and child caretaking: a cross-cultural view. In, M. E. Lamb and B. Sutton-Smith (eds.), *Sibling Relationships, Their Nature and Significance Across the Lifespan*, pp. 305-328. Lawrence Erlbaum Asociates, Hillsdale NJ.

White, L. 1994. Coresidence and leaving home: young adults and their parents. *Annu. Rev. Sociol.*, 20:81-102.

White, L. K. and A. Booth. 1985. The quality and stability of remarriages: the role of stepchildren. *Am. Sociol. Rev.*, 50:689-698.

White, L. K. and A. Reidmann. 1992. Ties among adult siblings. *Soc. Forces*, 71:85-102.

Williams, G. C. 1957. Pleiotropy, natural selection and the evolution of senescence. *Evol.*, 11:3948-411.

Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton University Press, Princeton.

Prediction	Suggested Rewording to be applicable to *Homo Sapiens*
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.	Not Applicable, as continued familial interaction does not necessarily imply sacrifice of reproductive status.
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.	Not generally applicable, as the need for familial support may often be higher in families with low material resources.
3. Assistance in rearing offspring (cooperative breeding) will be more prevalent in family groups than in otherwise comparable groups composed of nonrelatives. 4. Assistance in rearing offspring will be expressed to the greatest extent between those family members that are the closest genetic relatives.	3. Unreciprocated assistance in rearing offspring will be more prevalent between related persons than between unrelated persons. 4. Unreciprocated assistance in rearing offspring will be expressed to the greatest extent between those family members that are the closest genetic relatives.
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.	No change.
6. Breeding males will invest less in offspring as their certainty of paternity decreases.	No change.

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. 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.	Not Applicable, as reproductive competition in human families is not usually between parents and offspring for a limited number of breeding vacancies.
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.	Replacement breeders (step-parents) will invest less in existing offspring than will genetic parents.
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. 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.	Replacement (step-) families will be inherently less stable than biologically intact families.
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 dominant's control over the subordinate will decrease as the severity of ecological constraints decreases, that is, as the expected profitability of the subordinate's option of dispersal increases.

13. Reproduction within a family will become increasingly shared as the asymmetry in social dominance between potential cobreeders decreases.	The dominant's control over the subordinate will decrease as the asymmetry in social dominance between potential cobreeders decreases.
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.	Reproduction within a family will be shared more equitably when the potential cobreeders consist of siblings than when they consist of reproductive aged parents and grown offspring.
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.	When dominants and subordinates are both capable of reproduction, 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.

Table 1. Emlen's 15 predictions (Emlen 1995), and our suggested changes.

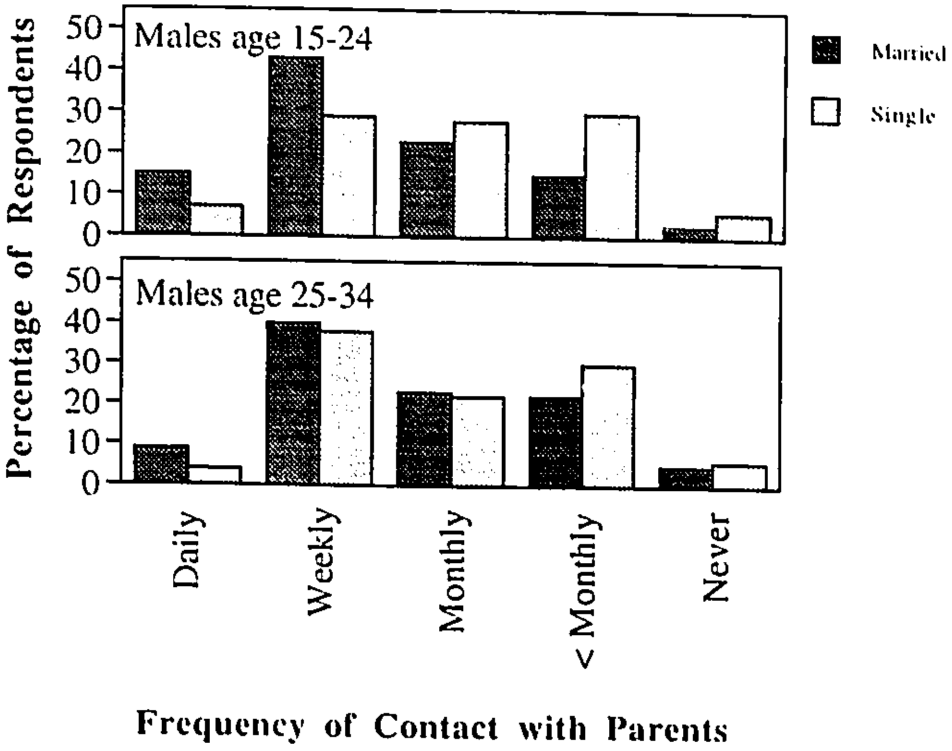
Figure 1.
Percentage of married and single male respondents who report seeing their parents daily, at least once a week, at least once a month, less than once a month, and never. Married male respondents in these age groups reported seeing their parents more frequently than single respondents. Data are from the Canadian General Social Survey, 1990 (Statistics Canada 1991).

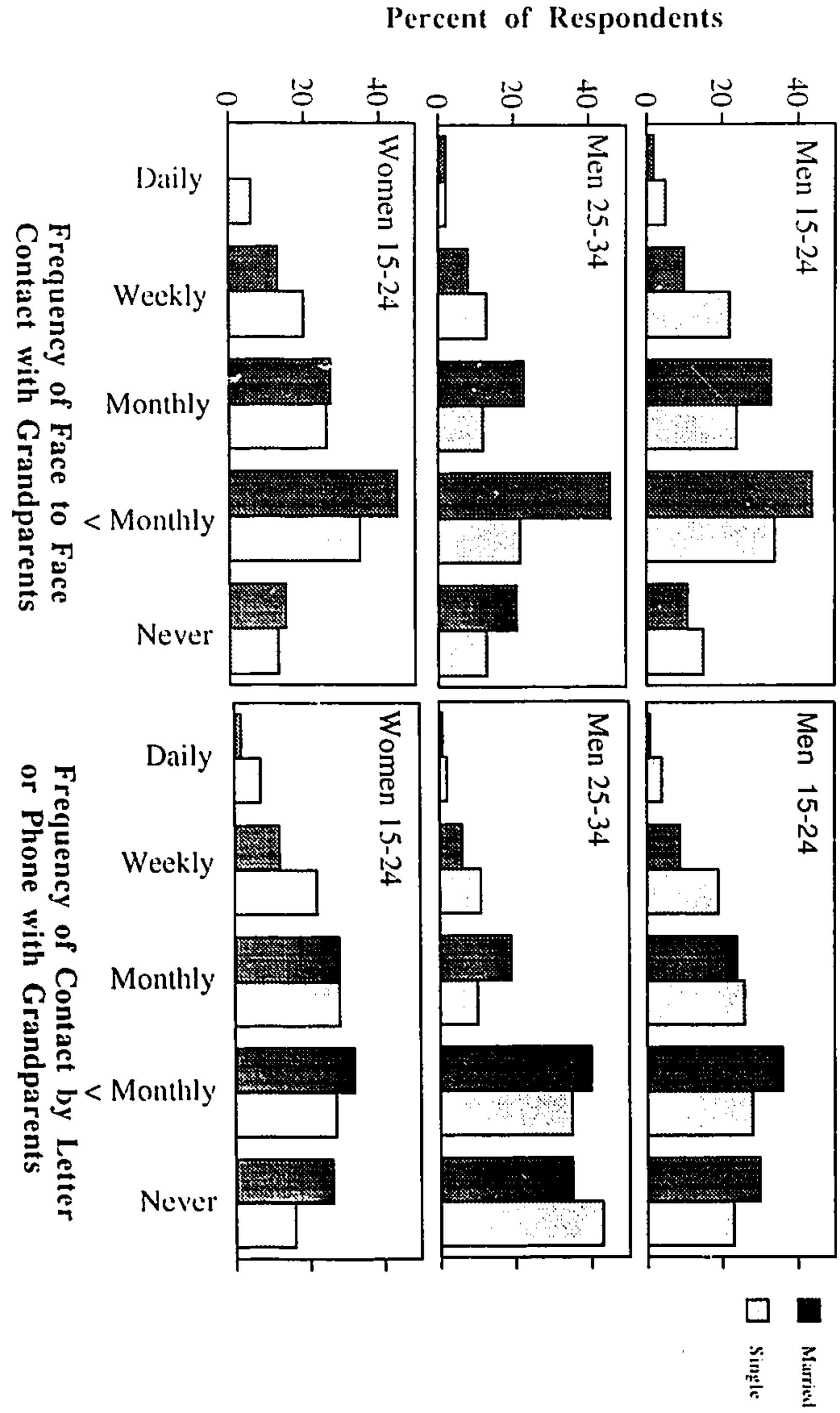
Figure 2.
Percentage of married and single respondents who report seeing their grandparents or contacting them by letter or phone daily, at least once a week, at least once a month, less than once a month, and never. Single respondents reported more frequent contact than married respondents.

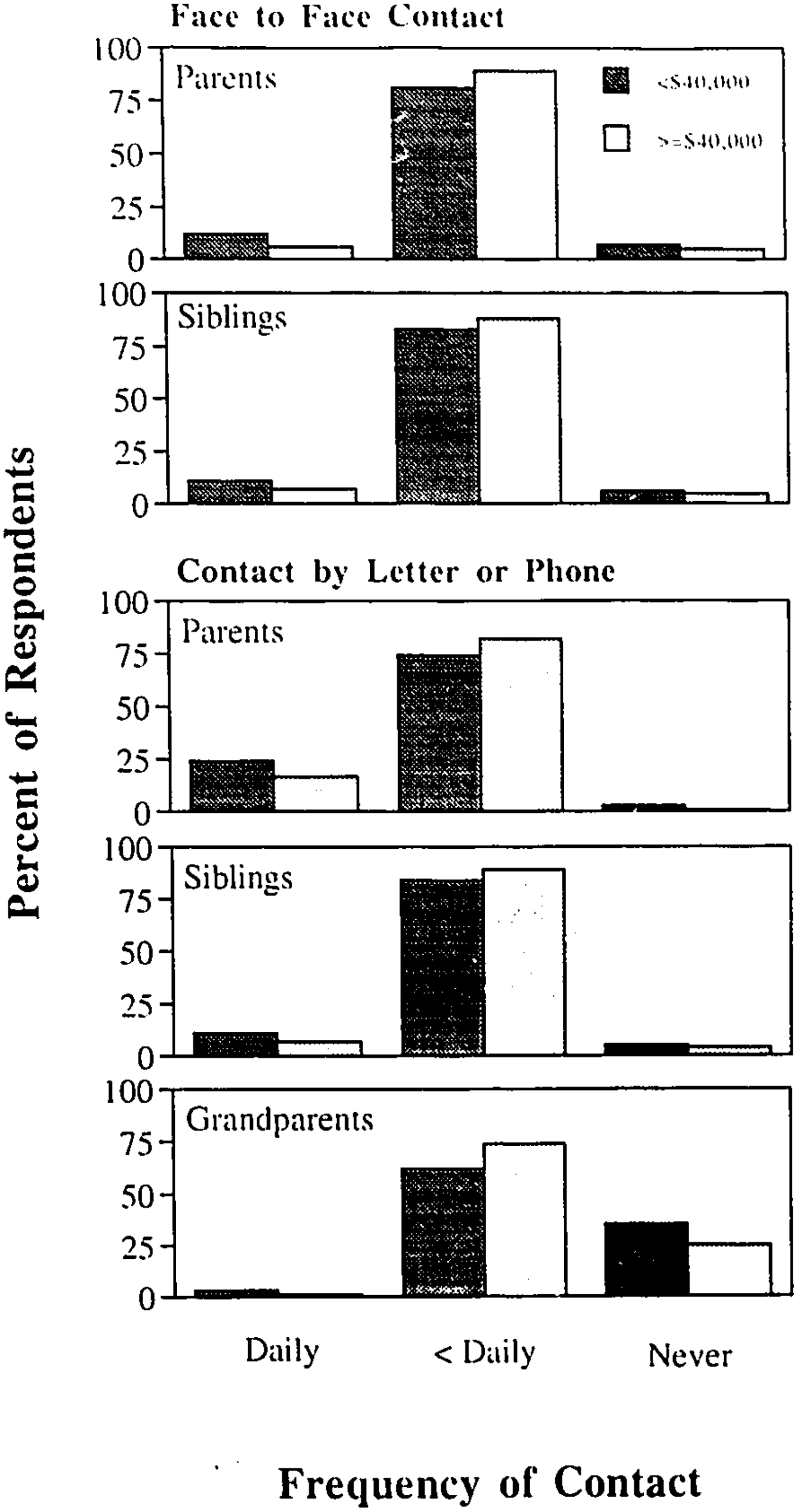
Figure 3.
Percentage of respondents below mean income (in the survey) versus above mean income that are in contact with relatives daily, less frequently then daily, and never. Data are summed across all significant age and sex categories for presentation. Respondents with lower incomes were more likely to be in contact with relatives daily, and also more likely never to be in contact with them at all.

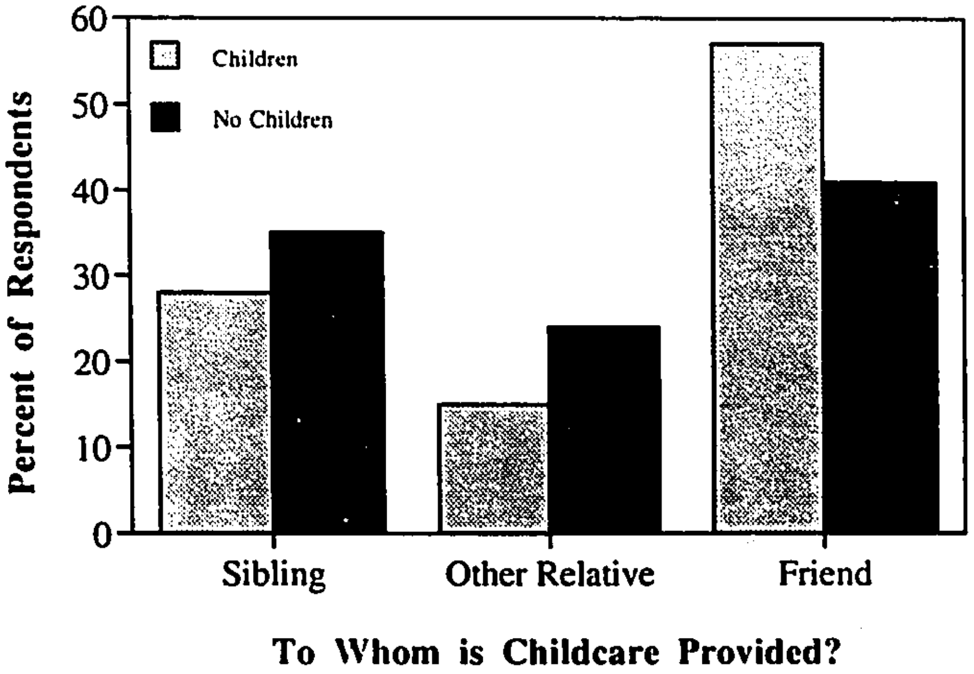
Figure 4.
Percentage of respondents 40 years old or younger with versus without children under the age of 13 who provided childcare assistance to their siblings, other relatives, or friends. Respondents with children were more likely to report assisting friends. Respondents without children were more likely to report helping relatives.

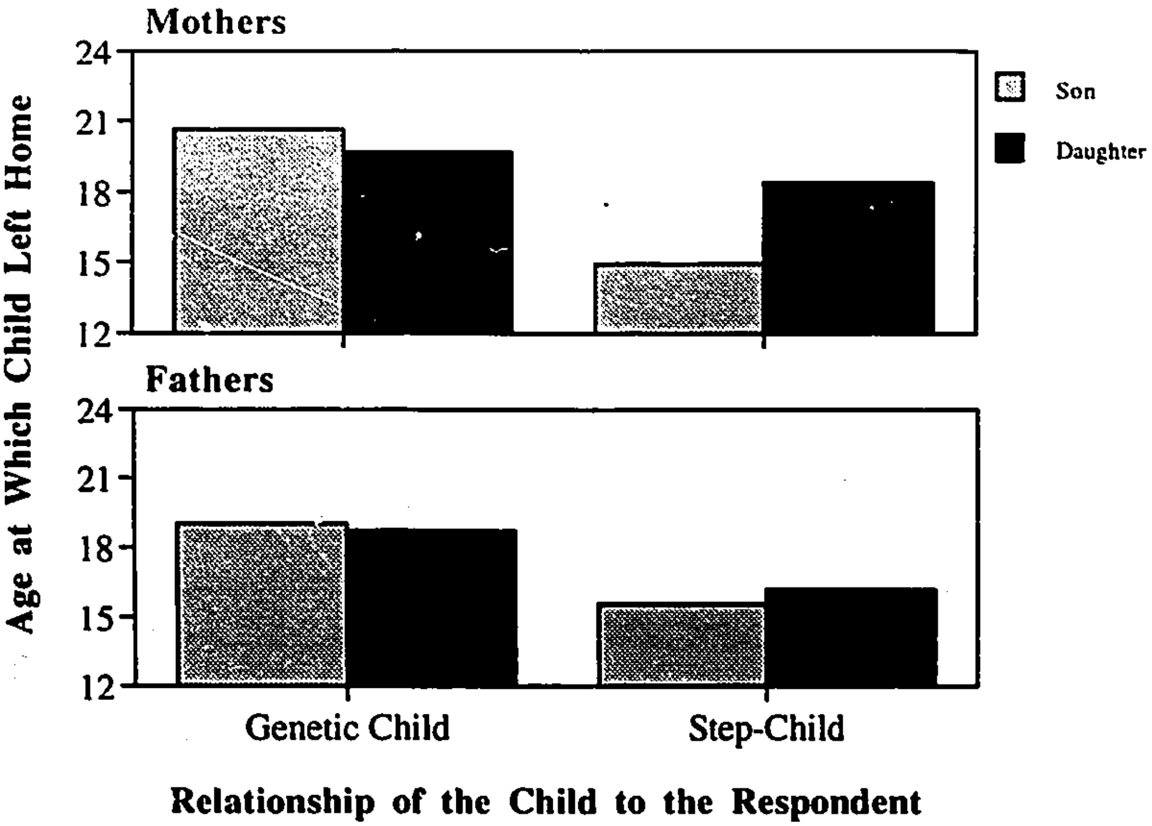
Figure 5.
Mean age at which sons versus daughters left home when their father or mother was a step-parent or their genetic parent. Both sons and daughters left earlier when living with a step-parent. Sons left later than daughters in genetic parent households, but they left earlier than daughters in step-parental households.


Males age 15-24
Males age 25-34
Percentage of Respondents
0
10
20
30
40
50
Daily
Weekly
Monthly
< Monthly
Never
Frequency of Contact with Parents
Married
Single


Percent of Respondents
0
20
40
Men 15-24
Men 25-34
Women 15-24
Daily
Weekly
Monthly
< Monthly
Never
Frequency of Face to Face Contact with Grandparents
Frequency of Contact by Letter or Phone with Grandparents
Married
Single


Face to Face Contact
Parents
<$40,000
>=$40,000
Siblings
Contact by Letter or Phone
Parents
Siblings
Grandparents
100
75
50
25
0
Daily
< Daily
Never
Percent of Respondents
Frequency of Contact


60
50
40
30
20
10
0
Children
No Children
Percent of Respondents
Sibling
Other Relative
Friend
To Whom is Childcare Provided?


Mothers
Fathers
24
21
18
15
12
Son
Daughter
Age at Which Child Left Home
Genetic Child
Step-Child
Relationship of the Child to the Respondent

Birth Order and Age of Dispersal in Modern Canada

<u>Submitted to Social Biology</u>

Jennifer Nerissa Davis
Department of Psychology
McMaster University
Hamilton, Ontario, Canada

The present study examines the relationship between birth order and the age at which children left home in a stratified random sample of modern Canadians. Analyses were carried out separately for only, oldest, and youngest children. The prediction that different variables would be relevant to the age at which each of these groups left home was upheld. In particular, the age at which only children left was unrelated to most variables measured, compared to children with siblings. Within multiple child families, sibling variables were more relevant to the age at which youngest children left than to the age at which oldest children left home. This result supports the hypothesis that the niche children fill within a family is related to birth order.

Birth order is a variable which has been both widely studied in psychology, and widely dismissed. Many researchers have sought, but have failed to find any significant birth order effects. This has led to the widespread conclusion that such differences do not exist or are of little importance (e.g. see Plomin and Daniels, 1987; Ernst and Angst, 1983). Some recent research challenges this conclusion.

According to behavior geneticists, within family environmental differences constitute the primary source of non-genetic variance in cognitive ability, personality, and psychopathology, and this variance makes two children in the same family almost as different from each other as children randomly selected from the population at large (Plomin and Daniels, 1987). Furthermore, these differences increase over time. Siblings and twins grow increasingly dissimilar to each other across childhood and adolescence (Loehlin, 1992; McCartney et al., 1990). This pattern has been interpreted as an attempt to assort into different family niches.

Parents may stand to benefit from encouraging their children to pick different niches. Humans are a highly social species. The environment in which individual children must survive and the social system into which they must integrate themselves are highly heterogeneous and potentially unpredictable. Under these conditions there may be a large benefit to simply being different in order to avoid unproductive competition with other family members. If one child excels at a certain task, parents may do best to encourage another child along an alternate path. Differential treatment might be thought of as a parental strategy to help all children achieve comparable success.

Why should these offspring differences predictably follow birth order? The birth order of a child will be strongly related to the family environment each one receives. If children do assort into different niches, this is one obvious means by which they might do so.

An additional rationale for the existence of birth order effects comes from Sulloway (1995) who has reanalyzed the vast pre-existing literature on personality. Although birth order effects are within family effects, most studies of them draw only one child from each family. This is likely to lead to a significant loss of statistical power unless a number of extraneous between family differences are controlled for. The results of a meta-analysis of all studies of the effect of birth order on the Big Five personality dimensions (extroversion, agreeableness, neuroticism, openness, and conscientiousness) that control for social class and sibship size, show a large and highly significant effect of birth order on all five dimensions (Sulloway 1995). Firstborns score higher than laterborns on measures of extroversion, neuroticism, and conscientiousness, while laterborns score higher on agreeableness and openness. Sulloway (1995) has also completed an historical study of the effect of birth order on willingness to accept radical innovation where he found that laterborns are significantly more likely to accept and champion radical innovations than firstborns.

Sulloway's research is based on the hypothesis that parental investment varies predictably with birth order. His argument is derived from the observation that, from an evolutionary standpoint, parents should value older children more than younger children. Older children, by virtue of simply being older, are more likely than their younger siblings to continue to survive and to reach an age where they can have children of their own. Parents, therefore, may be expected to have evolved behaviors that bias investment in favor of their oldest children.

Available evidence suggests that parents may, in fact, treat firstborns preferentially in at least some situations. In an analysis of the phenomenon of wet-nursing, Hrdy (1992) found that firstborn children were given preferential treatment (e.g. were nursed longer) in comparison to laterborns. In a study of nutritional status by birth order in the Philippines, Horton (1988) showed that firstborn children were less malnourished than lastborns. An analysis of British National Child Development Study data (Kaplan et al., 1992) found that firstborn children also received more medical surveillance.

If this bias is operative, then the amount of investment an individual child receives should be more dependent on the number of older siblings still receiving parental care than on the number of younger siblings. Each subsequent offspring will suffer from the existence of an additional and thus more highly 'valued' older sibling ahead of it. Within a brood, then, each subsequent offspring might receive less parental investment. If this is indeed the case, a comparison between brood sizes should reveal a much larger effect of brood size on the treatment received by lastborn offspring than on that received by firstborns regardless of whether there is a main effect of brood size on per capita investment.

Of course a demonstration that parents appear to discriminate between offspring on the basis of birth order in these situations does not mean that they always do so. While parental investment theory may predict such a discrimination in times when resources are scarce, there is no *a priori* reason to assume that this takes place as a matter of course. Given that parental investment decisions also include decisions about how many offspring to have, there is just as much reason to suppose that in the absence of extenuating circumstances an equal but age appropriate division of investment would be favored by selection. This is not a matter that can be resolved without further research. Similarly, the existence of birth order differences in personality does necessarily mean there are *investment* differences underlying them.

Even if differential parental investment is not the cause of birth order differences, however, this does not mean that birth order effects on personality and behavior are non-existent. The argument that these differences are merely a parsimonious means of differentiating children from each other in response to the need to survive in a heterogeneous and unpredictable environment is sufficient to predict them. Moreover, even under this niche filling hypothesis, the paths children take may still be more dependent on the number of older siblings they have than the number of younger ones, assuming that niches are filled in some semblance of sequential order.

The present study represents an attempt to determine whether birth order and sibship size do in fact affect behavior, and it does so by examining the relationship between birth order and dispersal age in modern Canada. Why use dispersal to test the hypothesis? The pattern of dispersal within a species has an enormous impact on nearly all aspects of its ecology and behavior. Different patterns of dispersal affect the likelihood that neighboring individuals will be close kin, and this, in turn, affects the evolution of behavioral interactions among individuals (Horn and Rubenstein, 1984). In a species like *Homo sapiens*, that thrives in a broad range of ecological and social environments, dispersal decisions may be expected to exhibit a large degree of plasticity and environmental contingency (Clarke, 1993). In a series of analyses of dispersal patterns in 19th century Sweden, Clarke and Low (1992) have demonstrated that human dispersal decisions are predicated on a number of factors, most importantly on an individual's expected inheritance or ability to accrue resources, and the liquidity of those resources.

If birth order is, in fact, predictably related to niche picking within the family and predictably related to the path children follow as adults, then a study of dispersal is one obvious place to begin the search for birth order differences. There are many aspects of dispersal that could be studied, such as the age at which a child leaves home, the distance the child moves, and the reasons for leaving. The present study focuses on age of leaving home.

Much remains unknown about patterns of human dispersal. The information that does exist comes primarily from studies of contemporary Western society. Although marriage is strongly associated with non-coresidence with parents (White, 1994; Davis and Daly, in prep.), according to Goldscheider and Goldscheider (1987; 1989), a majority of American adolescents expect to move away from home before marriage. An even larger majority of parents expect this of their children.

This trend of early dispersal has increased through this century, with fewer unmarried young adults residing with their parents now than in previous generations (White, 1994). The primary reason cited for this is the increase in affluence of modern society, whereby such widespread independence is made possible (Finch, 1989). Certainly, there is a very strong relationship between income and the likelihood that an adult child will not live with his or her parents (Michael et al., 1980). Children with more resources are less likely to live at home and less likely to return home once they have left (see White, 1994). Furthermore, it is the resource capacity of the child, not the parent, that is most likely to influence independence.

There is also some evidence that family structure affects coresidence patterns. Daughters leave earlier than sons (White, 1994). Children from families with more siblings leave earlier, as do children from step- and non-intact families (Aquilino, 1991; Mitchell et al., 1989; Kiernan, 1992). There appear to be no previous studies of the relationship between birth order and dispersal in contemporary society, but Clarke and Low (1992) have looked at this variable in relation to probability of dispersal (i.e. migration from natal community) in 19th century Sweden. They found greater probability of dispersal among laterborn children.

If dispersal age does, in fact, vary with factors that are related to an individual's life history, such as income and marital status, and if there is a predictable relationship between birth order and the choices an individual makes in these domains, that is, between birth order and the niches children fill, then different factors may be differentially relevant to the dispersal age of children depending on their birth order.

In order to test this, analyses were run on five different groups: only children, oldest children in two and three child families, youngest children in two and three child families, oldest children of all family sizes combined, and youngest children of all family sizes combined. Only children were included as a sort of control group, to see if there are any effects of simply having siblings on dispersal age. Analyses of two and three child families were conducted to help control for family size and to allow testing of factors that would be intractable to use on larger family sizes. Analyses of the full range of family sizes were included to allow testing of factors impossible to examine in the two and three child analyses.

Variables used for the analysis of the age at which only children left home were the age of the mother at the child's birth, total parental household income, sex of the child, and a variable measuring the amount of help the mother currently receives with daily tasks from family members other than her children. These variables were chosen as they are all factors related to the lifestyle of the family and potentially to the life goals of the child. The analyses run on two and three child families used these same variables, as well as the age disparity between the oldest and youngest child in the family, and sex of the focal child's siblings. The analyses run on all sibship sizes used the same variables as for only children except for help to mother, and included the number of younger or older siblings each child had as an additional variable.

Previous research on home leaving allows the formulation of several specific predictions about the nature of the relationship between several of these variables and the age at which children left. Clarke (1993) and Clarke and Low's (1992) research on dispersal in 19th century Sweden found a significant relationship between available resources and dispersal probability of children. Children with better local resource prospects were less likely to disperse. While the relationship between dispersal and parental circumstance in modern times is ambiguous (White, 1994), and more dependent on the child's earning capacity than that of the parent, the prediction can still be made that parental income, if and when it is significant, should be positively correlated with the age at which children leave home.

These same studies also found a significant relationship between sex of the child and probability of dispersal from the natal community. Daughters were more likely to disperse than sons. A similar relationship between sex and dispersal age exists in the modern West (White, 1994). Daughters leave earlier than sons. Therefore, in regards to the present study, it is predicted that if and when there is a significant sex of child effect daughters will leave earlier than sons.

Furthermore, the Sweden studies also showed a significant relationship between birth order, sibship size, and the probability of dispersal. Children born late in large families had a higher probability of dispersing. Although probability of dispersing from one's natal community and the age at which one moves out of one's parents' house are admittedly not quite the same thing, it is predicted that if a significant effect occurs for sibship size it will be larger for lastborn children than firstborns.

Finally, it is predicted that children in households where their parents receive help with daily tasks from other family members besides that child, will disperse at an earlier age. No directional predictions are made about the effects of mother's age, age disparity between children, or the sex of a child's siblings.

Methods

All data analyzed are from the General Social Survey (GSS) cycle 5 on Family and Friends, a telephone survey that was carried out in 1990 (Statistics Canada, 1991). It was conducted on a sample of all persons 15 years or older living in Canada except for residents of the Yukon and Northwest Territories and full-time residents of institutions. The survey also had a supplementary sample of the elderly and Ontario residents. To carry out the sampling procedure, each province was divided into geographic areas or strata representing census metropolitan areas (high population density) and census non-metropolitan areas (low population density). A random sample of phone numbers was generated for each stratum and an attempt was made to survey one randomly selected person from each household contacted. All interviewers were trained in phone survey techniques.

The survey consisted of two parts. The first, conducted before a household member was selected for the main questionnaire, determined each household member's age, sex, marital status and relation to the person being questioned. Following this a respondent was randomly selected from the eligible persons listed in part one to complete part two. The information collected in this section included the following: their children's birth histories and ages at which they left home if they had left; household help shared by persons living together and household help given to and received by persons not living in the household; and background socio-economic questions. All respondents gave their consent prior to being included in the survey.

The survey had a 75% response rate, and data were obtained from 13,495 households. Fifty-six percent of respondents were women and 44% were men. Refusal rates were higher for men than for women and for younger adults than for older adults.

All analyses were performed on SPSS/PC and, in order to get the most accurate measure of mother's age, were restricted to households in which a mother was the respondent. Households with step or adopted children were also removed, as the amount of parental investment received by these children is likely to be subject to additional factors not experienced by children living with their genetic parents (Daly and Wilson, 1988). Households with children who had not yet left home or who had left home either before 15 years of age or after 30 were excluded as well. These upper and lower limits were set in an attempt to remove from analysis as many people as possible who may have had extenuating reasons for leaving young or staying later that were not relevant to the present study. For example, children who may have been taken away from their parents, children with special needs who were not capable of living on their own, or children whose parents may need special care are not distinguishable from other children in this survey except that they might all be expected to show up disproportionately often as outliers on the age at which they left home.

Forced entry multiple regression was used for all analyses. The detail in which the variables were coded was the decision of Statistics Canada, and all analyses used the most complete codings available. The random sampling technique used in the GSS, coupled with the selection criteria used for this study, means that children born to younger mothers, and hence firstborn children will be slightly overrepresented in the sample. This bias should not affect any results, however, as the results of the analyses do not depend on the number of cases that fall into each level of the independent variables.

Because multiple analyses which often used some of the same data were run, α levels were adjusted using the Bonferroni procedure to correct for the increase in the chance of making a type I error. All significance levels were one tailed, except for mother's age, age disparity, and sex of the child's sibling(s), and all were set at $\alpha=.05/c$, where c equals the number of times the data in that variable were used for analysis. In the analysis of only children $c=3$ for mother's age, sex of the child, and income, and $c=1$ for help from family. In the analyses of 2 and 3 child families $c=4$ for household income, $c=2$ for mother's age, sex of the child, help from family, and age disparity, and $c=1$ for sex of sibling. In the analyses of all family sizes $c=5$ for household income, $c=3$ for mother's age and sex of the child, and $c=2$ for number of siblings.

Only children and the age of leaving home

The analysis for only children used the age at which children left home as the dependent variable, and the age of the mother at the child's birth, total household income, sex of the child, and a variable measuring the amount of help the mother currently receives from family members other than her children as the independent variables. The age at which children left home was specified in years, while age of the mother at the time of the child's birth was specified in years to the nearest 10th of a year. Total annual household income was divided into 9 categories by Statistics Canada where 1= <$5,000 CDN, 2= $5,000 to $9,999, 3= $10,000 to $14,999, 4= $15,000 to $19,999, 5= $20,000 to $29,999, 6= $30,000 to 39,999, 7= $40,000 to $59,999, 8= $60,000 to $79,999, and 9= ≥ $80,000. This was the most detailed coding of this variable available. It should be noted that the income variable is not coded on an interval scale. This does not prohibit the use of multiple regression for the analyses, but it does place some restrictions on the interpretations that can be made from the results. Rather than showing that there is a linear relationship between income and age of leaving home and being able to specify what that relationship is, any significant result is restricted to signifying that there is a monotonic trend in the relationship between the two variables (i.e. as one increases, the other either consistently goes up or down). This restriction is acceptable for the purposes of this study. In addition, the income measure was only available for the year when the household was surveyed, which often was not the same year the child left. This may add considerable noise to the measure. Sex of the child was coded as a binary variable. Help from family was also coded as a binary variable. This variable equaled 1 if the mother received help from any family member living outside the home other than her children, with at least one of the following: housework, household maintenance, transportation, personal care, or money. Otherwise it was 0. 190 cases of only children meeting the above stated criteria were available for analysis.

2 and 3 child families

The analyses performed on the oldest and youngest children in two and three child families also used the age at which children left home as the dependent variable. Two separate analyses were run, one on the oldest child of two and three child families, and one on the youngest child of two and three child families. Both analyses used the same set of independent variables: age of the mother at the time of the child's birth, total annual household income, the age disparity between the oldest and youngest child in the family, the sex of the child, the sex of the focal child's sibling(s), and help from family. Mother's age, sex of the child, household income, and help from family were measured as described in the analysis for only children. Age disparity was measured in years and was derived by subtracting the youngest child's current age from that of the oldest child. To simplify things, the three child families included for analysis were restricted to focal children with two same sex siblings. Sex of the child's sibling(s) was then coded as a binary variable. 609 and 493 cases, respectively, met the selection criteria for analysis of oldest and youngest children.

First and lastborns for all family sizes

The final two analyses carried out were run using data from the (1) oldest and (2) youngest children in each family in the survey. The independent variable of interest was the number of younger or older siblings each child had. Age of the mother at the time of the child's birth, total annual household income, and sex of the child were added to the equation to control for their effects. Once again the dependent variable was the age at which the child left home. Number of siblings was coded from 0 to 9. All control variables were coded as described above. 1452 and 1247 cases, respectively, met the selection criteria for oldest and youngest children.

Results

Only children

Table 1 shows that the age at which children without siblings left home was significantly associated with total annual household income. Children left later when they came from wealthier households and when they were born to older mothers. No other effects were significant.

2 and 3 child families

The age at which first born children with one or two younger siblings left home was significantly related to mother's age at the child's birth and sex of the child (Table 2). Children left later when they were born to older mothers. Boys left later than girls. No other effects were significant.

The age at which last born children with one or two older siblings left home was significantly related to mother's age at the child's birth, and to age disparity between the first and last children (Table 3). Children left later the older their mothers. They also left later the smaller the age disparity between themselves and their oldest sibling. Sex of the child, sex of sibling(s), household income, and help from family were all non-significant.

First and lastborns for all brood sizes

There was no significant effect of the number of younger siblings an oldest child had on the age at which he or she left home (Table 4). There was, however, a significant effect of the number of older siblings a youngest child had on the age at which he or she left (Table 5). Youngest children left later the fewer older siblings they had. Mother's age at the time of the child's birth and sex of the child were significant for both analyses. Again, children left later when they were born to older mothers, and boys left later than girls. Total household income was significant for the analysis of oldest, but not youngest, children. Oldest children left later when they came from wealthier households.

Conclusion

For variables for which predictions were made, all significant results were in the expected direction. These analyses, which show that sons leave later than daughters, and that laterborn children in large families leave earlier, are in accord with previous research on human dispersal. Although parental income was only significant in two analyses, it was positively correlated with age of leaving home, suggesting that in at least some circumstances high resources serve to delay dispersal.

The results of these analyses also support the idea that children in multiple child households do, to some extent, pick niches, and that this niche picking is related to birth order. Fewer factors were found to be relevant for the age at which only children leave home than for any of the other analyses. The factors that were significant were also different for children with siblings than for those without. Of course the smaller sample size of this group also means that power, or the ability to detect real differences, is lowest for the analysis of only children. Within multiple child families the variables significantly related to age of dispersal varied for oldest and youngest children. The age at which oldest children left home was not related to any sibling related measures, while the age at which youngest children left home was.

Although the causal factors mediating birth order effects are not yet clearly understood, the present study lends further support to the idea that such effects do, in fact, exist. Whether they are driven by differential parental investment, as suggested by Sulloway (1995) or are simply the result of adaptive niche picking in a heterogeneous and unpredictable environment cannot be addressed with these data, and this is an obvious issue for further research.

Acknowledgments

I thank M. Daly for helpful comments for this manuscript, as well as three anonymous reviewers for their comments on an earlier incarnation of this paper. Thanks also to M. Wilson and P. Robinson for procurement of the SPSS data file. This research derived financial support from a Natural Sciences and Engineering Research Council of Canada grant awarded to M. Daly.

References Cited

Aquilino, W. S. 1991. Family structure and home-leaving: a further specification of the relationship. *J. Marriage Fam.* 53:999-1010.

Clarke, A. L., 1993. Women, resources, and dispersal in nineteenth-century Sweden. *Hum. Nat.* 4:109-135.

Clarke, A. L., and B. S. Low, 1992. Ecological correlates of dispersal in nineteenth century Sweden. *Anim. Behav.* 44:677-693.

Daly, M., and M. Wilson, 1988. The Darwinian psychology of discriminative parental solicitude. *Nebraska Symposium on Motivation* 35:91-144.

Davis, J. N., and M. Daly, in prep. Women, power, reciprocity and an evolutionary theory of the human family.

Ernst, C. and J. Angst, 1983. *Birthorder: Its Influence on Personality.* Springer-Verlag, New York.

Finch, J. 1989. *Family Obligations and Social Change.* Polity, Oxford.

Goldscheider, C. and F. K. Goldscheider, 1987. Moving out and marriage: what do young adults expect? *Am. Sociol. Rev.* 52:278-285.

Goldscheider, F. K. and C. Goldscheider, 1989. Family structure and conflict: nest-leaving expectations of young adults and their parents. *J. Marriage Fam.* 51:87-97.

Horton S., 1988. Birth order and child nutritional status: evidence from the Philippines. *Economic Development and Cultural Change* 36:341-354.

Hrdy S. B., 1992. Fitness tradeoffs in the history and evolution of delegated mothering with special reference to wet-nursing, abandonment, and infanticide. *Ethol. Sociobiol.* 13:409-442.

Kaplan B.A., C. G. N. Mascie-Taylor, and J. Boldsen, 1992. Birth order and health status in a British national sample. *J.Biosoc. Sci.* **24**: 25-33.

Kiernan, K., 1992. The impact of family disruption in childhood on transitions made in young adult life. *Pop. Stud.* 46:218-234.

Loehlin, J. C., 1992. *Genes and Environment in Personality Development*. Sage, Newbury Park CA.

McCartney, K. M. J. Harris, and F. Bernieri, 1990. Growing up and growing apart: a developmental meta-analysis of twin studies. *Psych. Bulletin* 107:226-237.

Michael, R. T., V. R. Fuchs, and S. R. Scott, 1980. Changes in the propensity to live alone: 1950-1976. *Demography* 17:39-53.

Mitchell, B. A., A. V. Wister, and T. K. Burch, 1989. The family environment and leaving the parental home. *J. Marriage Fam.* 51:605-613.

Plomin, R., and D. Daniels, 1987 Why are children in the same family so different from one another? *Behav. Brain Sci.* 10:1-59.

Statistics Canada, 1991. The 1990 general social survey cycle 5: family and friends. Public use microdata file, documentation, and user's guide

Sulloway, F. J., 1995 Birth Order and Evolutionary Psychology: A Meta-Analytic Overview. *Psych. Inquiry* 6:75-80.

White, L., 1994. Coresidence and leaving home: young adults and their parents. *Annu. Rev. Sociol.* 20:81-102.

Table 1.

Analysis of the age at which only children left home

Variable	Beta	t	p Value	Adjusted α	Direction of Relationship	
					predicted	observed
Mother's Age	.0845	2.225	.0273	.0084	none	n.s.
Household Income	.2760	2.493	.0135*	.0167	+	+
Sex of the Child	-.6060	-1.410	.1663	.0167	boys leave later	n.s
Help from Family	.6640	1.239	.2171	.05	+	n.s.

Results of a step-wise multiple regression analysis using the age at which children with no siblings left home as the dependent variable. Independent variables are listed in the table. Mother's age refers to the age of the mother when the child was born. Household income is total annual household income for the year in which the survey was conducted. Help from family is a measure of whether or not mothers were receiving assistance with various things from family members other than their children . Because of the multiple analyses performed on these data, alpha levels had to be adjusted, and the adjusted rejection levels are listed. Beta values are the standardized regression coefficient. Starred p values are significant. R^2=.06, n=172, Sig. F <0.05.

Table 2.
Analysis of the age at which oldest children with 1 and 2 siblings left home

Variable	Beta	t	p Value	Adjusted α	Direction of Relationship	
					predicted	observed
Mother's Age	.0977	3.796	.0002*	.0125	none	+
Household Income	.1244	2.274	.0233	.0125	+	n.s.
Sex of the Child	-.8000	-3.479	.0005*	.025	boys leave later	boys left later
Help from Family	-.4620	-1.596	.1111	.025	+	n.s.
Sex of the Sibling(s)	.3485	1.132	.2581	.025	none	n.s.
Age Disparity	.0249	0.725	.4688	.025	none	n.s.

Results of a step-wise multiple regression analysis using the age at which first born children in families of 2 or 3 kids left home as the dependent variable. Independent variables are listed in the table. Age disparity is the age difference between the oldest and youngest child in the family. Beta values are the standardized regression coefficient. Starred p values are significant. R^2=.05, n=609, Sig. F <0.05.

Table 3.
Analysis of the age at which youngest children with 1 or 2 siblings left home

Variable	Beta	t	p Value	Adjusted α	Direction of Relationship predicted	Direction of Relationship observed
Mother's Age	.1588	4.414	.0000*	.0125	none	+
Household Income	.0970	1.177	.2399	.0125	+	n.s.
Sex of the Child	-.4147	-1.263	.2170	.025	boys leave later	n.s.
Help from Family	-.2840	-0.684	.4944	.025	+	n.s.
Sex of the Sibling(s)	-.0031	-0.006	.9950	.025	none	n.s.
Age Disparity	-.1606	-2.630	.0088*	.025	none	-

Results of a step-wise multiple regression analysis using the age at which last born children in families of 2 or 3 children left home as the dependent variable. Independent variables are listed in the table and are coded as in the analysis using the oldest child in two and three child families. R^2=.05, n=493, Sig. F <0.05.

Table 4.
Analysis of the age at which oldest children (with up to 9 siblings) left home

Variable	Beta	t	p Value	Adjusted α	Direction of Relationship	
					predicted	observed
Number of Siblings	.0194	0.711	.2384	.025	-	n.s.
Mother's Age	.1308	4.867	.0000*	.0084	none	+
Household Income	.0742	2.818	.0025*	.010	+	+
Sex of the Child	-.1291	-5.000	.0000*	.0167	boys leave later	boys left later

Results of a step-wise multiple regression analysis using the age at which first born children left home as the dependent variable. R^2=.04, n=1452, Sig. F <0.05.

Table 5.
Analysis of the age at which youngest children (with up to 9 siblings) left home

Variable	Beta	t	p Value	Adjusted α	Direction of Relationship predicted	Direction of Relationship observed
Number of Siblings	-.0811	-2.450	.0072*	.025	-	-
Mother's Age	.1857	5.572	.0000*	.0167	none	+
Household Income	.0302	1.064	.1438	.010	+	n.s.
Sex of the Child	-.1555	-5.604	.0000*	.0084	boys leave later	boys left later

Results of a step-wise multiple regression analysis using the age at which last born children left home as the dependent variable. R^2=.05, n=1247, Sig. F <0.05.

Birth Order, Sibship Size and Status in Modern Canada

submitted to Human Nature

Jennifer Nerissa Davis
Department of Psychology
McMaster University
Hamilton, Ontario, Canada

Abstract

This paper investigates the possibility that birth order affects the degree to which individuals seek out or attain higher status. Humans give birth to a variable number of (usually) single offspring spaced one to many years apart, and continue to maintain contact with them for greatly extended periods of time. The continued presence of older siblings, and arrival of younger ones, means that each child is reared in a different family environment. Research findings from the field of behavior genetics suggest that these differences have a significant impact on the development of individual differences between children in the same family. Although no two families are likely to be exactly the same, factors such as birth order vary predictably within them. The present study examines the relationships between birth order, sibship size, and several variables thought to measure status ambitions in a random sample of Canadians. Firstborn children appear to be more status oriented than lastborns, and this effect is mediated by sibship size. While firstborn children are unaffected by the number of younger siblings they have, the status ambitions of youngest children decrease the more older siblings they have. Birth order effects on status attainment are not as strong, suggesting that goals strived for are not always reached, or that perhaps both groups engage in status striving tactics, but go about this in different ways.

Research from behavior genetics has shown that there are remarkable differences between children in the same family. Siblings raised together are almost as different from each other as children randomly pulled from the population (Plomin and Daniels 1987). The present study is an attempt to determine whether certain differences between siblings follow a predictable pattern across families. Do birth order and sibship size affect the paths children follow? More specifically, are birth order and sibship size related to attempts to increase or maintain status?

This paper is divided into two parts. The first part describes what is meant by the term status striving, and attempts to explain, from an evolutionary perspective, why people might be expected to strive for high status. The argument is made that status striving is an adaptation, and several analyses are presented to explore the nature of this adaptation through an analysis of the behavior of modern Canadians, as the way it plays itself out could potentially have an impact on patterns of status striving seen in this population. The second part considers the relationship between birth order and factors thought to measure status striving. It presents analyses of this relationship in the same modern Canadian sample and discusses several possible explanations for the pattern of results seen.

Status Striving

What exactly is meant by the term status striving? From the perspective of evolutionary biology, status striving is seen as an evolved motivational system that helps to maximize the reproductive success (RS) of individuals in social species. That is, high status individuals are expected to leave more surviving offspring, on average, than low status individuals. There is a benefit to attempting to increase or maintain status and thus status striving should be selected for. In general, the correlation between status and RS in non-human animals is good, though not perfect (Dewsbury 1982; Fedigan 1983).

The same might be expected to be true for humans as well. Wealthy and powerful people should leave more offspring than those lower on the socio-economic ladder. In fact, this relationship does not always seem to hold, particularly in modern industrialized nations (see Pérusse 1993); indeed, the correlation is often reversed. If status striving is an adaptation, how could this be? People (or other species) are unlikely to achieve maximal RS by consciously trying to do so. Instead such ends are achieved through the development of adaptations that track more readily determined things that have been reliably correlated with high RS. Once such an adaptation is in place dissociation from its original purpose may occur, that is to say, it can become non-adaptive. Status seeking may be one such adaptation.

The correlation seen between status and RS in many non-human animals constitutes one line of evidence that this is a widespread adaptive phenomenon (Dewsbury 1982; Fedigan 1983). Similarly, evidence from human societies suggests that status seeking could be a good way to achieve high RS in many situations, at least for men. Wealthy and powerful men obtain sexual access to the greatest number of women in many cultures and have obtained it in the Western world throughout much of history (Betzig 1986, 1994). While most sire only a few legitimate offspring, they may sire many illegitimate children. This correlation breaks down in modern democracies, where status striving may no longer be adaptive. In a study of the relationship between status and mens' sexual opportunities in modern Quebec, Pérusse (1993) has shown that mens' opportunities, and hence presumably their fertility were it not for contraception, are positively correlated with social status. The contribution of status to expected fitness is likely to have been largely mediated by polygynous opportunity in men, but in women, as in other female primates, high social rank may have a positive effect on reproductive success for other reasons, such as priority of access to scarce resources (Fedigan 1983).

The link between high status and high RS is thus thought to have been broken by the advent of modern contraception and other evolutionarily novel aspects of modern life. The nature of status striving as an adaptation cannot be understood, however, without an understanding of why this breakdown occurs.

Reasonably effective birth control has been in existence for at least two thousand years and is found in cultures other than the modern Western world. Attempts to limit fertility, through contraceptive techniques, abortion, or infanticide, are so ubiquitous as to be considered a human universal (Himes 1936; McLaren 1990). The ancient Greeks and Romans, for example, are known to have used effective contraceptives and abortifacients derived from plants which recent research has shown do, in fact, serve their desired purpose (Riddle 1992). In addition, the mere availability of modern birth control methods does not guarantee their use. Women in overpopulated third world countries may use them in place of their traditional techniques to regulate birth intervals, but they do not use them to limit their family size (McLaren 1990). Thus, it would appear that a woman's regulation of her own fertility is not as novel as is sometimes assumed.

Why would people try to limit fertility? Interestingly, these efforts, primarily engaged in by women, seem somehow to be linked to attempts to either increase status or to prevent a decrease in status. As for men, a woman's status is likely to also have been related to her reproductive success. Such relationships are known to exist for non-human primates (Fedigan 1983). In a review of the relationship between social mobility and fertility, Kasarda et al. (1986) argue that the status of women has a critical influence on their reproductive behavior and that women limit fertility when they have the ability to influence their own status independently of that of their husbands and fathers. This ability comes primarily from increases in the amount of education women receive, increases in women's participation in the labor force (but only if the job held provides the opportunity for advancement and cannot be combined with child care), and decreases in the value of children as net wage or labor producers in the household. When having children drains resources and lowers status, women have fewer children.

The solution to the puzzle of the breakdown of the relationship between status and reproductive success in humans thus seems to be that it is a result of status seeking itself. A similar argument can be found in the economics literature (Donaldson 1991). Why bother raising this issue? It serves to underscore the notion that status is keenly sought after. This ambition was most likely selected for in a context where it increased RS, and even if it no longer serves this end in a particular society, it still remains.

As this study examines the relationship between birth order and status striving in modern Canada, given Pérusse's (1993) demonstration that high status is correlated with access to a larger number of sexual partners in modern Quebec, a logical place to start would be to examine the relationship between wealth and number of offspring in Canada. Is status striving adaptive in this group? More importantly, is there any evidence that Canadians behave as though it is?

To answer these questions, survey data on a stratified random sample of Canadians were analyzed to see 1) if there is a positive correlation between wealth and number of children or grandchildren for men and women in this sample, 2) if the probability of having any children, as opposed to number of children, is affected by wealth, and 3) if a Trivers-Willard sex ratio effect (see below) occurs in this population, that is, are wealthy people more likely to have sons and poor people more likely to have daughters? Trivers and Willard (1973) hypothesized that under certain circumstances which may apply to humans, the sex ratio of offspring within a population should be correlated with condition or status of parents. The existence of such an effect in modern Canada would be evidence that at some subconscious level, reproductive decisions are made as though status and RS are linked.

The first analyses are a straightforward test of the status-RS correlation. They assess the relationship between total household income and both the number of children and the number of grandchildren people have. Depending on the nature of the adaptation, status striving could still occur even if this correlation does not hold. Indeed, the evidence reviewed above suggests that status striving should be manifest regardless. Still, it is useful to test for the existence of the correlation between status attainment and RS. In the absence of detailed knowledge of the ways in which this correlation has been disrupted the possibility exists that any disruption might affect the relationship between birth order and status striving as well. If, for example, the link is broken in such a way that individuals no longer make reproductive decisions as though status and RS are linked, then the relationship between status striving and both parent and child status motivations may become suspect unless it can be shown that status striving is unaffected by this disruption.

The second analysis is an attempt to probe the nature of any disruption in the status-RS correlation. Perhaps having low status affects the probability of having children at all, even if it does not affect the total number of children among those who have them. Although status may no longer be positively correlated with family size, it may still affect the ability of individuals, particularly men, to find a mate, and thus their ability to have any children at all. Cross cultural research has shown that women prefer men with greater resources (Buss 1989). Following this, decisions of how many children to have may no longer be positively correlated with status, but whether an individual has any children at all may still be correlated with status.

This analysis, as well as the previous one, is carried out for men and women separately as it is conceivable that different patterns would emerge for the two sexes. Should there be a sex difference in the relationship between status and RS, it is likely that any correlation, positive or negative, will be stronger for men than for women. In polygynous species, and humans on the whole are mildly polygynous (Daly and Wilson 1983), variance in male reproductive success is typically greater than variance in female reproductive success. Assume, as is true in many if not most species, that the number of offspring males can sire is limited by the number of females they can fertilize, while the number of offspring a female can bear is a function of the amount of investment she needs to put in to them and is thus less variable and not constrained in the same manner. If the sex ratio in the population is approximately equal to 1, then for every extra mate a given male has, there must be another male in the population who has none. This drives up the variance in RS. Each female, on the other hand, can have a mate, which leads to low variance in RS.

The third analysis, of the existence of the Trivers-Willard effect, is an attempt to determine whether the reproductive investment of Canadians suggests that at some level they still behave as though a correlation between status and RS exists. According to Trivers and Willard (1973), in species with effectively polygynous breeding systems and where condition of the young at the end of parental investment is correlated with parental condition, parents in good condition are expected to favor sons and parents in poor condition are expected to favor daughters. These differences can be measured in terms of biased sex ratios as well as biased behavior. The rationale for this prediction is based on the previously mentioned observation that in polygynous systems, males exhibit greater reproductive variance than females. If an individual's subsequent breeding success is linked to parental condition, then the sons of parents in poor condition are not likely to produce as many offspring as their daughters. On the other hand, parents in good condition are likely to produce sons that outreproduce their daughters.

Trivers and Willard (1973) hypothesized that socioeconomic status is an index of condition in human societies. Thus, wealthy and powerful people may be expected to produce and/or invest more heavily in sons, and their poorer counterparts are expected to do the reverse. Several studies have looked at sex differential investment as a function of status or wealth in humans with mixed results. Some have found the predicted effect (Abernathy and Yip 1990; Betzig and Turke 1986; Boone 1988; Cronk 1991; Dickemann 1979; Gaulin and Robbins 1991; Mealey and Mackey 1990; Voland 1988), some have failed to find any effect or found mixed results (Essock-Vitale 1984; Hrdy and Judge 1993; Low 1991), and at least one has found the opposite effect. Voland et al. (1991) discovered that the prosperous farmers in 18th and 19th century Krummhörn, Germany, raised more daughters than sons. The authors explained this outcome as the result of a highly saturated social and economic environment, with little opportunity for marriage of sons, but not daughters, without loss of social status. Voland et al. (1991) interpret this pattern as a parentally motivated means of concentrating property to maintain social standing. That is, the pattern of sex-biased parental investment did not simply track status, it tracked attempts to maintain status. This daughter bias was not seen in the sex ratio at birth, which was male biased, but manifested itself in the sex ratio of children who reached age 15.

Methods

All analyses were performed on SPSS for Windows. All data analyzed are from the General Social Survey (GSS) cycle 5 on Family and Friends, a telephone survey that was carried out in 1990 (Statistics Canada 1991). It was conducted on a sample of all persons 15 years or older living in Canada except for residents of the Yukon and Northwest Territories and full-time residents of institutions. The survey also had a supplementary sample of the elderly and Ontario residents, i.e. these two groups were overrepresented in the sample. To carry out the sampling procedure, each province was divided into geographic areas or strata representing census metropolitan areas (high population density) and census non-metropolitan areas (low population density). A random sample of phone numbers was generated for each stratum and an attempt made to survey one randomly selected person from each household contacted. All interviewers were trained in phone survey techniques.

The survey consisted of two parts. The first, conducted before a household member was selected for the main questionnaire, determined each household member's age, sex, marital status and relation to the person being questioned. Following this a respondent was randomly selected from the eligible persons listed in part one to complete part two. This section collected information on the following: aspects of the respondent's relationship with parents, grandparents, siblings, grandchildren, and friends; relationships with their children, their children's birth histories, ages at which they had left home if they had left; fertility intentions; marriage and common-law history; and background socio-economic questions. All respondents gave their consent prior to being included in the survey.

The survey had a 75% response rate, and data were obtained from 13,495 households. Fifty-six percent of respondents were women. Refusal rates were higher for men than for women and for younger adults than for older adults. In the GSS, total annual household income was coded into 9 levels. These levels covered highly variable ranges of income and contained highly variable numbers of respondents. For the present analyses income was recoded as a binary variable, divided at the median income for the group being tested.

Number of children was coded in the GSS from 0 to 9, with all larger brood sizes scored as 10, and was used without further modification for analysis. Number of grandchildren was similarly coded. The childlessness variable was created for these analyses and was coded as a binary variable: each respondent either had children or did not. Sex of child was also coded as a binary variable.

The relationship between wealth and number of children was analyzed with a two-way ANOVA, with number of children as the dependent variable and sex of the respondent and income group as the independent variables. Analysis of the relationship between wealth and number of grandchildren was carried out in the same fashion. A first analysis was restricted to respondents between the ages of 55 and 65. Women of this age are no longer capable of having children, and an inspection of men who had reached the age of 75 revealed that fewer than a dozen of them had had any further children after age 55. The upper age limit was imposed to attempt to control for any cohort effects. A second analysis was restricted to respondents over the age of

70. The median split of income for the first analysis occurred at \$30,000 CDN, and for the second analysis at \$14,000.

The relationship between the probability of having any children and income was examined with a χ^2 test using presence or absence of children and income group as the test variables. This analysis was performed separately for men and women, and was also performed only on respondents between the ages of 55 and 65.

The presence of a Trivers-Willard sex ratio effect was tested by χ^2, using the variables sex of child and income group. To simplify analysis this test was run only on firstborn children of female respondents, and was run only on firstborn children who were no more than 2 years old at the time of the survey. This restriction was placed on the age of children in order to get as accurate a measure of familial income at the time of the child's birth as possible. Since larger families also require greater income to achieve the same economic status the restriction on birth order of the child controlled for this potential confound. The low and high income groups were split at the median, which was \$14,000 for this analysis due to the large number of low income mothers with young children.

Results

The status-RS correlation appears not to hold in modern Canada. There was no main effect of income on number of children in this sample ($N=1174$, $F=1.604$, $p<0.206$). There was, however, a significant interactive effect of sex of the respondent by income ($F=8.101$, $p<0.001$). Men in the high income group had the same number of children, on average, as men in the low income group (simple effects of income for men F=1.0925, $p>0.05$) while women had significantly more children in the low income group than in the high income group (simple effects of income for women F=8.6712, $p<0.01$). Although these results may at first seem hard to reconcile, they are not in fact contradictory when you consider the effects of single parenthood: single mothers tend to have very low incomes, while single fathers are not similarly affected. These results are not consistent with the notion that wealth is correlated with larger numbers of children (high RS). There was a main effect of income on the number of grandchildren respondents had, but the results were in the opposite direction from the prediction. Wealthier people had fewer grandchildren than poorer people (N=1234, F=24.525, $p<0.000$). Again, these results are inconsistent with the idea that wealthier people will leave more descendants, although it is possible that the poor have grandchildren earlier and the wealthier catch up at a later age.

Income is related to the likelihood of having at least one child, at least for men. Men in the low income group were significantly more likely to remain childless than men in the high income group (Fig. 1, N=597, $\chi^2=23.345$, $p<0.00001$). There was no effect of income on childlessness for women (Fig. 1, N=577, $\chi^2=0.037$, p=.847).

Income is also related to the sex of firstborn children. Low income mothers were significantly more likely to give birth to girls, and high income mothers were more likely to have boys (Fig. 2, N=224, $\chi^2=6.292$, $p<0.01$). This pattern is consistent with expectations from the Trivers-Willard effect, and parallels results found in other studies of this effect in contemporary North America (Abernathy and Yip 1990;

Gaulin and Robbins 1991). Partial correlations were also run to be certain that this effect was not spurious and instead due to parental age differences or differences in the presence or absence of a father in the household, which have also been hypothesized to affect parental 'condition' (Clutton-Brock 1991). The relationship between sex and income still held after these additional effects had been partialled out.

Thus, while the RS-status correlation does not hold in modern Canada, this lack of effect seems to occur in the number of children people have, and not in whether they have any at all. Wealthy men, at least, are more likely to have children than poor men. When they do have them, they simply have fewer. Furthermore, the existence of a Trivers-Willard effect on sex ratio of offspring can be interpreted as evidence that Canadians still behave as though status was relevant to RS, even though it appears not to be. Thus, although the link between status and RS does appear to have deteriorated in this population, the results of these analyses, together with Pérusse's (1993) data on the relationship between status and sexual access for men, suggest that modern Canadians still behave as though the two are linked in several ways. While these results are not necessarily proof that Canadians treat status as though it were a proxy for fitness, this evidence reinforces the adaptationist rationale for seeking patterns of status striving in relation to birth order.

Birth Order and Sibship Size

My purpose is not merely to suggest that status striving is an adaptation, but also to investigate the relationship between birth order, sibship size and status striving in modern Canada. If people do strive to increase status, how might this vary by birth order, and why?

One of the most surprising findings to come out of the field of behavior genetics is the striking degree to which children in the same family differ from one another. These environmental differences constitute the primary source of environmental variance in cognitive ability, personality, and psychopathology, and this variance makes two children in the same family as different from each other as children randomly selected from the population at large (Plomin and Daniels 1987). Siblings and twins grow increasingly dissimilar to each other across childhood and adolescence (Loehlin 1992; McCartney et al. 1990). These differences have been interpreted as attempts to find different family niches.

If niche picking does occur within families, then birth order could be one convenient way to organize this differentiation. The number of older siblings present in the household is perhaps the most predictable source of variance in the environment into which different children are born.

Birth order has been extensively studied in personality psychology, and extensively dismissed. Many studies have failed to find significant differences between individuals based on birth order. This has led to the widespread conclusion that such differences do not exist or are of little importance (e.g. see Ernst and Angst 1983; Plomin and Daniels 1987). This conclusion may, however, be in error.

Birth order effects are, by definition, within family effects, yet the vast majority of birth order studies draw only one child from each family. This is likely to lead to a significant loss of statistical power unless a number of extraneous between family differences, most notably social class and sibship size, are controlled for. Sulloway (1995) has completed a meta-analysis of all studies of the effect of birth order on the Big Five personality dimensions (extroversion, agreeableness, neuroticism, openness, and conscientiousness) that control for social class and sibship size, and has found a large and highly significant effect of birth order on all five dimensions. Firstborns score higher than laterborns on measures of extroversion, neuroticism, and conscientiousness, while laterborns score higher on agreeableness and openness. Sulloway (1995) has also completed an historical study of the effect of birth order on willingness to accept radical innovation. Laterborns are significantly more likely to accept and champion radical innovations than firstborns.

Several previous studies have already shown effects of birth order on factors that could be interpreted as status striving and status attainment measures. Compared to laterborns, firstborn children attain higher levels of education, and attain greater occupational achievement, both of which are linked to higher status (Adams 1972; Taubman and Behrman 1985). Marjoribanks (1988, 1989) found that birth order was significantly related both to status aspirations of Australian adolescents, and to their status attainment at age 21. Firstborns have also been found to score higher on measures of self-esteem (Zajonc et al. 1979).

There is also evidence that birth order not only affects the way children behave, it also affects the way their parents treat them across a wide range of situations. The evidence generally points to parents giving firstborn children preferential treatment over laterborns. In an analysis of the phenomenon of wet-nursing, Hrdy (1992) found that parents paid for their firstborn children to be nursed longer than their laterborns. Taubman and Behrman (1985) presented data from the U.S.A. showing that firstborn children spent more years in school than laterborns. In a study of nutritional status by birth order in the Philippines, Horton (1988) showed that laterborn children were more malnourished than firstborn ones. An analysis of British National Child Development Study data (Kaplan et al. 1992) found that firstborn children also received more medical surveillance. Thus, if status striving is such a strong motivation, and serves as a proximate measure of success, parents should help children to strive, and birth order effects on status striving may likely reflect variations in parental treatment.

If sibling differences are in fact the result of parental discrimination, and if this discrimination typically favors firstborn children, then the specific niche an individual offspring occupies should be more dependent on the number of older siblings still receiving parental care than on the number of younger siblings. That is, the way in which parents divide up investment should be predictably related to the birth order of the child. Within a brood each subsequent offspring might receive increasingly different treatment and select different niches. If this is indeed the case, a comparison between brood sizes should reveal a much larger effect of brood size on the treatment received by lastborn offspring than by firstborns regardless of whether there is a main effect of brood size on per capita investment.

The present study is designed to test the hypothesis that niche differentiation within a family is related to birth order. More specifically, the present study tests the hypothesis that first born children are more status striving than their later born siblings, and that this disparity increases the more older siblings a laterborn child has.

A number of variables were used to index status striving in this study. Some, namely education, age of first marriage, number of children desired and age at which first child was born, can collectively be thought of as measures of attempts to attain or maintain high status. High status individuals in modern Western society typically attain a higher level of education, marry later, begin having children later, and have fewer children than low status individuals (Donaldson 1991; Kasarda et al. 1986). The other variables, total annual household income and the number of children respondents actually had, can be thought of as measures of status attainment. Firstborns are predicted to rank higher on measures of status striving, and the degree of such striving should not be affected by the number of siblings they have. Laterborns, on the other hand, should rank lower on measures of status striving, and this decline should be correlated with the number of older siblings they have. If these status striving strategies are effective, then firstborns should also show higher status attainment.

Methods

These analyses used the same GSS data set described previously. All analyses were performed on SPSS/PC using forced entry multiple regression. The detail in which the variables were coded was the decision of Statistics Canada, and all analyses used the most complete codings available. Respondents who had no siblings were excluded from analysis. A number of control variables were added to the models. These included age (in years) and sex of the respondent (0=female, 1=male), number of siblings (1-10), and mother's age at the time when the respondent was born (in years). Although hypotheses could be generated about the relationship between mother's age or number of siblings and any of the dependent variables, any significant main effects of these variables in these analyses should be ignored as they are confounded with socio-economic status (SES). The GSS does not supply any measure of childhood SES, so it is impossible to partial out the correlation between status striving or attainment measures and these control variables.

The prediction that oldest children would receive more education was tested by adding birth order to the equation as a dummy variable where 0=lastborn and 1=firstborn. The prediction that , compared to lastborns, the amount of education firstborns receive would be less affected by the number of siblings they have was tested by the addition of the interaction between birth order and number of siblings to the model. The interaction between sex of the respondent and number of siblings was also included to see whether firstborn males were especially favored, and to control for this effect if it existed. Sex and age of respondent, number of siblings, and age of mother when the respondent was born were also included as control variables. The dependent variable was the highest level of education received by the respondent. This variable was coded as follows: 1=elementary school or less, 2=at least some secondary school, 3=at least some trade or technical school, 4=at least some college, 5=at least some university, 6=at least some postgraduate work. After removing cases with missing data, 3098 respondents remained and were used for this analysis.

The analysis of the relationship between birth order, its interaction with sibship size, and the age at which respondents were first married was run twice. The first model was set up identically to the analysis of education, except with age of first marriage (in years) as the dependent variable. The second model added two additional independent variables, education (coded as above) and total annual household income, to determine whether any significant birth order effect seen in the first model was truly due to the effect of age at first marriage, or whether it was instead due to its correlation with either of these variables. For this analysis, and all analyses in which it was included, income was coded as follows: 1=$0 to $19,999, 2=$20,000 to $39,999, 3=$40,000 to $59,999, 4=$60,000 to $79,999, 5=$80,000+, in order to turn it into approximately an interval scale. The number of respondents in these analyses was 2234 and 1929 respectively.

The analysis of the relationship between birth order, its interaction with sibship size and the age of respondents when their first child was born was also run twice. The first model contained birth order (coded as first or last born) and the interaction between birth order and sibship size as independent variables. Age of respondent, sex of respondent, mother's age when the respondent was born, number of siblings and the interaction between birth order and sex were added as control variables. The second model added total education, annual household income, and age at first marriage as additional independent variables to determine whether any significant birth order effect was in fact due to them. Age at birth of first child was coded in years. These analyses were run on 1889 and 1520 respondents respectively.

The analysis of the number of children respondents wanted to have was restricted to respondents between the ages of 15 and 25. Presumably, respondents in this age group are the most likely to still give birth to additional children. In addition to the two test variables, the control variables added to this model were age of the respondent, sex of the respondent, mother's age when the respondent was born, number of siblings, education, total annual household income, and the sex by birth order interaction. 396 respondents fit the criteria for this analysis.

The next analysis used total annual household income as the dependent variable. As the relationship between age of respondent and income is likely to be non-linear, this was tested for in these data. Curve fitting confirmed that there was, in fact, a strong quadratic component to the relationship. Age squared was therefore added to the model as a control variable in addition to age. Other control variables added to this model were sex of the respondent, mother's age when the respondent was born, number of siblings, education, and the sex by birth order interaction. After removing cases with missing data, 2691 respondents remained and were used for analysis.

The final analysis, using the number of children respondents actually had as the dependent variable, was restricted to respondents over the age of 55, as this question is most meaningfully asked of people who have finished having children. The control variables used in this analysis were age of the respondent, sex of the respondent, mother's age when the respondent was born, number of siblings, and the sex by birth order interaction. 602 respondents were included in this analysis.

Results

The results of these analyses show that oldest children receive more education, get married later, are older when they have their first child, and intend to have fewer children than youngest children (Table 1). These effects are not independent, however. The relationship between birth order and age of marriage is partially accounted for by the relationship between income, education, and age of marriage. Similarly, the relationship between the respondent's age when the first child is born and birth order is almost entirely accounted for by education, income, and age at marriage.

For most indices of status striving, the results also show that the number of older siblings a youngest child has affects his or her outcome to a greater degree than does the number of younger siblings an oldest child has. Although in general having more siblings is associated with a lower level of education (remember, however, that this could be due in part to the effect of SES rather than purely family size), being the oldest child reduces the slope of the regression line by about half (Fig. 3a). Similarly, although having more siblings is associated with earlier age at first marriage, being the oldest child almost completely eliminates this effect (Fig. 3b). Being the oldest child also reduces the negative relationship between number of siblings and age when the respondent's first child was born (i.e. reduces the slope of the regression line) by a little more than half (Fig. 3c).

The pattern seen for number of children desired, however, is a bit different. Oldest children intended to have fewer children of their own than youngest children, and the number they wanted to have increases the more siblings they have. On the other hand, there was no effect of sibship size on the number of children youngests wanted to have. For the smallest sibship size oldest children desired fewer children of their own than youngest children, and this effect reversed when sibship size increased beyond 3 (Fig. 3d).

The analyses of status attainment yield somewhat different results from those of status striving (Table 1). As adults oldest children earned more overall than youngest children (Fig. 4). Unlike in the analyses of status striving, however, the relationship between number of siblings and total household income was not different for first and lastborns. And while there was a significant interaction between birth order and sibship size for the number of children desired, these same independent variables were not related to the number of children respondents actually had.

Discussion

The results of these analyses support the idea that firstborn children may be preferentially socialized to strive for high status. The hypothesis that this effect would be the result of sequential niche filling within a family was also supported, as the degree to which oldest children strived (i.e. attained higher levels of education, delayed marriage and childbirth) was largely unaffected by the number of younger siblings they had, but the degree to which youngest children strived decreased the more older siblings they had. The status attainment analyses, on the other hand, showed a main effect of birth order on status, as measured by total household income, but failed to replicate the differential effect of number of siblings on first and lastborns, nor was any birth order effect seen in the number of children respondents had. Thus, this research is in accord with previous studies on birth order differences in potential measures of status striving. Why might these effects occur? And, more specifically, why is it oldest children that seem to strive the most? There are several possible explanations. Each will be considered in turn.

Perhaps the best place to start is with Sulloway, who is one of the only researchers in this area to offer a theoretical rationale for his results. His research is based on the specific hypothesis that the amount parents invest in a child varies predictably with birth order. He argues, from an evolutionary standpoint, that parents should value older children more than younger children. This is because older children, by virtue of simply having survived longer, are more likely to continue to survive and to reach an age where they can have children of their own. Parents, therefore, may be expected to have evolved to bias their investment in favor of them.

If parents were choosing between the life and death of their offspring this argument makes some evolutionary sense. If you can only save one, save the one most likely to make it to adulthood. This rationale has been used to explain the birth order pattern of chick mortality in siblicidal birds (Mock et al. 1990), and is basic to the most common explanation of hatching asynchrony in birds in general (Clark and Wilson 1981; Lack 1954).

If parents are forced to choose a child to encourage to climb the socioeconomic ladder, they should, then, generally choose their eldest. This reasoning is similar to that of the resource dilution hypothesis that has been advanced in the sociological literature to account for the frequently occurring negative relationship between family size and educational outcomes (Heer 1985; Powell and Steelman 1993). This argument has also been used to explain decreases in educational attainment when children within a family are very close in age (Powell and Steelman 1993). The results of these analyses are consistent with this interpretation.

However this is necessarily a post hoc explanation. If the outcome of these analyses were reversed, explanations as to why youngest children would strive harder for status could just as easily have been made using the same theoretical arguments as Sulloway. If parents are favoring their older children, then in order to attain the same things youngests could arguably have been predicted to have to strive harder. In other words, if youngest children are receiving less investment, then they might be expected to have to expend greater effort than oldest children to achieve equal status to their elder siblings.

Extending Sulloway's original argument, as parental resources are exhausted in the domain of status enrichment the degree of childrens' status striving should decline. Thus with each subsequent child, status striving should decline. As previously mentioned, oldest offspring might be relatively unaffected by the number of younger siblings they have, because, by being firstborn, they all receive the same parental investment strategy. With each subsequent offspring, however, parental resources in various domains become used up on preceding siblings, and competition for these various resources with siblings may increase. Analysis of status striving should reveal a much larger effect of brood size on lastborn offspring than firstborns regardless of whether there is a main effect of brood size.

In fact, the analyses of what are presumed to be manifestations of status striving did show this effect. Analyses of status attainment, however, did not. One possible reason for this lack of consistency is that this interaction effect may be weaker than the birth order main effect. Certainly, the beta weights bear this out. Given the large amount of unexplained variance in these analyses, further research may be required to determine whether this effect truly does not exist, or whether it exists but is masked by unaccounted for error.

Of course, there are other possible explanations for these effects in addition to Sulloway's rationale. The parental forced choice scenario upon which Sulloway bases his theoretical argument may be fundamentally different from the choices parents make about how to partition investment among offspring when there is enough to go around. There is no *a priori* rationale for supposing that parents should achieve the greatest fitness benefits (i.e. end up with more surviving grandchildren) by investing highly in some children and not in others. It is certainly possible that this is the case, but it is just as plausible that parents would do best by treating all children equally, or that the optimal bias in investment between children may be highly variable and environmentally contingent. The optimal parental strategy should be driven by the payoff matrices to parents of partitioning investment in different ways. Without further research into this area it is impossible to determine which of these alternatives would represent the optimal parental strategy.

Clark and Wilson (1981) have challenged the facilitation of brood reduction hypothesis commonly used to explain hatch asynchrony in birds. As explained above, this hypothesis, like Sulloway's, is based on the argument that the reproductive value of a given offspring increases as it ages, so that, when resources are in short supply, parents will preferentially care for older offspring. In situations where resource availability is unpredictable, then, parents may be selected for hatch asynchrony to facilitate this brood reduction when necessary. Clark and Wilson (1981) suggest instead that asynchronous hatching may result from attempts by parents to increase the total number of chicks raised, and that it does not represent a decrease in the amount of investment in younger chicks in at least some species.

A similar explanation may be true for people as well. Human infants require a great deal of time and energy. Caring for more than one at a time may not often be possible. Staggered birth interval in humans is quite likely to be a means for increasing the total number of children that can be raised to adulthood (Blurton-Jones 1986). While parents may treat their children differently, then, these differences could simply be the result of parents engaging in age appropriate interactions. When parental interactions towards their children are scored when those children are at a fixed age, parents have been shown to treat their children remarkably similarly (Dunn et al. 1985, 1986). The hypothesis that parents stand to gain the most by treating all children equally cannot be ignored or rejected.

Just because parents may not invest more heavily in one child than in another, however, they may still stand to benefit from encouraging their children to follow different paths. Humans are a highly social species. The environment in which individual children must survive and the social system into which they must integrate themselves are highly heterogeneous. In order to avoid unproductive competition with other individuals and with other family members, there may be a large benefit to simply being different. If one child excels at a certain task, parents may do best to encourage another child along an alternate path. This is not to say that there is no sibling competition. Siblings certainly do compete with each other, but if intrafamilial competition in a given domain truly imposes costs on the competing individuals, they ought to compete primarily by channeling their energies in different directions. That is, they may compete to succeed, but what they try to succeed in should differ. This hypothesis requires further testing.

The possibility remains that there is no real difference by birth order in the degree to which individuals actually strive for status. The real difference may simply be that children within a family differ in the means by which they attempt to attain the same goal. In this scenario differential treatment could be thought of as a parental strategy to help all children achieve success, rather than a forced sequential devaluation due to diminishing resources. This interpretation is consistent with the greatly reduced relationship between birth order and status attainment, compared with status striving. If all children are, in fact, striving for high status, birth order should not be related to status attainment. If they take different routes to this goal, then birth order effects could exist for measures of status striving.

Of course, the routes children take are not necessarily under parental control. Parental strategies are expected to be determined by the relative costs and benefits of investing in various ways. From a parent's standpoint, the maximal division of parental investment may or may not be equal among offspring and may vary widely with the context. It is impossible to predict parental optima without constructing detailed models of parental payoffs. One thing is certain, however, and that is that whatever the optimal parental division of investment is, children are not likely to agree with the division. Because parents are equally related to all their offspring, while children are more related to themselves than to their siblings, these two parties are expected, from an evolutionary perspective, to be somewhat at odds (Trivers 1974). Specifically, offspring should be selected to try to obtain more investment for themselves than parents are selected to want to give them. For each additional portion of investment a given offspring manages to procure, his or her siblings will necessarily receive less, and thus the benefit to a given offspring of procuring that extra investment will depend on both the degree to which it benefits that child and the degree to which it harms its siblings. Although this will affect the degree to which a child may fight for extra investment, there is still an inherent conflict of interest. Unquestioningly accepting parental manipulation is not likely to be in the child's best interest.

There is evidence that children do spend a lot of time monitoring parental interactions with their siblings and are very good at detecting parental biases. From a very young age, children are remarkably sensitive to any parental discrimination and will attempt to intervene when they perceive that their siblings are receiving too much attention from their parents (Dunn and McGuire 1994).

Birth order differences could be a result of differing payoffs to children of accepting parental attempts at control. The younger a child is, the more investment it is likely to require from its parents. The degree to which the loss of any of this investment harms a child is also likely to be greater the younger it is. For an extreme example, think of the effect on an infant of not being fed by its parents for a day versus the effect on a teenager. One is clearly capable of feeding him or herself should the need arise, the other is not. Thus, for the oldest child in a family, the procurement of extra investment from parents will have a larger effect on his or her siblings than the same behavior will on the part of a youngest child. That oldest child "needs" less to begin with, and his siblings may suffer more from his greed than he will benefit by it. That youngest child, on the other hand, will benefit more from being greedy, and has siblings who will not suffer as much from the loss of a little investment. Of course much of this argument is hypothetical and requires more careful testing before it can be set forth as a real hypothesis, but it is at least a plausible scenario.

How could this affect status striving? If firstborn children stand to gain less from demanding increased investment this may be expected to manifest itself as decreased conflict with parents. To the extent that parents attempt to control their children's behavior, and encourage them to stay in school and get good jobs, firstborns may listen more. In general, because of this decreased parent-offspring conflict, they may simply be more obedient. Subsequent offspring may be less so. This hypothesis does not automatically predict the sibship size effect seen in the data, but it may provide part of the explanation.

It is difficult to know exactly how to interpret the results of these analyses without greater knowledge of the details of parent-offspring and sibling-sibling influences on behavior and of the link between these influences and success in the extra-familial social environment. Nevertheless, the present analyses did provide support for the notion that differences in birth order and sibship size are related to differences in an individual's life strategy. Despite some claims to the contrary, there is evidence that birth order affects the niches children fill. The reasons behind this predictable relationship, however, are still unclear. They could be a result of oldest children receiving more from parents, of the benefits to parents of treating different children differently, or even of the benefits to different children of treating parents differently.

Acknowledgments

I thank M. Daly, H. Kaplan, B. Low, and F. Sulloway for enlightening conversation about birth order issues. I thank M. Daly, L. Gibbs, R. Morrison and J. Quinn for helpful comments on this manuscript. I thank R. Morrison for statistical advice, M. Wilson and P. Robinson for procuring the GSS database, and C. Salmon for helping with some of the references. This research derived financial support from a Natural Sciences and Engineering Research Council of Canada grant awarded to M. Daly.

References Cited

Abernathy, V. and R. Yip

1990 Parent Characteristics and Sex Differential Infant Mortality: the Case in Tennessee. *Human Biology* 62:279-290.

Adams, B. N.

1972 Birthorder: a Critical Review. *Sociometry* 35:411-439.

Bateman, A. J.

1948 Intra-Sexual Selection in *Drosophila. Heredity* 2:349-368.

Betzig, L. L.

1986 *Despotism and Differential Reproduction: A Darwinian View of History.* New York: Aldine.

1994 The Point of Politics. *Analyse und Kritik* 16:20-37.

Betzig, L. L. and P. W. Turke

1986 Parental Investment by Sex on Ifaluk. *Ethology and Sociobiology* 7:29-37

Blurton-Jones, N.

1986 Bushman Birth Spacing: A Test for Optimal Interbirth Intervals. *Ethology and Sociobiology* 7:91-105.

Boone, J. L.

1988 Parental Investment, Social Subordination, and Population Processes among the 15th and 16th Century Portuguese Nobility. In *Human Reproductive Behavior: a Darwinian Perspective,* L. Betzig , M. Borgerhoff Mulder, and P. Turke, eds. Pp. 201-219. Cambridge: Cambridge University Press.

Buss, D. M.

1989 Sex Differences in Human Mate Preferences: Evolutionary Hypotheses Tested in 37 Cultures. *Behavioral and Brain Sciences* 12:1-46.

Clark, A. B. and D. S. Wilson

1981 Avian Breeding Adaptations: Hatching Asynchrony, Brood Reduction, and Nest Failure. *Quarterly Review of Biology* 56:253-277.

Clutton-Brock, T. H.

1991 *The Evolution of Parental Care.* Princeton: Princeton University Press.

Cronk L.

1991 Preferential Parental Investment in Daughters over Sons. *Human Nature* 2:387-417.

Daly, M., and M. Wilson

1983 Sex, Evolution, and Behavior, second ed. Boston: Duxbury Press.

1984 A Sociobiological Analysis of human Infanticide. In *I nfanticide: Comparative and Evolutionary Perspectives*, G. Hausfater and S. B. Hrdy eds. Pp. 487-502. Hawthorne NY: Aldine de Gruyter.

Dewsbury, D. A.

1982 Dominance Rank, Copulatory Behavior, and Differential Reproduction. *Quarterly Review of Biology* 57:135-158.

Dickemann, M.

1993 Human Reproductive Plasticity. *Behavioral and Brain Sciences* 16:290-291.

Donaldson, L.

1991 *Fertility Transition*. Cambridge MA: Basil Blackwell.

Dunn, J. and S. McGuire

1994 Young Children's Nonshared Experiences: A Summary of Studies in Cambridge and Colorado. In *Separate Social Worlds of Siblings: The Impact of nonshared Environment on Development*, E. M. Hetherington, D. Reiss, and R. Plomin, eds. Pp. 111-128. New Jersey: Lawrence Erlbaum Associates.

Dunn, J., R. Plomin, and M. Nettles

1985 Consistency of Mother's behavior Towards Infant Siblings. *Developmental Psychology* 21:1188-1195.

Dunn, J., R. Plomin, and D. Daniels

1986 Consistency and Change in Mother's Behavior to Two-Year-Old Siblings. *Child Development* 57:348-356.

Ernst, C. and J. Angst

1983 *Birthorder: Its Influence on Personality.* New York: Springer-Verlag.

Essock-Vitale, S. M.

1984 The Reproductive Success of Wealthy Americans. *Ethology and Sociobiology* 5:45-49.

Fedigan, L. M.

1983 Dominance and Reproductive Success in Primates. *Yearbook of Physical Anthropology* 26:91-129.

Gaulin, S. J. C., and C. J. Robbins

1991 Trivers-Willard Effect in Contemporary North American Society. *American Journal of Physical Anthropology* 85:61-69.

Heer, D. M.

1985 Effect of Number, Order, and Spacing of Siblings on Child and Adult Outcomes: An Overview of Current Research. *Social Biology* 33:1-4.

Himes, N. E.

1936 *Medical History of Contraception.* Baltimore: Williams and Wilkins.

Horton S.

1988 Birth order and Child Nutritional Status: Evidence from the Philippines. *Economic Development and Cultural Change* 36:341-354.

Hrdy S. B.

1992 Fitness Tradeoffs in the History and Evolution of Delegated Mothering with Special Reference to Wet-Nursing, Abandonment, and Infanticide. *Ethology and Sociobiology* 13:409-442.

Hrdy S. B. and D. S. Judge

1993 Darwin and the Puzzle of Primogeniture. *Human Nature* 4:1-45.

Kaplan B.A., C. G. N. Mascie-Taylor, and J. Boldsen

1992 Birth order and Health Status in a British National Sample. *Journal of Biosocial Science* 24: 25-33.

Kasarda, J. D., J. O. G. Billy, and K. West.

1986 *Status Enhancement and Fertility.* Orlando FL: Academic Press.

Lack D.

1954 *The Natural Regulation of Animal Numbers.* London: Oxford University Press.

Loehlin, J. C.

1992 *Genes and Envorinment in Personality Development.* Newbury Park CA: Sage.

Low, B. S.

1991 Reproductive Life in Nineteenth Century Sweden: An Evolutionary Perspective on Demographic Phenomena. *Ethology and Sociobiology* 12:411-448.

Marjoribanks K.

1988 Sibling, Family Environment and Ability Correlates of Adolescents' Aspirations: Ethnic Group Differences. *Journal of Biosocial Science* 20:203-209.

1989 Ethnicity, Sibling, and Family Corelates of Young Adults' Status Attainment: A Follow-Up Study. *Social Biology* 36:23-31.

McCartney, K. M. J. Harris, and F. Bernieri

1990 Growing Up and Growing Apart: A Developmental Meta-Analysis of Twin Studies. *Psychological Bulletin* 107:226-237.

McLaren, A.

1990 *A History of Conception*. Cambridge, MA: Basil Blackwell.

Mealey, L. and W. Mackey

1990 Variation in Offspring Sex Ratio in Women of Differing Social Status. *Ethology and Sociobiology* 11:83-95.

Mock, D. W., H. Drummond, and C. H. Stinson

1990 Avian Siblicide. *American Scientist* 78:438-449.

Pérusse, D.

1993 Cultural and Reproductive Success in Industrial Societies: Testing the Relationship at Proximate and Ultimate Levels. *Behavioral and Brain Sciences* 16:2647-322.

Plomin, R. and D. Daniels

1987 Why are Children in the same Family so Different from One Another? *Behavioral and Brain Sciences* 10:1-59.

Powell, B. and L. C. Steelman

1993 The Educational Benefits of Being Spaced Out: Sibship Density and Educational Progress. *American Sociological review* 58:3647-381.

Riddle, J. M.

1992 *Contraception and Abortion from the Ancient World to the Renaissance.* Cambridge MA: Harvard University Press.

Statistics Canada

1991 The 1990 general social survey cycle 5: family and friends. Public use microdata file, documentation, and user's guide

Sulloway, F. J.

1995 Birth Order and Evolutinary Psychology: A Meta-Analytic Overview. *Psychological Inquiry* 6:75-80.

Taubman P. and J. R. Behrman

1986. Effect of Number and Position of Siblings on Child and Adult Outcomes. *Social Biology* 33:22-34.

Trivers, R. L.

1972 Parental Investment and Sexual Selection. In *Sexual Selection and the Descent of Man 1871-1971,* B. Campbell ed. Pp. 136-179. Chicago: Aldine.

Trivers, R. L. and D. E. Willard

1973 Natural Selection of Parental Ability to vary the Sex Ratio of Offspring. *Science* 179:90-92.

Voland, E.

1988 Differential Infant and Child Mortality in Evolutionary Perspective: Data from Late 17th to 19th Century Ostfriesland (Germany). In *Human Reproductive Behavior: a Darwinian Perspective,* L. Betzig , M. Borgerhoff Mulder, and P. Turke, eds. Pp. 253-261. Cambridge: Cambridge University Press.

Voland, E., E. Siegelkow, and C. Engel

1991 Cost/Benefit Oriented Parental Investment in High Status Families: The Krummhörn Case. *Ethology and Sociobiology* 12:105-118.

Williams, G. C.

1966. *Adaptation and Natural Selection.* Princeton: Princeton University Press.

Zajonc, R. B., H. Markus, and G. B. Markus

1979 The Birth Order Puzzle. *Journal of Personality and Social Psychology* 37:1325-1341.

Analysis	Variable	Beta	t	p Value
Education	Sex	.1044	2.006	.0449
	Age	-.1053	-5.736	.0000
	Mother's Age	.2286	10.151	.0000
	# of Siblings	-.2529	-8.411	.0000
	Birth Order	.1899	3.033	.0024 *
	# Sibs x Birth Order	.1305	3.216	.0013 *
	Sex x Birth Order	.1452	1.916	.0555
Age of First Marriage	Sex	.4875 *.4192*	8.235 *6.734*	.0000 *.0000*
	Age	.0723 *.0901*	3.468 *4.128*	.0005 *.0000*
	Mother's Age	.1567 *.1079*	6.056 *3.932*	.0000 *.0001*
	# of Siblings	-.1119 *-.5605*	-2.999 *-1.415*	.0027 *.1571*
	Birth Order	.2171 *.1273*	3.002 *1.693*	.0027 * *.0907*
	# Sibs x Birth Order	.1071 *.0814*	2.162 *1.574*	.0308 * *.1157*
	Sex x Birth Order	.2557 *.1711*	2.900 *1.857*	.0038 *.0635*
	Education	*.2324*	*10.246*	*.0000*
Age When First Child Born	Sex	.4270 *.1011*	6.762 *1.941*	.0000 *.0525*
	Age	.1419 *.0634*	6.443 *3.527*	.0000 *.0004*
	Mother's Age	.2202 *.0621*	7.975 *2.703*	.0000 *.0070*
	# of Siblings	-.2055 *-.0729*	-5.252 *-2.135*	.0000 *.0329*
	Birth Order	.1820 *.0419*	2.369 *0.685*	.0179 * *.4936*
	# Sibs x Birth Order	.1252 *.0147*	2.434 *0.335*	.0150 * *.7377*
	Sex x Birth Order	.1700 *.0387*	1.812 *0.512*	.0702 *.6090*
	Education	*.0770*	*4.026*	*.0001*

	Age of Marriage	*.6414*	*33.907*	*.0000*
Number of Children Respondent Desires	Sex	-.1571	-0.996	.3198
	Age	.0452	0.847	.3976
	Mother's Age	.0172	0.262	.7934
	# of Siblings	.0381	0.594	.5529
	Birth Order	-.3981	-2.169	.0307 *
	# Sibs x Birth Order	.3691	3.873	.0001 *
	Sex x Birth Order	-.2299	-1.033	.3021
	Education	.0647	1.285	.1997
	Income	-.0270	-.514	.6076
	Current # of Children	.1815	3.473	.0006
Total Annual Household Income	Sex	.1490	2.877	.0040
	Age	1.6837	16.895	.0000
	Age Squared	-1.5332	-15.376	.0000
	Mother's Age	.0328	1.425	.1542
	# of Siblings	-.0690	-2.272	.0231
	Birth Order	.1224	1.981	.0477 *
	# Sibs x Birth Order	.0001	0.005	.9962
	Sex x Birth Order	.0882	1.176	.2398
	Education	.2359	13.089	.0000
Number of Children Born	Sex	-.1744	-1.413	.1581
	Age	.2617	6.330	.0000
	Mother's Age	-.0212	-.434	.6642
	# of Siblings	.1657	1.252	.2109
	Birth Order	-.1288	-0.969	.3329
	# Sibs x Birth Order	-.0454	-0.296	.7676
	Sex x Birth Order	-.1634	-0.972	.3317

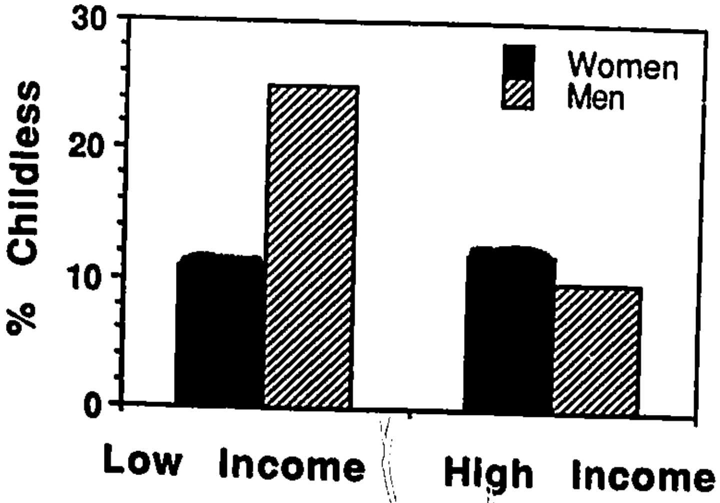
Table 1. Results of the regression analyses for birth order. Each analysis is presented separately. Where two regression models were run with the same dependent variable the values for the first model are in plain text and the values for the second are in italics. Most variables are control variables. The two of interest, birth order and birth order x sibship size are starred where significant. The beta weights presented are standardized.

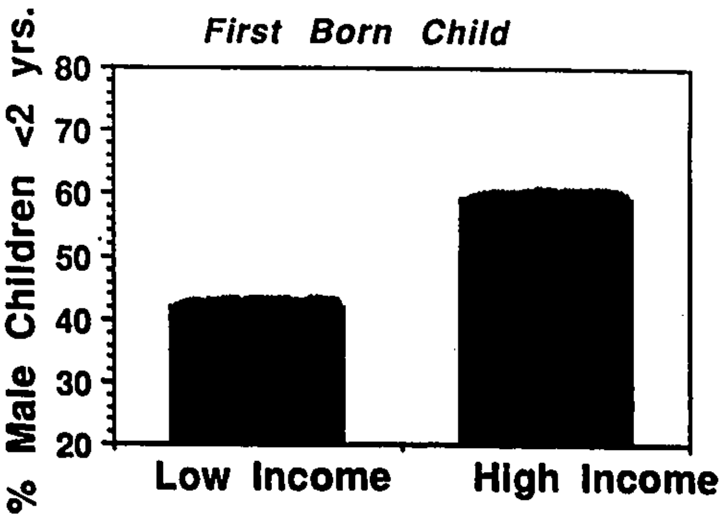
Figure 1. The percentage of men and women between the ages of 55 and 65 in the upper versus lower 50 percent income brackets who did versus did not have any children during their lifetimes. Data from the general Social Survey, cycle 5, conducted in 1990 by Statistics Canada.

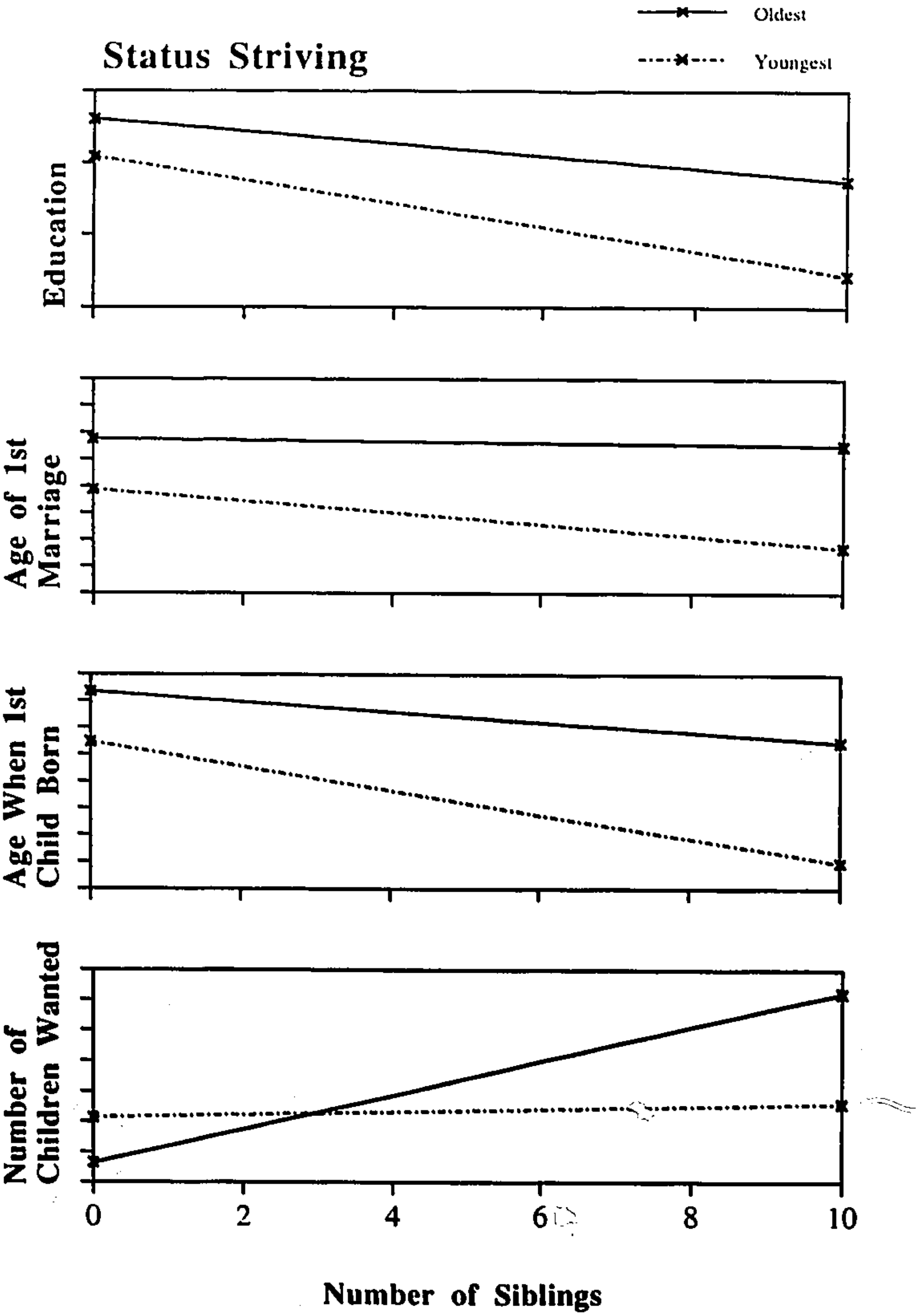
Figure 2. The percentage of mothers in the upper vs. lower 50 percent income brackets with male vs. female firstborn children less than 2 years old at the time of the survey.

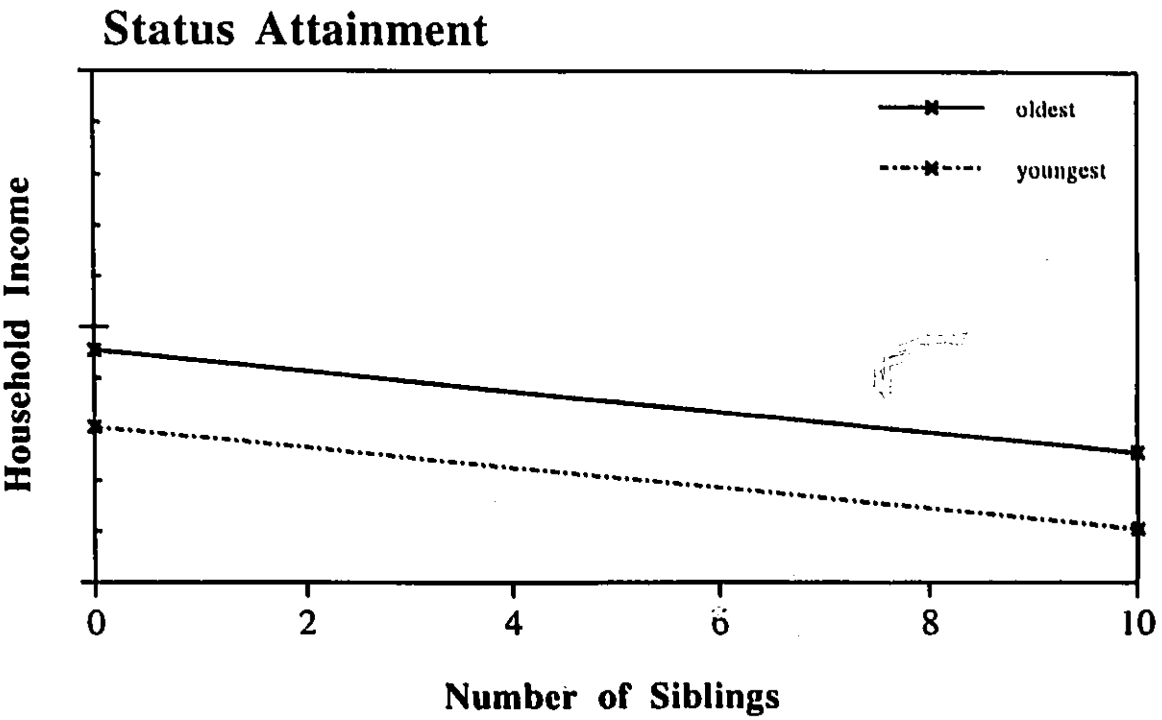
Figure 3. Results of the analyses of the effects of birth order and sibship size on various phenomena which may be interpreted as status striving. Graphs are designed to portray the relative strengths of relationships, not absolute values, which are dependent on all variables in the analysis, not just the ones shown. Each tick on the y-axis represents one unit increase, but no numbers are given. (a) represents the relationship between number of siblings and highest level of education completed for first and lastborn children. (b) portrays the same relationship for age at first marriage. (c) shows the relative effect of sibship size on the age at which the first child was born to first and lastborn respondents. (d) represents the relationship between birth order, sibship size, and the number of children respondent's age 25 or younger intend to have. Note the significant interaction effect (non-parallel lines on the graph) between sibship size and birth order for all four analyses.

Figure 4. Results of the analyses of the effects of birth order and sibship size on status attainment as measured by adult income. This graph is designed to portray the relative strength of the relationship, not absolute values, which are dependent on all variables in the analysis, not just the ones shown. Each major tick on the y-axis represents one unit increase. See methods for ordinal unite of teh income variable. Note the parallel lines; there is no significant interaction effect in this analysis. Although oldest children appear to earn slightly more than youngest children overall, the effect of sibship size on income is similar for first and lastborn respondents.


30
20
10
0
% Childless
Women
Men
Low Income
High Income


First Born Child
% Male Children <2 yrs.
80
70
60
50
40
30
20
Low Income
High Income


Oldest
Youngest
Status Striving
Education
Age of 1st Marriage
Age When 1st Child Born
Number of Children Wanted
0
2
4
6
8
10
Number of Siblings


Status Attainment
oldest
youngest
Household Income
0
2
4
6
8
10
Number of Siblings

Distribution of Parental Investment and Sibling Competition in the Herring Gull, *Larus argentatus.*

Under review at the Condor

Jennifer Davis
Department of Psychology
McMaster University
Hamilton, Ontario L8S 4K1
Canada

James S. Quinn
Department of Biology
McMaster University
Hamilton, Ontario L8S 4K1
Canada

Running Head: Parental Investment and Sibling Competition in Herring Gulls

Abstract

Herring gulls, *Larus argentatus*, typically lay three eggs. The third laid egg is smaller, hatches later, and hatches a lighter, smaller chick than the first two. The third hatched chick also has a lower chance of survival. This size asymmetry and hatch asynchrony have been thought to facilitate brood reduction when there is insufficient food to raise three young. It has been suggested that parents continue this pattern of unequal resource distribution by behaviorally discriminating against the third chick after it hatches. Observations of parent-chick and chick-chick interactions were conducted at two Ontario sites in the Great Lakes to determine whether and how parents might behaviorally bias investment after the incubation period, and how interactions among chicks might add to the third chick disadvantage. Little evidence was found for behavioral discrimination against the third chick by either its parents or its siblings. In fact, third hatched chicks were the most likely to peck siblings.

Key Words

Herring Gull, parental investment, hatch order, aggression, begging

The herring gull, *Larus argentatus*, is a ground nesting colonial waterbird found widely in marine and fresh water environments throughout the northern parts of the northern hemisphere. Herring gulls typically lay three eggs which hatch precocial young. As in most gulls, the third laid egg is generally smaller and hatches later than the first two (Parsons 1975, Graves et al. 1984, Pierotti & Bellrose 1986, Hébert & Barclay 1988). When the first and second (or A and B) chicks hatch, the parents begin to feed and brood them. This disrupts incubation of the remaining, unhatched egg, and leads to a significant drop in its temperature. There is evidence, however, that the third egg is adapted to this circumstance. Lee et al (1993) have shown that hatchability and time to hatch of this egg are unaffected by natural levels of neglect.

Nevertheless, the third hatched, or C chick, does seem to be at a disadvantage. In addition to hatching later, it hatches at a smaller size and lighter weight than its siblings, grows at a slower rate, and has a higher pre-fledging probability of mortality (e.g. Parsons 1975, Hébert & Barclay 1988).

Several explanations have been offered for the pattern of disadvantage that accrues to the C chick in herring gulls. The two most common ones will be considered here. One, following Lack's (1954) hypothesis, interprets it as evidence of an adaptive response to an unpredictable food supply which allows parents to reduce brood size to fit the availability of food. Evidence for this comes primarily from experiments showing that artificially created synchronously hatching nests fledge fewer chicks than asynchronous ones (herring gulls: Parsons 1974, laughing gulls: Hahn 1981).

Graves et al. (1984) have offered a different explanation. Based on the results of a food provisioning experiment and data that suggest the parental effort required to fledge three chicks instead of two is very high, they argue that the third-laid egg functions primarily as insurance against the loss of one of the first two. By setting up an age and size asymmetry parents facilitate the survival of the A and B chick and the demise of the C chick, should all three hatch. The mechanism of brood reduction posited by Graves et al. is starvation of the C chick due to reduced ability to compete for food.

Despite the well documented observation that the C chick does seem to suffer from a disadvantage compared to its siblings, few studies attempt to document the nature of this disadvantage. Graves et al. (1984) made the observation that parents fed chicks 60 to 100 cm from the nest, and suggested that this decreased C's ability to reach the food in the first couple of days after hatching. However, they provided no direct evidence to support this claim.

Herring gull parents feed their chicks by regurgitating chunks of food onto the ground. Chicks then feed from the regurgitated bolus. This should leave little room for parental control of chick feeding hierarchies. Hébert and Barclay (1986) reasoned that parents might be able to control which chicks obtain food by moving around the territory and making chicks chase them. The younger, sma[illegible]r C chicks should be less able to keep up. They measured the order at which chicks arrived at food in three chick nests. While they found no overall difference in the order of arrival, when they did paired comparisons they found that C arrived significantly later than B, but not A. The statistics used for this comparison, however, were not the most appropriate for their data. Upon reanalysis we found that this difference is not quite significant (χ^2=3.78, p>0.05, crit.value=3.84). Hébert and Barclay (1986) also found that A and B participated in a greater number of feedings than C. This difference is significant.

Here we attempt to determine the nature of the C chick disadvantage by addressing the question: are C chicks *behaviorally* discriminated against, or is any disadvantage they suffer simply due to differences in competitive ability among chicks? This can be divided into three sub-questions: 1) do parents discriminate against the C chick? 2) do the A and B chicks discriminate against the C chick? 3) are C chicks at a competitive disadvantage compared to their siblings?

Methods

Data were collected from two populations of herring gulls over two years. One colony, nesting in Hamilton Harbor on the western end of Lake Ontario (45° 15'/79° 51'), was studied during the breeding seasons of 1994 and 1995. The other, nesting in Port Colbourne on the eastern end of Lake Erie (45°15'/79°46'), was studied in 1995 only.

Colony nests were marked with numbered stakes for identification. Because of the flat, open habitat at the Hamilton Harbor colony, territories were fenced to reduce the mortality risk to chicks from running off their territory for cover when experimenters entered the colony. Territories at Port Colbourne contained abundant hiding places for the chicks and were not fenced.

In 1994, for the first two weeks after chicks began to hatch, nests were censused every day. For the rest of that season, and for the entire 1995 season they were censused every other day, weather permitting. New eggs were weighed and marked when found. Newly hatched chicks were weighed, measured for length from the back of the head to the tip of the bill, web tagged, and dyed for individual identification. Chicks were dyed on the head, throat, or wings with Nyanzol (brown, used at Hamilton Harbor) or Rhodamine-B (pink, used at Port Colbourne). Dye pattern was random with respect to hatch order at Hamilton Harbor, but not at Port Colbourne.

Behavioral observations were made from blinds situated within the colonies. Only the data from nests in which 3 chicks hatched are considered here. A total of 14, asynchronous three chick nests were observable from the blinds. Behavioral observations were conducted when the C chick was between 0 and 9 days old, because this is the highest period of C chick mortality and hatch order effects on feeding ability have been hypothesized to be greatest during this period(e.g. Graves et al. 1984, Hébert and Barclay 1986). Observations were made daily on up to 4 nests at a time for 1 1/2 hour intervals. Observations were conducted between 6:00 and 11:00, and between 17:00 and 20:00.

Data were recorded on begging and feeding behavior, and aggressive interactions between chicks. Herring gull chicks beg in two ways. Chicks will either peck the red spot on their parent's bill, or perform a 'sighing' display in which they alternately raise and drop their heads while vocalizing (Tinbergen 1960). The latter begging method is not commonly performed by young chicks and was rarely observed in this sample, but was still recorded as begging when seen.

Every time a chick began begging the identity of the beggar was recorded as was information on whether or not the parent fed the chick before the end of the begging bout. Begging bouts began when a chick begged and ended when both the chick and the parent ceased watching each other.

Each time a parent fed chicks the following information was recorded: the estimated distance of each chick from the parent, the order in which chicks ate, and whether or not any of the chicks engaged in tug-of-wars over the food. Tugs-of-war occurred when one chick tried to take food away from another and generally ended with two or three chicks pulling on a piece until one managed to pull it away from the other(s). When tugs-of-war occurred, the identity of the initiator, the chick whom the action was initiated against, and the victor were all recorded.

The only other aggressive action observed and recorded between chicks was pecking. When chicks pecked each other the identities of the aggressor and victim were recorded.

Observations of nest groups were made by one or two people at a time. All observers were trained and tested to insure inter-observer consistency in scoring behaviors before collecting data alone. Observers were blind to chick hatch orders, though slight size differences between the chicks may have enabled them to accurately guess hatch orders.

All observational data were analyzed using non-parametric methods (Friedman or Sign tests). These tests were chosen because of the wide variation in number of hours watched and number of behaviors recorded between nests, and because of the unknown reliability of certain measures like exact distances of chicks from parents. By taking only the rank of scores or direction of difference between scores into account these tests remove any possible bias that tests which take the magnitude of differences into account might introduce. To provide some measure of the power of the analyses performed when null results are reported we also report the minimum sample size that would be required to get a significant result given the effect size seen in the data. While this is not a traditional way to present power calculations, we were unable to find a way to perform power calculations with Friedman's test, and we believe that this method provides an intuitive means to assess the strength of our results.

Just to be sure the age range chosen for observation was not too long, when possible all analyses were also performed for data collected on days 0-4 only. In no case did the results of the day 0-4 analysis differ from the results of day 0-9, so only the day 0-9 data are reported here. Although a total of 14 nests were studied, not all behaviors were observed at all nests, so the n varies slightly for different comparisons.

Results

Parent-Chick Interactions

It has been hypothesized that parents feed farther from the C chick and that this leads to C arriving at the food last. Before addressing this we ask: is there a benefit to being closer? In this sample the closest chick was most likely to eat first (Fig. 1, sign test, n=10, +=10, p<0.001). However, eating later did not mean a chick missed getting food. In this sample, especially for chicks of such young ages, order of arrival at the food never appeared to influence an individual chick's ability to eat. Parents always regurgitated more than a single chick could swallow, and frequently reswallowed leftover portions of food after the chicks had finished eating.

Given that closer chicks were still more likely to eat first, did hatch order affect whom parents fed closest to? In this sample it did not (Friedman test, n=12, Fr=0.125, n needed for significance=575). Parents were no more likely to feed closer to A or B than to C. Results of an analysis of whom parents fed farthest from were also not significant (Friedman test, n=12, Fr=0.542, n needed for significance=133).

Although parents did not appear to be feeding farther from the C chick it is possible that they discriminated against it in other ways, perhaps in their response to begging. Hatch order did not affect the likelihood of parents feeding a chick when it begged (Friedman test, n=13, Fr=0.4319, n needed for significance=169).

Chick Competition

All the arguments made about biased parental treatment have hinged on the assumption that the C chick is at a competitive disadvantage with respect to its siblings. Is there any evidence of such a disadvantage in this sample?

Given the developmental disadvantage of C chicks it is plausible that they might still get to the food last even if they start no farther from it than the A and B chicks. Results of analyses of the effects of hatch order on who gets to the food both first and last showed no significant effects (Friedman test, n=12, First: Fr=2.042, n needed for significance=35, Last: Fr=1.167, n needed for significance=62).

Another possible means of chick competition is begging behavior. Begging chicks in this sample were more likely to be closest to the parent when fed (Fig. 2, Sign test, n=6, +=6, p<0.016). Begging chicks were also more likely to eat first, though not significantly so (Fig. 2, Sign test, n=6, +=5, p=0.109, n needed for significance=10). Although it might seem that the method herring gull chicks use to beg would necesitate that beggars be closer, there was almost always a brief time lag before parents actually fed, which did give chicks the opportunity to change positions.

Given this, does hatch order affect who begs the most? The A chick begged the most and C the least, as expected, but this difference was not significant (Friedman test, n=13, Fr=5.538, n needed for significance=15). Similarly, the A chick ate more often than B or C, though this effect is also not significant (Friedman test, n=12, Fr=3.792, n needed for significance=19).

It should be noted that when a chick failed to eat, it was not for lack of sufficient food or lack of ability to get it. Chicks that did not eat at a feeding were invariably observed in the vicinity of the food bolus, but made no attempts to go over to or eat it. The overwhelming impression left by their behavior was that they simply were not hungry.

Chick-Chick Interactions

Even if parents are not behaviorally discriminating against chicks it is still possible that chicks discriminate against each other.

Given the age and size disadvantage of the C chick, and the hypothesized reasons for this difference, C chicks might be expected to be targets of aggression. Surprisingly, analysis of the effect of hatch order on who pecks siblings the most found that C was significantly more likely to peck than A or B (Fig. 3, Friedman test, n=11, Fr=7.7535, p<0.05).

Regardless of who pecks the most, however, hatch order could still affect who gets pecked. That is, although A and B peck less often, when they do peck they might still choose C as their target. This does not appear to be the case. Neither the A, B, or C chick picked one sibling to peck more often than the other (Sign test, A: n= 7, +=4, B: n=6, +=2, C: n=9, +=3, for all p>0.05, n needed for significance= 147 for A, 30 for B and C).

The same analyses can be done for data on tugs-of-war. Hatch order did not affect who initiated tugs-of-war over food, when the number of tugs-of-war started was scaled by opportunity to start them (i.e. the number of times that chick was not the first one to eat; Friedman test, n=8, Fr=1.3125, n needed for significance=37). Hatch order did, however, affect whom tugs-of-war were started against, when this value was once again scaled by opportunity, in this case the number of times that chick had food. When A and B started tugs-of-war they were more likely to start them against C than against each other (Fig. 4, Sign test, n=8, +=0, p=0.0039). One reason why C might be targeted is that A and B, due to their greater age and larger size, might be more likely to win against C. Analysis of who won tugs-of-war with C, however, shows that this was not the case (Sign test, n=8, +=5, p=0.8555, n needed for significance=56).

Chick Size and Hatch Date Asymmetries

Data from all 3-chick nests at Hamilton Harbor from the 1994 season were analyzed with respect to chick size asymmetries and hatch date asynchrony so that comparisons could be made between this sample and others reported in the literature. Data from 1995 were not included in these analyses due to small sample size and less frequent nest checks which do not allow for accurate hatching synchrony assessment.

There was a surprising amount of intrabrood hatching synchrony in the colony. A total of 28 three chick nests hatched at HH in 1994 during the period in which nest checks were made every 24 hours, excluding nests hatching around a day when the check was cancelled due to inclement weather. Of these, the B and C chicks hatched on the same day in 7, or 25% of them. In 3 of those, or 11% of the 28 three chick nests, A, B, and C all hatched within 24 hours. Synchronously hatching nests were excluded from behavioral analyses.

Analysis of the head to tip measures taken on asynchronous broods revealed no significant effect of hatch order on head size. There was, however, a significant difference in the hatching mass of chicks. The A and B chicks were significantly heavier than the C chick, but did not significantly differ from each other (ANOVA, $n=21$, Mass: $F= 6.428$, $p<0.005$, Size: $F=0.586$, $p>0.5$). Interestingly, in 3 of the 21 nests used for this comparison the C chick was not the lightest in the brood.

Discussion

Results show little evidence of behavioral discrimination against C chicks in these populations. In terms of feeding distance and response to begging, parents appear to treat all chicks equally.

Analyses of feeding and begging behavior reveal very little, if any competitive disadvantage of the C chicks in this sample. Despite suggestions in the literature to the contrary, the C chick was not less likely than A or B to get to the food first. Although there was a non-significant tendency for the A chick to beg more than the others, which could be interpreted as a competitive advantage given that begging is associated with being closer to the food, it is not clear that this behavior necessarily constitutes a direct benefit to the begging chick, especially given the feeding method herring gulls use. In begging more frequently, A would not only attain more food for itself, but for its siblings as well. This could lead to indirect fitness benefits for the A chick. However, the existence of such benefits does not address the question of whether there are competitive asymmetries within broods. It is also possible that the order of eating, and hence frequency of begging, increases food acquisition for older chicks or for chicks in a food limited environment, but that did not appear to be the case here.

The A chick also ate more frequently than others, though not significantly so. This result is in agreement with similar findings by Hébert and Barclay which did reach significance (1986), but again it is questionable as an indicator of competitive asymmetries within the brood. Observations showed that C received food less often than A because C tried to eat less often, though able to reach the bolus. Given the smaller size and especially the younger age of the C chick it would not need as much food as its older, larger siblings, especially in the first couple of days after hatching when it is likely to still have yolk reserves to survive on, and its siblings have higher metabolic costs and lower or no yolk reserves.

In terms of chick interactions, while A and B were more likely to target C when trying to steal food, they were not more likely than C to attempt food stealing, even when the likelihood of doing so is scaled by opportunity to do it, and they did not target C for pecking. If anything, C appeared to be the most aggressive chick: it pecked siblings the most, and, despite its younger age and smaller size, was *not* more likely to lose battles over food with its siblings. Why would C be so aggressive?

A study by Hunt and Hunt (1976) on the glaucous winged gull (*Larus glaucescens*) found that hungrier chicks were more active than sated ones. While it is possible that C chicks are generally more aggressive because they are hungrier, observations showed that throughout the first 10 days of its life C always got some food when it tried to eat. Whether it got enough food to be sated is unknown, but given that C occasionally failed to attempt eating even when food was available, it is at least plausible that it ate enough, which would render this hypothesis unlikely.

It is also possible that C was more aggressive *because* of its size and age disadvantage. Schwabl (1993) found that last hatched canary chicks were more aggressive than their siblings, presumably so that they could better compete for food. It is possible that this behavior is also a compensatory mechanism in herring gulls. If so this may call into question the assumption that the function of the third chick disadvantage is to create feeding hierarchies within broods. Whether this behavior is controlled by parents as it is in canaries, or is the C chick's evolved response to attempted parental control (i.e. the result of parent-offspring conflict) is unknown at this time.

One piece of evidence not in question is that C hatched lighter than its siblings. Although C chicks in Hamilton Harbor did not hatch with smaller body dimensions than their siblings, in accordance with previous findings (e.g. Parsons 1975, Hébert & Barclay 1988) they still hatched at significantly lower masses. This leaves the question: why is the C chick lighter? Quinn and Morris (1986) argue that in the Caspian tern, which also has hatch asynchrony and egg and chick size asymmetry but only lays two eggs per clutch, B eggs are lighter because the B chick's survival is more dependent on the fate of its older sibling than on its initial size. The same is not true for A chicks. Thus they interpreted the age-specific size difference between A and B eggs as a parental response to the differences in reproductive value of asynchronously hatching chicks.

Although parents apparently put less investment into the C chick before it hatched, no post hatching behavioral bias was found, the competitive disadvantage expected was not found, and very little bias against C appears to exist on the part of siblings. Most analyses, however, focused on interactions over food. It is possible that food is not the relevant parameter to study.

The populations used in this study did not appear to be food limited, nor were populations studied by Graves et al. (1984), yet size and hatch asymmetry were still found in both places. Supplementing food does appear to increase chick survivorship (VanKlinken 1980, Graves et al. 1984), but it is not clear what, exactly, it is about the supplement that does this. Although Graves et al. (1984) found increased growth rates of supplemented chicks, VanKlinken (1980) did not. It is possible that the increased survivorship of supplemented chicks was due to decreased death by starvation, but more needs to be learned about the causes of mortality in very young chicks before reaching that conclusion. Hunt and Hunt (1976) suggest that starvation, which has been previously assumed to be the cause of most C chick deaths, is not a major mortality factor in gull chicks. In a study of mortality in glaucous winged gulls they found conspecific predation to be the primary cause of death for young chicks, followed by adverse weather.

This does not mean that food supply is irrelevant to the issue of why the third chick is smaller, but the available evidence suggests that it may be at best an indirect explanation of the phenomenon.

Regardless of which environmental factors turn out to be most relevant for the maintenance of hatch and size asymmetries in herring gull chicks, it is likely that the locations where this study was conducted provide a relatively easy environment in which to raise chicks compared to the marine populations observed in other studies. Food for gulls is plentiful and, being inland, temperatures are warmer and storms less frequent than in coastal regions. Given this, parents might be expected to reduce chick asymmetries if they are able. There is evidence that Western gulls are capable of adjusting the degree of third chick disadvantage to fit local conditions (Pierotti and Bellrose 1986). The same might be occurring in the herring gulls in this sample. There seemed to be a fairly high degree of hatching synchrony in Hamilton Harbor. In 7 out of 28 nests the C chick hatched on the same day as the B or A and B chicks. Previous reports of any such synchronous hatching could not be found (Parsons 1975, Graves et al. 1984, Hébert and Barclay 1986, Lee et al. 1993).

In conclusion, this study fails to provide support for the notion that Herring gull parents and siblings behaviorally discriminate against the last hatched chick, at least over food. Parents seem to treat chicks equally, and, contrary to expectations, the C chick is the most aggressive in the brood. Whether these results are generalizable to other domains of parental care or other Herring gull populations is unknown, though several features of the environment where these gulls were studied suggest that these populations breed in particularly favorable locations.

Acknowledgments

We thank the Canadian Wildlife Service and Hamilton Harbour commissioners for permission to study the Hamilton Harbour colony and R. Morris for permission to collect behavioral data at the Port Colbourne site. We thank H. Bickerton, L. Leaver, and P. Wehr for assistance with observations, L. Biasin, H. Bickerton, K. Brown, S. Godin, L. Leaver, E. Macedo, J. Newman, J. Sirdevan, and C. Yauk for assistance with many aspects of the study. We thank R. Morrison for his statistical advice and assistance and we thank M. Daly for comments on this manuscript. This research derived financial support from the McMaster EcoResearch Project (Tri-Council Green Plan) , and Natural Sciences and Engineering Research Council of Canada grants awarded to J. Quinn and M. Daly.

References

Graves, J., A. Whiten, and P. Henzi. 1984. Why does the herring gull lay three eggs? Animal Behaviour 32:798-805.

Hahn, D.C. 1981. Asynchronous hatching in the laughing gull: cutting losses and reducing rivalry. Animal Behaviour 29:421-427.

Hébert, P.N. and R.M.R. Barclay. 1986. Asynchronous hatching: effect on early growth and survivorship of herring gull, *Larus argentatus*, chicks. Canadian Journal of Zoology 64:2357-2362.

Hébert, P.N. and R.M.R. Barclay. 1988. Prental investment in herring gulls: clutch apportionment and chick survival. Condor 90:32-338.

Hunt, G.L. and M.W. Hunt. 1976. Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology 57:62-75.

Lack, D. 1954. The naturla regulation of animal numbers. Oxford University Press.

Lee, S.C., R.M. Evans, and S.C. Bugden. 1993. Benign neglect of terminal eggs in herring gulls. Condor 95:507-514.

Parsons, J. 1975. Asynchronous hatching and chick mortality in the herring gull *Larus argentatus*. Ibis 117:517-520.

Pierotti, R. and C.A. Bellrose. 1986. Proximate and ultimate causation of egg size and the "third-chick disadvantage" in the western gull. Auk 103:401-407.

Quinn, J.S. and R.D. Morris. 1986. Intraclutch egg-weight apportionment and chick survival in Caspian terns. Canadian Journal of Zoology 64:2116-2122.

Schwabl, H. 1993. Yolk is a source of maternal testosterone for developing birds. Proceedings of the National Academy of Sciences 90:11446-11450.

Tinbergen, N. The Herring gull's world. Doubleday, New York.

Van Klinken, A. 1980. The impact of additinal food provisioning on chick growth and breeding output in the herring gull *Larus argentatus*: a pilot experiment. Ardea 80:151-155.

Table 1.

Head to tip		Mean	S.E.
	A	48.98	± 0.42
	B	48.96	± 0.40
	C	48.60	± 0.32
Weight			
	A	68.41	± 1.49
	B	67.68	± 1.37
	C	63.35	± 1.53

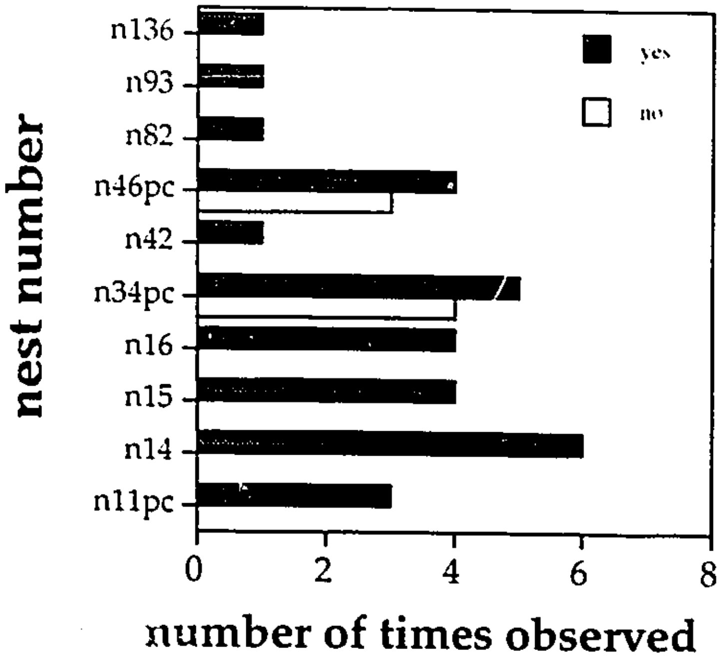
Hatch day measurements from non-synchronously hatching nests at Hamilton Harbor 1994.

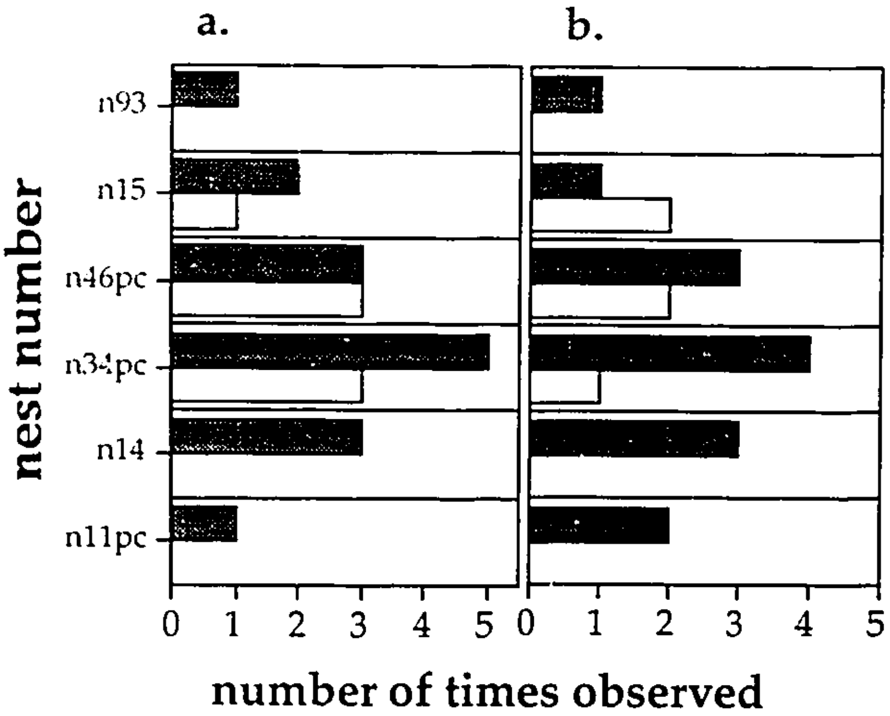
Figure 1. Number of times the closest chick did and did not eat first for each nest for which there were relevant data. This result is significant at $p<0.001$.

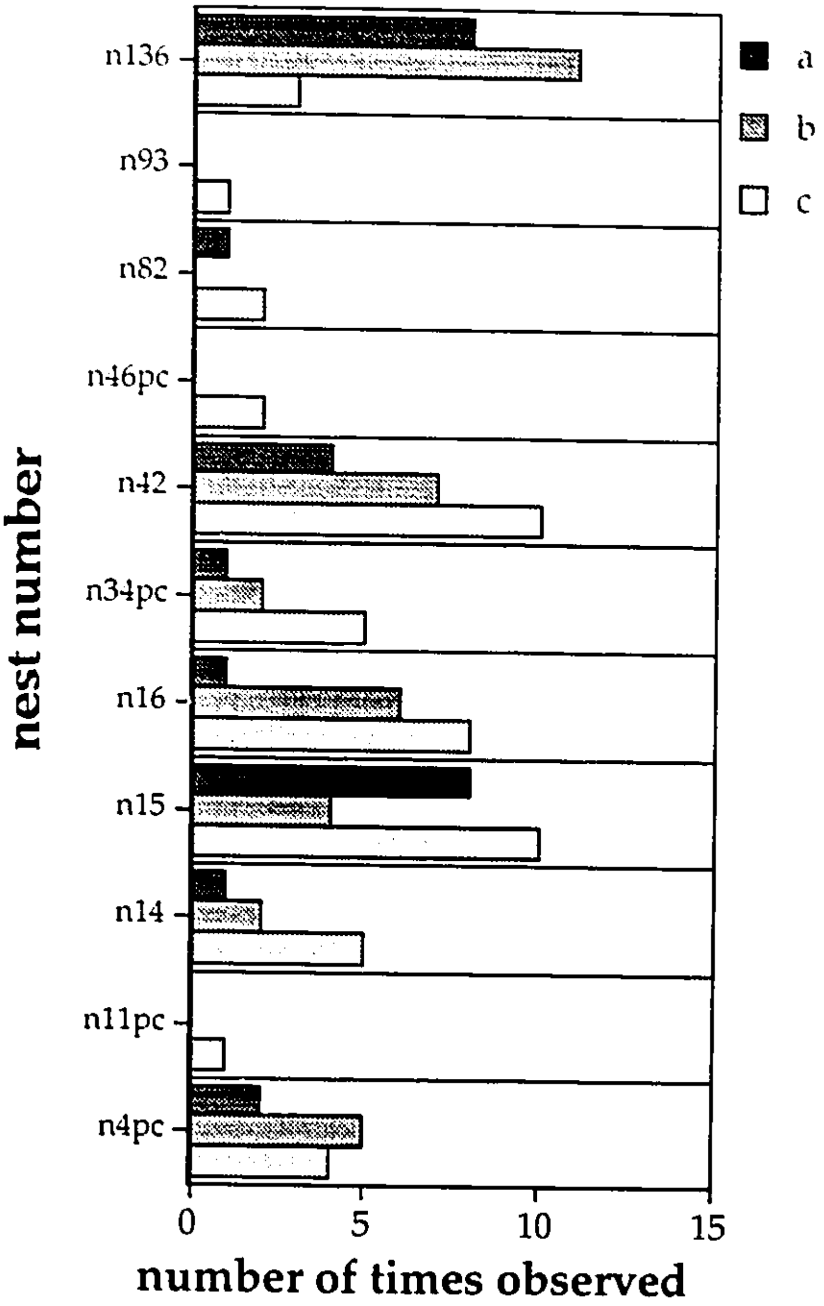
Figure 2. (a) The number of times begging chicks were and were not closest to the food, and (b) the number of times they did and did not eat first, by nest. Begging chicks were significantly more likely to be closest ($p<0.016$), but not significantly more likely to eat first.

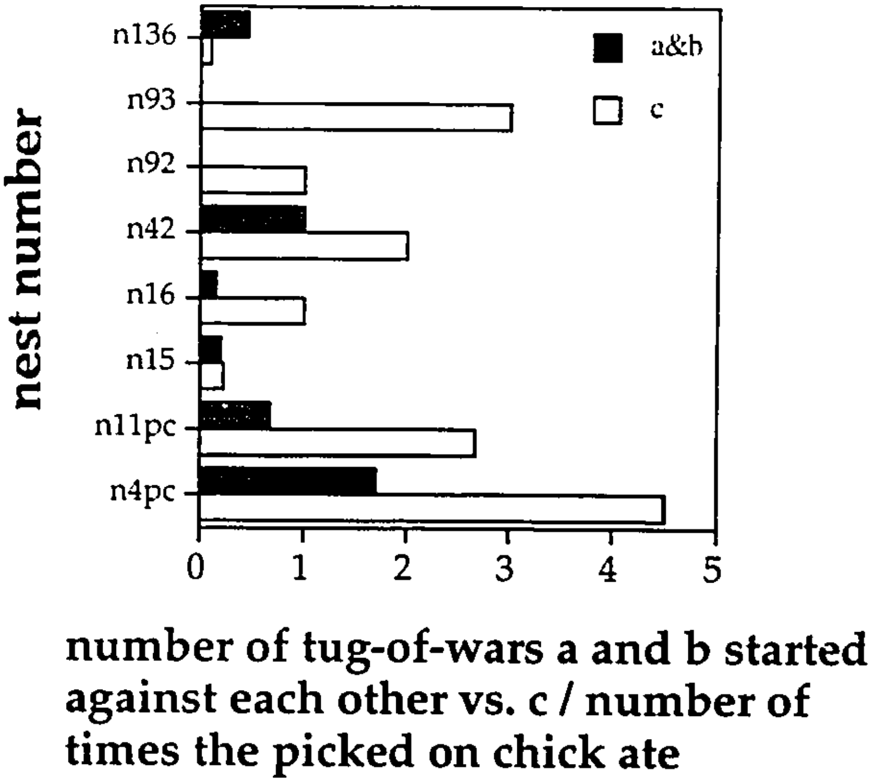
Figure 3. The number of times the A, B, and C chicks pecked each other. The C chick was significantly more likely to peck than A or B ($p<0.05$).

Figure 4. The number of times A and B started tug-of-wars against each other and the number of times they were started against C, graphed by nest. The A and B chicks were significantly more likely to start tug-of-wars with C than with each other ($p<0.004$).


nest number
n136
n93
n82
n46pc
n42
n34pc
n16
n15
n14
n11pc
yes
no
0
2
4
6
8
number of times observed


a.
b.
nest number
n93
n15
n46pc
n34pc
n14
n11pc
0
1
2
3
4
5
0
1
2
3
4
5
number of times observed


n136
n93
n82
n46pc
n42
n34pc
n16
n15
n14
n11pc
n4pc
nest number
0
5
10
15
number of times observed
a
b
c


nest number
n136
n93
n92
n42
n16
n15
n11pc
n4pc
■ a&b
□ c
0
1
2
3
4
5
number of tug-of-wars a and b started against each other vs. c / number of times the picked on chick ate