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**THE STRUCTURE OF ENERGY PRODUCTION AND
REDISTRIBUTION AMONG TSIMANE' FORAGER-
HORTICULTURALISTS**

BY

PAUL L. HOOPER

A.B., Near Eastern Studies, Princeton University, 2003
M.S., Anthropology, University of New Mexico, 2008

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy

Anthropology

The University of New Mexico
Albuquerque, New Mexico

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For Annie and Josephine

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ABSTRACT

This dissertation constitutes an integrated analysis of the Tsimane' economic subsistence system. Its analyses are guided by a body of evolutionary theory which posits that life history traits, the structure of social relationships, and nature of economic production co-evolve in patterned and predictable ways. This theory specifically suggests that, for humans, the returns to embodied capital development and declines in reproductive efficiency late in life interact to produce: prolonged development, extended lifespan, menopause, and a predominantly downward three-generational system of energetic provisioning. The current analyses of Tsimane' work effort, production, and transfers are consistent with this theory in the following ways.

(1) Tsimane' young remain in net caloric deficit until around age 20. From the 20s onward, both sexes produce a substantial net surplus, with men in middle adulthood producing the bulk of dietary fat and protein. The contributions of post-reproductive men and women to total productivity within the population are substantial even when mortality is taken into account.

(2) The benefits of subsidizing young kin have predictable effects on individual workloads, and variation in these benefits interact with the time-paths of strength and skill acquisition to determine the life history of Tsimane' resource production and transfers. Mothers decrease production with nursing children, but increase production with the presence of additional weaned offspring. Fathers and grandparents of both sexes also show greater productivity when more offspring and grandoffspring are present.

(3) The life history of resource production leads to systematic differences in the benefits of receiving and the costs of giving calories across life, motivating net downward transfers between relatives across generations. Caloric transfers between families are predicted by the interaction of relatedness and relative caloric need. The analysis of transfers also reveals signatures of reciprocal consumption smoothing, and specialization and exchange across and within generations.

The energetic approach taken in this dissertation complements existing demographic methods for evaluating the role of kin in promoting offspring success by directly examining the material means of investment in kin. Its results flesh out the structure of social relationships that constitute the core human pattern of cooperative reproduction.

TABLE OF CONTENTS

| | |
|---|-------------|
| LIST OF FIGURES | xi |
| LIST OF TABLES | xiii |
| CHAPTER 1. BACKGROUND AND THEORY | 1 |
| Introduction | 1 |
| The Social Nature of Human Energetics | 3 |
| Effects of Dependent Need on the Life History of Production | 8 |
| Asymmetries in Caloric Availability and Need Drive Transfers..... | 11 |
| Guide to the Dissertation..... | 14 |
| CHAPTER 2. STUDY POPULATION AND METHODS | 15 |
| Tsimane Population | 15 |
| Data Collection..... | 19 |
| Data Preparation..... | 21 |
| CHAPTER 3. THE LIFE HISTORY OF TSIMANE' PRODUCTION AND CONSUMPTION | 30 |
| Introduction | 30 |
| Production by Economic Domain | 33 |
| Methods..... | 33 |
| Results and Discussion | 41 |
| Net Production and Need of Individuals and Families | 44 |
| Methods..... | 44 |
| Results and Discussion | 47 |
| Conclusion..... | 49 |

| | |
|---|------------|
| CHAPTER 4. EFFECTS OF DEPENDENT KIN ON TSIMANE' PRODUCTIVITY | 50 |
| Introduction | 50 |
| Methods..... | 54 |
| Results | 71 |
| Discussion and Conclusion | 75 |
| CHAPTER 5. THE DEMOGRAPHIC STRUCTURE OF TSIMANE' ENERGY TRANSFERS | 81 |
| Introduction | 81 |
| Methods..... | 84 |
| Results | 90 |
| Discussion and Conclusion | 103 |
| CHAPTER 6. SUMMARY AND CONCLUSION | 106 |
| APPENDICES..... | 111 |
| APPENDIX A. SUPPLEMENTARY MATERIALS ON RICE SALES DATA..... | 111 |
| APPENDIX B. DESCRIPTION OF KINSHIP ALGORITHM..... | 113 |
| APPENDIX C. COMPOSITION OF RETURN RATE SAMPLES..... | 119 |
| APPENDIX D. ADDITIONAL FIGURES FROM THE ANALYSIS OF CALORIC TRANSFERS BETWEEN FAMILIES | 120 |
| REFERENCES..... | 121 |

LIST OF FIGURES

| | |
|--|----|
| Figure 2.1. Rice harvested per hour by age and sex | 23 |
| Figure 2.2. BMR by age and sex | 26 |
| Figure 3.1. Mean return rates from, time allocation to, and production from hunting by sex and age category | 35 |
| Figure 3.2. Mean return rates from, time allocation to, and production from fishing by sex and age category..... | 36 |
| Figure 3.3. Mean time allocation to horticultural labor by sex and age category | 37 |
| Figure 3.4. Mean harvest return rates, daily harvest rates, and production of non-rice horticultural products by sex and age category | 38 |
| Figure 3.5. Mean harvest return rates, daily harvest rates, and production of rice by sex and age category..... | 39 |
| Figure 3.6. Mean daily production of rice for subsistence by sex and age category | 40 |
| Figure 3.7. Tsimane' mean daily production and consumption by age and sex..... | 45 |
| Figure 3.8. Proportional energetic contribution by age and sex | 46 |
| Figure 3.9. Mean net daily production by age for Tsimane' nuclear families | 48 |
| Figure 4.1. Effect of removing the estimated effects of dependent kin from the age- schedule of time allocation to production | 78 |
| Figure 4.2. Effect of removing the estimated effects of dependent kin from the age- schedule of caloric production | 78 |
| Figure 5.1. Proportions of production received by recipient categories, by producer age and sex..... | 87 |

| | |
|---|-----|
| Figure 5.2. Relative magnitude of caloric transfers to recipients, by producer age and sex | 88 |
| Figure 5.3. Proportional contributions of producers toward recipient categories, by producer age and sex..... | 89 |
| Figure 5.4. Bidirectional transfers of calories from game and fish within the extended family | 92 |
| Figure 5.5. Bidirectional transfers of horticultural calories within the extended family..... | 93 |
| Figure 5.6. Net caloric transfers within the extended family | 94 |
| Figure 5.7. Mean net transfers of meat, horticulture, and all calories to closely families as a function of family age | 98 |
| Figure 5.8. Predicted independent effects of family age on gross calories transferred between closely related families | 100 |
| Figure 5.9. Predicted effects of donor and recipient net need on gross calories transferred between families as a function of relatedness and family age | 101 |
| Figure 5.10. Predicted combined effects of age and need on gross caloric transfers between closely related families | 102 |
| Figure D.1 Predicted independent effects of family age on gross meat calories transferred between closely related families | 120 |
| Figure D.2. Predicted independent effects of family age on gross horticultural calories transferred between closely related families | 120 |

LIST OF TABLES

| | |
|--|-------|
| Table 2.1. Sample characteristics by region..... | 19 |
| Table 2.2 Coefficients for estimating BMR | 25 |
| Table 3.1 Age- and sex distribution of the production and sharing sample..... | 34 |
| Tables 4.1-4.42 Regression models predicting production effort and output as a function of the presence of siblings, children and grandchildren | 57-68 |
| Table 4.43 Significant relationships between male production and the presence of siblings, children, and grandchildren across life..... | 69 |
| Table 4.44. Significant relationships between female production and the presence of siblings, children, and grandchildren across life | 70 |
| Table 5.1. Linear mixed model predicting gross meat calories transferred between families per day..... | 96 |
| Table 5.2. Linear mixed model predicting gross horticultural calories transferred between families per day..... | 99 |
| Table 5.3. Linear mixed model predicting gross total calories transferred between families per day..... | 100 |
| Table A.1. Regression model predicting amount of rice already sold based on amount harvested and amount planned to sell in the future | 111 |
| Table A.2. Regression model predicting amount of rice sold on basis of amount of rice harvested and region | 112 |
| Table B.1. Definition of pedigree vector | 114 |

| | |
|---|-----|
| Table B.2. Definition of kinship match matrix..... | 115 |
| Table C.1. Composition of return rate samples | 119 |

In these bodies we will live, in these bodies we will die.

Where you invest your love, you invest your life.

(Mumford & Sons)

The family is one of nature's masterpieces.

(George Santayana, *The Life of Reason*)

CHAPTER 1. BACKGROUND AND THEORY

1. Introduction

Demographic patterns in traditional human societies are characterized by remarkably late maturation, reproductive cessation preceding general somatic decline, and extended lifespan relative to other primates and mammals (Bogin and Smith 1996, Ellison 2010, Gurven and Kaplan 2007). Fieldwork with extant hunter-gatherer groups and other small-scale traditional societies has also revealed the remarkable extent of social interdependence in our species. This interdependence is metabolically manifest in extensive flows of calories between individuals, both within and between families. Human young rely on substantial caloric provisioning and care from parents, grandparents, and other kin (Gray and Anderson 2010, Hrdy 2009, Sear et al. 2000). Food is also shared extensively between both kin and non-kin throughout life (Gurven 2004).

Interest in the cooperative nature of reproduction in human societies has grown in recent years, as manifested in the literature on grandmothering (Coall and Hertwig 2010, Hawkes et al. 1998, Scelza 2009, Volland et al. 2005), intergenerational transfers (Chu and Lee 2006, Kaplan and Robson 2002, Lee 2003), and “cooperative breeding” in humans (Hill and Hurtado 2009, Hrdy 2009, Kramer 2005a, Kramer and Ellison 2010, Mace and Sear 2005). Despite general consensus on the basic facts of human demography and sociality in the preceding paragraph, important empirical and theoretical questions remain unanswered: Who exactly contributes to the biological welfare of whom, and in what ways? What relation do these patterns of social support have to human-typical rates of growth, reproduction, and survival? Ultimately, what evolutionary and ecological factors are responsible for selection to have favored these characteristics of sociality and life history in our species, but not others?

To make progress toward answering these questions, this dissertation investigates the energetic basis of growth, maintenance, and reproduction in one

traditional small-scale human society, the Tsimane'. It asks who in the society produces the calories that fund these fundamental biological goals; to whom these calories are redistributed; and how the need of those recipients affects the productive effort of their donors. In doing so, it shows the extent to which human life histories are socially subsidized, and provides an explanation for why this must necessarily be the case. It shows that the need for this subsidization has predictable effects on individual workloads, and that variation in this need interacts with time-paths of physical strength and skill acquisition to determine the life history of resource production and transfers.

This chapter introduces a theoretical framework for understanding the energetic systems of small-scale human societies. This framework draws on the theory of embodied capital developed by Kaplan and colleagues (Kaplan 1997, Kaplan et al. 2010, Kaplan et al. 2000) to develop the conceptual links between human life history patterns of energy production, consumption, and transfers, on the one hand; and growth, reproduction, and survival, on the other. It specifically advances this body of evolutionary theory by leveraging Hamilton's theory of inclusive fitness (Hamilton 1964) to predict the specific patterning of energetic flows between individuals, and the effect of the consumption requirements of energy recipients on the work effort of producers.

Section II of this chapter describes the interactions between age-patterns of productivity, fertility, and mortality that motivate a three-generational system of energetic provisioning in human families. Section III then develops predictions from this theory for the effect of kin need on the work effort of individuals across life. Section IV builds on this theory to develop a more fine-grained framework for predicting the direction and volume of energetic transfers on the basis of the returns to kin investment, specialization by age and sex, and risk reduction. The chapter concludes with a road-map of the empirical studies that follow in this dissertation.

II. The social nature of human energetics

In most mammals, energetic provisioning of offspring is primarily limited to gamete formation, gestation, and lactation; after weaning young must be capable of meeting their own energetic needs (Kramer and Ellison 2010). In traditional small-scale human societies, on the other hand, parental provisioning beyond weaning is extensive, with important inputs from both mothers and (with some exceptions) fathers (Hrdy 2009, Lancaster and Lancaster 1983, Winking 2006). There are also significant inputs to an individual's biological success from other consanguineous kin, affinal kin, and non-kin (Gurven 2004, Sear et al. 2000). Some of these energetic transfers are bi-directional and fairly balanced, while others are unidirectional or bi-directional but significantly asymmetric.

Embodied capital theory provides a particularly parsimonious explanation of the co-evolution of such high levels of energetic interdependence with prolonged development, extended lifespan, and menopause. This approach roots the evolution of these features of human life history and sociality in the gains to investment in brain growth and skill development, which are characteristic of our species' foraging niche. The effects of such embodied capital investments are manifest in the human age-schedule of production: young remain unproductive for longer as they invest in brain growth and skill development; older adults, on the other hand, produce large caloric surpluses, as the gains to a lifetime of accumulated knowledge and skill pay off later in life. Life history models show that such a shift in the age-schedule of productivity increases the gains to investing in survival to later ages, leading to low adult mortality rates and extended lifespan (Kaplan and Robson 2002, Robson and Kaplan 2003). At the same time, the prolonged period in which offspring remain in caloric deficit—consuming more calories than they are able to produce per unit time—both encourages and necessitates high levels of energetic subsidization from other individuals in later, more productive phases of life (Kaplan and Robson 2002, Lee 2008).

Parental provisioning

The first line of energetic support for offspring growth and development naturally comes from parents themselves (Lancaster and Lancaster 1983). Theories to explain the unique energetic role of fathers in supporting human reproduction have matured in recent years, emphasizing both the outright volume of offspring need, as well as the gains to complementary specialization of male and female inputs to offspring success (Chapais 2011, Gray and Anderson 2010, Gurven and Hill 2009, Winking et al. 2007). Human females share with other primates a commitment to internal gestation, nearly continuous mother-infant contact, and lactation; humans, on top of this, exhibit even deeper commitments to offspring quality. One result of these commitments is that dangerous and physically demanding production activities that are incompatible with keeping an infant safe become prohibitively costly for mothers while children are young and directly dependent on maternal care (Hurtado et al. 1992). Because of this, women may also be unlikely to be able to invest the time to master activities such as hunting that are both incompatible with safeguarding an infant *and* require high levels of experience. Taking on the risks and skill investments of foraging pursuits such as hunting are thus rarely economically feasible for human mothers, despite their high yield of valuable fat and protein for somatic growth and encephalization.

The unique energetic contributions that men can provide in such childcare-incompatible and skill-intensive arenas create a complementarity between male and female inputs into household wellbeing. Such a complementarity (rather than substitutability) of parental inputs is able to stabilize an equilibrium of parental investment from both sexes by the logic of ESS models of animal parental investment (Grafen and Sibly 1978, Kokko and Johnstone 2002, Maynard Smith 1977). Variation across ecologies can result in higher or lower levels of complementarity, as well as determine different sources of complementarity; among South American horticulturalists, for example, men are also in a position to contribute differentially in the clearing and burning of forest for new fields. While recognizing this variation, a growing body of evidence confirms the important role of paternal provisioning across

most traditional small-scale human societies, motivated for that purpose (Gurven and Hill 2009, Marlowe 2001, Marlowe 2007, Winking 2006, Wood 2006).

Why the third generation contributes

Focus was brought to the energetic contributions of kin beyond parents by Hawkes' examination of grandmaternal contributions to grandoffspring success among the Hadza. Hawkes found that the grandchildren of grandmothers who spent more hours in foraging enjoyed better nutritional health (Hawkes et al. 1989). This led to a proposal that the contributions of grandmothers to their reproductive-age daughters and grandchildren allowed selection to favor survival to post-reproductive ages (Hawkes 2003, Hawkes et al. 1998, Hawkes et al. 2000, see also Lancaster and King 1985, Williams 1957). While Hawkes and colleagues have remained steadfast in emphasizing grandmaternal contributions (but not those of male kin), this insight has been generalized in demographic models of lifespan evolution and "indirect reproduction" via intergenerational transfers (Chu and Lee 2006, Kaplan and Robson 2002, Lee 2003, Lee 2008, Robson and Kaplan 2003).

Given traditional human age-schedules of fertility and caloric production, the economic necessity of downward transfers across three generations is clear: the need of younger nuclear families with multiple dependent offspring outstrips production, while older nuclear families, who have high productivity but few or no remaining dependent offspring, run a caloric surplus which can be invested in adult offspring and dependent grandoffspring (Hill and Hurtado 2009, Kaplan et al. 2010, chapter 3 of this dissertation). Simply taking the human fertility pattern as a given, however, neglects the fact that it is oddly atypical. Despite the fact that other human biological rates (i.e. growth, mortality) have slowed relative to other apes in the face of humans' high investments in embodied capital, mortality-reduction, and offspring quality, fertility rates during the reproductive period are relatively higher than would be expected for an ape of our size (approximately 0.3 births per year in traditional human societies, versus 0.2 for chimpanzees; Alvarez 2000, Walker et al. 2006). If women were to maintain lower

fertility rates on par with other apes, the demand for outside provisioning would be reduced, as there would be fewer overlapping dependents at one time. Conversely, it is only because women cease to produce dependents of their own mid-way through their adult lifespan—likewise atypical among primates (Levitis and Lackey 2011)—that a sizeable surplus is available to channel to descendent families (Kaplan et al. 2010). Importantly, differences in human and chimp fertility rates more or less disappear when births are averaged over both the reproductive and post-reproductive lifespan: in essence, total lifetime fertility is conserved, at the same time that is concentrated earlier in the life course (Burger et al. 2010).

Why is it, then, that this pattern of concentrated early-life reproduction with support from older, post-reproductive individuals is the equilibrium, rather than a more even spread of fertility across the lifecourse without significant non-parental subsidization, or a concentration of fertility later in the life course with support provided by younger, pre-reproductive “helpers at the nest”? We have argued elsewhere (Kaplan et al. 2010) that the condition of maternal reproductive physiology and oocyte reserves—themselves endogenously modifiable through costly investments in maintenance of reproductive capital—are important determinants of the benefits and costs of direct reproductive effort across different stages of the lifespan. The mother's optimization problem should weigh these benefits and costs of direct reproductive effort (and the maintenance investments required to sustain it) against the returns to alternative investments: namely, somatic maintenance, mortality reduction, and indirection reproduction via transfers.

Empirical studies of mammalian physiology indicate that declines in the quality of oocyte reserves with age result in higher rates of spontaneous abortion and genetic and developmental defects in offspring conceived by older mothers (Ottolenghi et al. 2004, vom Saal et al. 1994). These increasing costs with age are likely to weigh more heavily for humans than less embodied-capital oriented species because of our remarkably high commitment to investment in each offspring. Consistent with this proposition, human reproductive physiology appears to be particularly sensitive to

embryo quality, employing a more stringent selective sieve to prevent inferior embryos from implanting (compared to standard mammalian physiology; Ellison 2001, Haig 1993). Scaling back direct reproductive effort later in life may also be favored in the human production niche because of the importance of surviving to the ages of high late-life productivity in good physical condition. By doing so, women avoid risks of mortality in childbirth and losses due to maternal depletion and immunosuppression (particularly in terms of survival and economic productivity; Heyborne and Silver 1996, Louden 1992, Tracer 1991), which are likely to be higher for older, senescent women than younger women in prime physical condition. In societies where long-term monogamy is predominant, older men face high returns to investing their economic production in descendent kin, but low expected success in pursuing new reproductive opportunities in the mating market, rendering indirect reproduction through provisioning in old age the most likely fitness-maximizing strategy for men as well as women (Kaplan et al. 2010).

The embodied capital model posits that these factors combine to favor a human life history of early-age specialization in subsidized direct reproduction, and old-age specialization in production and subsidization, rather than other potential age-schedules of fertility and social support (Kaplan et al. 2010). While it is plausible that a species in a high embodied-capital niche may be capable of manifesting three-generational transfers without menopause, in the human case, the optimality of more rapid early reproduction and programmed reproductive cessation certainly seals the deal.

Children's contributions

On the whole, the skill- and learning-intensive nature of human production, combined with high altriciality and slow pace of development, renders human children less productive than other primates, with remarkably late ages of self-sufficiency (around 18-22 in many foraging societies, compared to around 5 for chimpanzees; Hill and Hurtado 2009, Kaplan et al. 2000). The ability of children to contribute to the household economy through caloric production, however, varies with ecological circumstance (Kramer 2005a). In foraging societies, when valuable resources such as

fruits and fish are abundant and easy to harvest, children are more productive and less dependent on resource flows from other kin (Bliege Bird and Bird 2002, Blurton Jones et al. 1989, Tucker and Young 2005). In horticultural and agricultural economies, children can perform less strength- and skill-intensive tasks such as weeding and harvesting; other tasks, such as manually clearing and burning forest plots and planning the placement of fields and timing of activities, remain the domain of adults, especially men, who have the strength and experience to successfully carry them out (Gurven et al. 2009).

Children's time allocation is expected to be oriented toward both current production and future skill investment, through play, "practice" productive effort, or accompanying older, more skilled producers (Bock and Johnson 2004, Stieglitz 2009). Children's labor can substitute for that of parents in less skill- and strength-intensive tasks, allowing parents to shift time toward more skill- and strength- intensive tasks (Bock 2002a, Bock 2002b). Children can also assist significantly in childcare and other tasks outside primary production such as food processing (Bove et al. 2002, Kramer 2005a, Kramer 2005b). Several studies have found associations between the presence of older sub-adult helpers and indicators of household success, presumably as a result of these contributions during the latter half of dependency (Crognier et al. 2001, Stinson 1980, Turke 1988).

III. Effects of dependent need on the life history of production

Embodied capital theory, as developed to this point, provides a means of understanding changing efficiency through time as a function of physical ability and skill development. The life history of production, however, depends not only on ability, but also the level of effort allocated to production. If production is motivated by the gains to subsidizing the growth and reproduction of close kin, the degree of need of individuals in the producer's kin network should have predictable impacts on their productive

effort. Examining whether or not this is the case serves a test of the motivations for production.

Consider a simple model in which an individual faces the choice of how much effort to expend in producing calories, and how to divide those calories produced amongst an array of possible consumers (including the individual herself) in order to maximize her inclusive fitness (Hamilton 1964). Since production effort entails costs to the producer, effort levels should be optimized to balance these costs against the benefits of the calories produced. The producer's inclusive fitness benefit from a recipient's consumption of calories depend on the relatedness of the recipient to the donor (r) as well as the relative need of the recipient: the fewer the calories the recipient enjoys from other sources, the greater the direct marginal benefit (i.e. need) of the transfer to the recipient, and thus the greater the inclusive fitness benefit to the donor. (It is reasonable to assume that there are diminishing marginal benefits of consumption, but increasing costs of productive effort; these costs may include opportunity costs, as time or energy is diverted from other fitness-enhancing activities, such as mating effort or embodied capital development.) At the producer/donor's optimum, the marginal inclusive fitness benefit of the transfer multiplied by the marginal productivity of effort should equal the marginal cost of productive effort. Increases in either the inclusive fitness benefit of the transfer or the productivity of effort should thus drive the producer to expend greater productive effort (and incur a higher marginal cost of effort at the optimum). Productive effort is thus predicted to increase as a function of the number of kin in need, their relative degree of need, and the relative efficiency of the producer.

Differential efficiency across activities (in returns rates from or costs of effort) should also impact the specific domains of production in which kin need registers its effects, a prediction which emerges from this same logic of inclusive fitness maximization. The effect of greater kin need on a hunting specialist (i.e. one who is differentially more proficient in hunting than in other activities), for example, should thus be manifest in hunting effort, while its effect on a horticultural specialist should be

manifest in horticultural labor. Substitution effects may also register themselves in the effects of kin presence on the focal producer's effort: in the activity where others' labor may substitute for that of the focal producer, the presence of substitutes will have a negative effect on the producer's effort in that activity; in the activities to which the focal producer may profitably redirect his effort, the presence of substitutes will have positive effects (Bock 2002a, Gurven and Kaplan 2006).

These considerations also serve to link inclusive fitness and life history theory with Chayanov's economic theory of consumption-labor balance, and other studies in anthropology which drawn on it. Chayanov's theory posited that productive effort in family farms should be responsive to the relative need of the household, as indexed by the ratio of producers to consumers in the household (Chayanov 1966). Sahlins (1974) later imported Chayanov's model into anthropology, and a number of studies in economic anthropology (e.g. Chibnik 1984, Sahlins 1974, Smith 1979) and human behavioral ecology (Berté 1988, Kramer and Lee 2002, Marlowe 2003, Stieglitz 2009, Turke 1988) have tested its predictions for the relationship between consumer need and work effort in a variety of ethnographic settings. Chapter four of this dissertation tests for effects of descendent kin need on both time allocation and daily productivity across ages within the Tsimane' sample.

Evaluating the degree to which the age-schedule of human productivity is due to the age-schedule of kin need also tests an important assumption of the embodied capital model of human life history evolution. Namely, embodied capital theory posits that productivity is constrained by the age-pattern of embodied capital development (Kaplan and Robson 2002). If it were to turn out that the age-schedule of production is governed entirely by differences in need across life, and not at all by differences in ability, it would cast doubt on embodied capital theory to explain the evolution of social provisioning.

IV. Asymmetries in caloric availability and need drive transfers

Fitness benefits of transfers derive from variance in the ability to provide and the benefits of receiving calories, manifest across a number of dimensions and time-scales. There are three ways in which such asymmetries motivate transfers that are particularly worth highlighting in the human context. First, life-history based variance in the ability to produce calories motivates altruistic provisioning of needy kin during periods of high productivity. Second, variance across individuals in the productivity and cost of effort motivates specialization and exchange. Finally, variance in productivity due to luck or ill-fortune motivates reciprocal provisioning in order to smooth consumption rates through time. We examine each of these motivational factors in turn.

Life historical variance in the costs and benefits of kin altruism

Hamilton's theory of inclusive fitness predicts that kinship-based altruism should be favored by natural selection when the benefits of the altruistic act to the recipient (b) devalued by the relatedness of the two individuals (r) exceed the cost to the donor (c), or $br > c$ (Hamilton 1964). The life history of resource production, fertility, and mortality combine to structure systematic differences in the benefits of receiving calories, and the costs of giving them away across life. On the one hand, individuals in less productive phases of life gain a greater marginal benefit from receiving calories from others. For more productive individuals, on the other hand, the marginal cost of giving away calories is reduced, as they have more to spare. Likewise, families with fewer dependents and/or with high productivity can afford to share out calories more generously, while families with more dependents and/or lower productivity receive greater marginal gains from receiving calories from others.

Human parents are thus in a position to subsidize the growth of their non-productive young, while grandparents—who have high productivity, but few remaining direct dependents of their own—are in a position to subsidize the need of their adult children's families, who are often in caloric deficit due to the need of multiple

dependent offspring (Kaplan et al. 2010). By the same logic, a pair of adult siblings and other close kin facing differences in productivity or dependent need—due to birth order, stochasticity in rates of fertility and mortality, or other factors—should also be motivated by inclusive fitness maximization to help each other fulfill unmet needs.

Gains to specialization by age and sex

At the same time, there is life-period-scale variance in the return rates from and costs of effort in specific activities, as a function of individuals' sex, embodied capital investments and physical condition. This variance creates returns to age- and sex-specific specialization and exchange (Bock 2002a, Gurven and Kaplan 2006). Reproductive-age women, for instance, specialize in direct child care (including lactation), with costs to their direct caloric productivity (Hurtado et al. 1992). Men at their peak hunting ability (typical in mid-life, when significant skill has accumulated, yet the body is still in good condition for dangerous and physically demanding activities) specialize in production of foods rich in fats and protein. Older adults, as they experience physical senescence, may optimally shift effort away from potentially injurious tasks in favor of more low-impact routes to fitness promotion (Gurven and Kaplan 2006).

Such specialization by age and sex in different domains of caloric production can lead to bi-directional energy flows, with each individual producing a surplus of those products which they are differentially suited to produce (as a function of their own age- and sex- specific efficiency and cost of effort). Specialization of some family members in other fitness-enhancing tasks outside direct production—such as child care or food processing—on the other hand, can yield apparently asymmetric flows when only calories alone are considered, but which may (or may not) be more balanced upon consideration of all currencies. Kramer's work has focused in particular on quantifying these non-caloric inputs into household success (Kramer 2005b, Robinson et al. 2008).

Reciprocal insurance against risk

Finally, variance in return rates across shorter time spans (days, weeks, months, or potentially years) produce returns to forming relationships of reciprocal food sharing. Variance in returns implies that on successful days, families face low marginal costs to gifting part of the returns to others; while on unsuccessful days, they face high marginal gains from receiving calories from others. Families can thus benefit from smoothing each other's rates of consumption as they experience periodic asymmetries in relative need (Gurven 2004, Kaplan and Hill 1985, Winterhalder 1986). The same logic supports reduction in longer-term variance in productive ability due to illness or injury (Gurven et al. 2000, Sugiyama 2004, Sugiyama and Chacon 2000). Such bilateral relationships of mutual support are predicted to be robust to the costs of free-riding and defection when agents interact repeatedly, and can preferentially maintain relationships with those who return the favors done them (Axelrod and Hamilton 1981, Trivers 1971). Optimal strategies for inter-temporal variance reduction may differ substantially for domesticated plant and animal resources compared to foraged goods, with increased capacities for storage, greater synchronicity of shortfalls between households, and longer time-scales at which variance in income is manifest (i.e. seasons and years rather than days or weeks; Cashdan 1985).

Whether relationships of specialization and exchange and reciprocal variance-reduction are best, more easily, or more often established with kin or non-kin are important theoretical and empirical questions. On the one hand, inclusive fitness benefits may facilitate the formation of reciprocal relationships (Axelrod and Hamilton 1981), and if kin tend to live nearer to each other, the costs of giving may be lower. On the other hand, non-kin may have more different commodities to offer, or experience more asynchronous patterns of risk (which might be more correlated within a kin group) which increase the returns to exchange with non-kin; these considerations, however, may not be especially important for a simple subsistence economy such as the Tsimane's, but may be more germane to more complex human societies with more extensive divisions of labor and trade.

VI. Guide to the dissertation

The subsequent chapters of the dissertation are organized as follows. Chapter 2 provides a brief introduction to the Tsimane' population, its economy, and its social organization. It then describes the methods utilized to collect data on economic production and redistribution in 11 Tsimane' villages, and describes the procedures used to prepare these data for analysis. Chapter 3 presents an analysis of the life history of Tsimane' productivity in terms of return rates, time expenditures, and total daily output across different domains of production: hunting, fishing, and horticulture. Chapter 4 then evaluates the impact of the need of siblings, children, and grandchildren on productive effort across the lifespan. Chapter 5 then presents an analysis of the pattern of caloric transfers between individuals and families. These patterns of productivity and redistribution are discussed in light of the theory laid out in this introductory chapter. Chapter 6 summarizes the results of these analyses, and discusses them in light of the current state of research in human evolutionary ecology.

CHAPTER 2. STUDY POPULATION AND METHODS

This chapter describes the empirical foundation for the analyses carried out in this dissertation, and is divided into three parts. Part I gives a brief introduction to the Tsimane' population, economy, and social structure. Part II then describes the data sample and field methods for data collection. Part III then describes the data preparation methods employed to construct the datasets analyzed in the subsequent chapters of this dissertation.

I. Tsimane' population

The indigenous Tsimane' population of some 10-12,000 individuals resides in the Beni Department in lowland Bolivia. Tsimane' settlements are located primarily along the Maniqui and Quiquibey rivers, their tributaries, and nearby forested regions. Detailed ethnographic and historical treatments can be found in Chicchón (1992), Ellis (1996), and Reyes-García (2001).

The Tsimane' practice a primarily subsistence lifestyle that includes hunting, fishing, and horticultural production of rice, sweet manioc, plantain, and maize. Tsimane' hunting targets a variety of game species, including collared peccary, tapir, gray and red brocket deer, paca, howler monkeys, white-faced capuchin monkeys, coati, armadillo, and cracid birds (Gurven et al. 2006). The Tsimane' employ bows and arrows, 12-gauge shotguns, 0.22 caliber rifles, and machetes to kill prey. Dogs are also often utilized to discover, corner, tree, or kill game. Flashlights are sometimes used for hunting at night. While hunting is undertaken almost exclusively by men—often alone or in small group of two or three—women sometimes accompany and assist in kills, especially on multi-day foraging trips. Boys begin to accompany men on hunting trips in adolescence in order to gain the skills necessary to track, encounter, and apprehend prey. Returns from hunting effort are highly variable; in the production and sharing

dataset described below, males aged 20+ return without success on 37% of hunting days.

The Tsimane' fish in rivers, streams, arroyos, and ox-bow lagoons utilizing a variety of methods, including hook and line, bow and arrow, and nets. Like many other native Amazonian groups, the Tsimane' also utilize plant poisons in combination with temporary dams, weirs, and water diversions to intoxicate and capture fish in large numbers. Toxin-producing plants are grown in families' yards or gardens, or are collected from the forest. A poison-fishing event is usually initiated by one or two experienced individuals who, after making the initial preparations, enlist the help of a wider group of friends and relatives to help corral and harvest the fish. When small fish are teeming near shore, they can be swept onto land using a machete or bare hands. In the larger rivers, migratory pulses of fish can provide an abundance of fish meat over the course of a few days or a week. Returns from fishing are less variable than hunting; in the production and sharing dataset, males aged 20+ return from fishing without success on only 13% of days. Meat and fish can be roasted, smoked, salted and dried in strips, or cooked in stews with rice or other carbohydrates.

Horticulture is land extensive in nature, and is primarily limited by the availability of labor, not land, although encroachment by non-Tsimane' ranchers and colonists has begun to restrict the availability of land for some communities. Land-use rights are informal, and few permanent claims to land are made or recognized (Gurven et al. 2010). New fields are cleared using metal axes and machetes, then burned, cleaned, and planted during the dry season each year (roughly July through November). Most families maintain between 1 and 6 fields at one time (mean = 2.9 fields per family) that range in size from 0.1 to 2 hectares (mean = 0.56 hectares per field). Fields are usually left fallow for 5-10 years before being re-used.

Plantain and manioc are harvested throughout the year. Plantains are usually roasted directly on embers and consumed alongside meat or fish. Manioc is commonly chopped, boiled, masticated, and fermented (1 to 4 days) to make chicha (Tsimane':

shocdye'), a sweet, viscous, and slightly alcoholic beverage common to many South American groups. Chicha is also sometimes supplemented with plantain or corn.

The rice harvest is seasonally concentrated in the months from February to May. The rice is gathered into handfuls and reaped with the aid of a knife, then set out to dry for one or two days. Rice is then either piled and stored in small roofed huts, or bagged for storage or sale. Families in this sample sell an average of 32% of rice harvested. Rice for sale can either be transported to town, husked, and sold to venders in the market at a price of 25-50 Bolivianos (Bs; 7 Bs = 1 USD) per arroba (1 arroba = 11.5 kg), or be sold to merchants who travel to the community and buy at lower rates of 15-20 Bs per arroba. Merchants often offer commercial goods on credit in the year preceding the rice harvest, and collect at the end of the harvest season, a practice which can particularly pinch the caloric budget of families in years with lower-than-expected yields. Horticultural yields can be undercut by flooding, consumption by insects or birds, poor maturation (e.g. leading to brittle rice stalks), ill-timed rain patterns, or a mismatch in the timing of harvest-readiness and the availability of harvest labor; stored rice is also vulnerable to ruining by mold, consumption by insects or birds, and theft. Before cooking, the rice is pounded in a hollowed log with a wooden mallet to husk the grains. Rice is usually either boiled and eaten alongside other foods, or cooked in a stew of meat or fish. While manioc and maize were cultivated in lowland South America prior to European contact, rice and plantains are both Old World imports (Crosby 1972).

Tsimane' social structure is manifest at relatively small scales, primarily at the levels of the nuclear and extended family. Closely related nuclear families often reside together in small residential clusters, within which are relatively high levels of cooperative labor, common and shared meals, and other forms of resource pooling. The median age at marriage is 16.5 for Tsimane' women, and 21.0 for men (Winking 2005). Marriage is not marked with formal ceremony, but is socially recognized as a couple begins to reside and sleep together. 5-10% of married men are polygynously married, almost always to two sisters. Parents sometimes play a role in arranging or encouraging marriages, and the woman's family is often consulted by a suitor or his family in the

informal process of courtship. While couples may reside near either the husband or the wife's kin, young couples often reside with the woman's family for some period after marriage as the husband contributes a loose form of bride service. Tsimane' marriages are relatively stable, with roughly 20% of marriages ending in divorce, most often within the first year or two of marriage (Winking et al. 2007). 95% of men whose wives undergo menopause do not go on to reproduce again, meaning that most older men cease reproducing at the same time as their wives (Kaplan et al. 2010).

Traditionally, the Tsimane' evidence relatively egalitarian distributions of wealth and social power, although recognized leadership roles and distinctions by wealth have become more pronounced in some settlements as a function of acculturation (Gurven et al. 2010). With prompting from the New Tribes missionaries, the Tsimane' Grand Council was formed in the 1980s, with offices in San Borja; as a part of this initiative, villages were instructed to elect 'chiefs' (Spanish: *corregidor*) to direct village meetings and facilitate relations with the Spanish-speaking outside world. Tsimane' communities in the Pilon Lajas Biosphere Reserve are also under the jurisdiction of the Tsimane' Mosetene Regional Council, based in Rurrenabaque.

Adult men engage in some wage labor, principally with ranchers and loggers. A typical daily wage is 20-30 Bs. Tsimane' families make occasional purchases of processed foods such as vegetable oil, sugar, salt, and alcohol, and other non-food items, such as ammunition for hunting, hooks, line, and nets for fishing, clothing, mosquito nets, and school supplies. Market transactions take place in town, or with Spanish-speaking merchants or ranchers.

Tsimane' mortality rates are high for western standards, but typical for foragers and forager-horticulturalists (Gurven and Kaplan 2007). Roughly 25% of children die before age 15. Mortality rates during adulthood stabilize around 1%, and begin to increase from the 30s onward. On average, those who reach age 15 can expect to live an additional 43 years; those who reach age 50 can expect to live an additional 17 years (Gurven et al. 2007). During the reproductive period, Tsimane' women maintain fertility rates of roughly 0.3 births per year. The total fertility rate is high, with 8.7 expected

births in a woman's lifetime (Kaplan et al. 2010). Most Tsimane' have only gained access to basic modern medical care in the last decade with the initiation of the NIH/NIA-funded Tsimane' Health and Life History Project.

II. Data collection

Study sample

The sample employed in this study is made up of 245 families (1245 individuals) residing in eleven villages. These villages are clustered in four regional groupings: four villages located on the Maniqui downriver from the town of San Borja (“Downriver”); five villages located in the forested region to the east of the Maniqui (“Forest”); one village located on a western tributary of the Maniqui upriver from San Borja (“Tributary”); and one, more acculturated village located along an arroyo a few kilometers outside of San Borja (“Ton’tumsi”). Research teams composed of North American anthropologists and Tsimane’ research assistants were resident in each sample village (or in a walkable neighboring village) between 4 and 30 months (mean = 15.2; *SD* = 8.1) from 2005 through 2009. The author assisted in data collection and entry beginning in 2005, visited the Forest villages and Ton'tumsi during the sample period in 2006, and resided Downriver in 2007 and in Tributary in 2008 and 2009. A breakdown of sample characteristics by region is given in Table 2.1.

Table 2.1. Sample characteristics by region

| <i>Region</i> | <i>Villages</i> | <i>Sample Period</i> | <i>Nuclear Families</i> | <i>Individuals</i> | <i>Individual Prod. & Sharing Sample Days</i> | <i>Field Interviews</i> |
|---------------|-----------------|----------------------|-------------------------|--------------------|---|-------------------------|
| Downriver | 4 | Aug 2006 - Nov 2007 | 61 | 289 | 19,268 | 76 |
| Forest | 5 | Jan 2005 - Jun 2006 | 73 | 366 | 18,220 | 50 |
| Tributary | 1 | Dec 2007 - Dec 2009 | 46 | 239 | 20,762 | 86 |
| Ton'tumsi | 1 | Jan 2005 - Jul 2006 | 65 | 351 | 19,680 | 52 |
| All Regions | 11 | Jan 2005 - Dec 2009 | 245 | 1245 | 77,930 | 264 |

Census and demography

In all sample communities, a detailed census was established and kept up-to-date which provided, among other data, each individual's sex, birth year, and biological parents and grandparents. Birth years were estimated using methods described in Gurven et al. (2007). Where incomplete, these census data were supplemented with data from demographic interviews also described in Gurven et al. (2007). Adult parents and their co-resident dependents (i.e. offspring and adopted dependents) were classified together as nuclear families. Body mass in kilograms, assessed using an electronic standing scale, was available from yearly physical exams conducted by Bolivian physicians and research assistants for 1198 individuals in the sample (96%).

Production and sharing interviews

Production and sharing interviews were conducted in the Tsimane' language by a trained Tsimane' research assistant roughly twice per week with each family. It was estimated how many hours each family member had spent engaging in subsistence activities during the preceding two days, including hunting, fishing, and horticultural labor. Horticultural labor was disaggregated by activity type, including clearing brush, clearing trees, burning, planting, weeding, and harvesting; the family owning the horticultural field(s) was also recorded.

Quantities and producers of edible products hunted, fished, or harvested during those two days were recorded. For each product, interviewees were asked which members of the nuclear family and other community members had consumed portions of the product in prepared meals, and which had received portions of the products as raw gifts; the reported quantities gifted were also recorded. Families were also asked whether they had received any gifts of food from other households, in which case the quantity, primary producer(s), and donor(s) of any gifts were recorded. Each family was interviewed an average of 45.5 times ($SD = 20.4$), yielding a mean of 92.8 sample days per individual ($SD = 40.0$).

In one village ('Tributary'), an additional questionnaire was administered focusing on the redistribution of horticultural products. For any plantain, manioc, or rice cooked in the previous two days, interviewees were asked who had harvested the product from which family's field, and who (within or outside the nuclear family) had consumed portions of the product. The quantities of any gifts of plantain, manioc, or rice to or from other families in the previous two days were also recorded.

Field interviews

In order to complement the finer time-scale but sample-error-prone horticultural data of the production and sharing interview, horticultural field interviews were also conducted with field owners on a yearly basis. These interviews included information on area of acreage cleared and planted with each of the major cultigens (rice, plantain, manioc, maize) in current fields, and the number of days worked by individuals within and outside the household who contributed labor to the preparation, maintenance, and harvesting of fields. The total amount of rice harvested (in arrobas of bagged rice; 1 arroba = 11.5 kg) from each field and the total amount of rice sold on the market were recorded; those families planning to harvest or sell more rice in the same year were asked to estimate how much more rice they expected to harvest or sell. Field interview data were available for 173 families in the study (71%), among which there are an average of 1.53 interviews ($SD= 0.73$) and 1.13 unique field owners ($SD= 0.37$) per family.

III. Data preparation

Caloric value estimates

For each product, unprocessed mass in kilograms was calculated from reported quantities produced (e.g. arrobas of rice, bunches of plantains, number of animals or fish); the raw mass of unitary products (e.g. animals, fish, fruits) was estimated based on mean mass measurements derived from field guides (Eisenberg 1989, Emmons 1990)

and previous research with the Tsimane' and other South American foragers (Gurven et al. 2006, Hill and Hawkes 1983). The product's total caloric value was then calculated based on estimates of mean dietary calories (assimilated by a human consumer after processing) per unprocessed kilogram for each item, derived from standard nutritional tables (INLASA 2004).

Individual hunting and fishing production measures

Credit for game and fish listed in the production and sharing interviews was assigned to the individual that located and killed the animal or fish; credit for animals that were located and killed by more than one hunter, or for fish that were produced collectively (e.g. from net fishing) was split evenly between the active hunters or fishers. Credit for game found or killed by dogs was also assigned to the human hunter(s) in the hunting party. To calculate daily individual production from hunting and fishing (in calories per day), total calories from game and fish produced per sample day were calculated for each month, then averaged across months in order to limit sampling error due to concentrated periods of dearth or bounty. Likewise, to calculate individual time allocation to hunting and fishing, total hours spent hunting/fishing per sample day were calculated for each month, then averaged across months. Individual return rates from hunting and fishing (in calories per hour of effort) were calculated by summing all calories of game/fish produced and dividing by the total number of hours spent hunting/fishing.

Individual horticultural production measures

As horticultural goods are produced through the combined effort of multiple individuals in a variety of tasks across the year, estimating individual credit for horticultural production requires more complex accounting techniques. The datasets employed in this dissertation fortunately provide a level of detail regarding field labor inputs to yield an unusually complete picture of individual roles in this area of the economy.

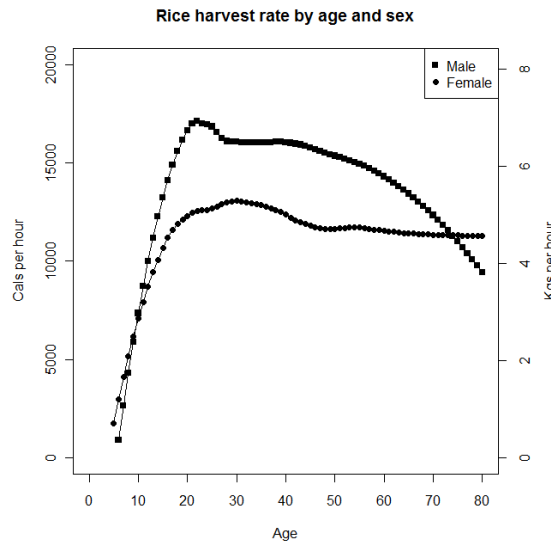


Fig 2.1. Rice harvested per hour by age and sex.
(N = 4431 harvest events, loess smoothing parameter = 0.6)

The number of hours each individual spent per day in horticultural labor in each family's fields was calculated separately for each month based on the production and sharing interviews, then averaged across months. Likewise, total calories of rice and non-rice horticultural products harvested per day by each individual from each family's fields was calculated separately for each month, then averaged across months. On the basis that harvesting time accounts for approximately 35% of hours spent in horticultural labor across the year, the harvesters of horticultural products were assigned credit for 35% of the calories they harvested. Credit for the remaining 65% of calories was distributed among those individuals who had contributed labor preparing and maintaining the fields of the field-owning family in the following way.

In order to account for variation in efficiency in horticultural labor, a relative labor efficiency curve was estimated as a function of age and sex based on rice harvest rates. A loess curve was fit (using the loess function in version R 2.11) to the harvest rate estimates (in kg per harvest hour) for each individual rice harvest day in the production and sharing dataset as a function of age, separately for each sex. These efficiency curves are given in Fig. 2.1. For each contributor to a focal family's fields, the number of hours

spent per day in preparation of those fields was weighted by his/her expected relative efficiency based on age and sex. Approximating that clearing trees with an axe carries a metabolic cost roughly 2-4 times that of other field preparation tasks (e.g. clearing brush, planting, weeding; Ainsworth et al. 1993), tree clearing hours were weighted 3 times more heavily than other field preparation hours. Preparation credit for each harvested item was then divided among field laborers in proportion to their weighted contribution of preparation hours per day.

Due to the seasonally concentrated nature of the rice harvest and the short time-scale of the production and sharing interview, a correctional procedure was employed to reduce variance due to sampling error for those 102 families with valid rice data from both the production and sharing interview and the field interview. On the basis that the number of personal harvest days per year reported annually by field owners in the field interview should be less prone to sampling error than the same number calculated from the production and sharing data, each family's total rice production per day as reported by the production and sharing interview was rescaled by a factor calculated as the ratio of the number of field owner harvest days reported in the field interview to the number of field owner harvest days estimated from the production and sharing interview.

Rice production data from the production and sharing interviews of 95 families who were not sampled in every month from February through May were discarded. Valid field interview rice production data were available and utilized for 45 of these families. Previous analysis suggested that field interview responses greatly underestimated the labor and productivity of non-field owners (e.g. wives and children). To correct for this under-estimation, and to bring the field interview production numbers in line with the equivalent numbers in the production and sharing interview, the rice harvest days contributed by non-owning family members were multiplied by a factor of 2.6, and those contributed by non-family members were multiplied by a factor of 1.1. These multipliers reflect the ratio of the total number of harvest days per year contributed by these types in the production and sharing interview, to the comparable,

under-estimated number in the field interview. Each of these families' rice production in the field interview was then adjusted according to the ratio of the expanded total number of harvest days per year, weighted by relative harvest efficiency of harvesters, to the reported number of days in the field interview weighted by relative harvest efficiency. Credit for rice production in these families was then divided according to individuals' weighted horticultural labor contributions (from the production and sharing interview) throughout the rest of the year.

The percent of harvested rice sold per year by each family was drawn from the field interview data. A comparison of those interviews in which field owners estimated the amount of rice they were still planning to sell in the same year with those that had complete rice sale data suggested a slight tendency of interviewees to overestimate the amount that they would finally sell. A regression model was used to evaluate the magnitude of this over-estimation (using the *lm* function in R version 2.11), and the quantities sold by families with estimated sales data were devalued accordingly; this procedure is described in appendix A. Rice sales data were missing or insufficient for 23 families possessing valid rice production estimates. For these families, amounts sold were predicted from a regression equation based on those families with both production and sales data, taking into account geographical region and total rice production from the family's fields (Table A.2 in the appendix A). The amount of rice sold was subtracted from each family's rice production to yield subsistence rice production per day.

Table 2.2. Coefficients for estimating BMR in kcal/day from body mass in kg, where $BMR = a + b \times \text{mass}$, from FAO (2001).

| <i>Age category</i> | <i>Males</i> | | <i>Females</i> | |
|---------------------|----------------------|-----------------------------|----------------------|-----------------------------|
| | <i>Intercept (a)</i> | <i>Mass coefficient (b)</i> | <i>Intercept (a)</i> | <i>Mass coefficient (b)</i> |
| 0-2 | -30.4 | 59.512 | -31.1 | 58.317 |
| 3-10 | 504.3 | 22.706 | 485.9 | 20.315 |
| 10-18 | 658.2 | 17.686 | 692.6 | 13.384 |
| 18-30 | 682.2 | 15.057 | 486.6 | 14.818 |
| 30-60 | 873.1 | 11.472 | 845.6 | 8.126 |
| 60+ | 587.7 | 11.711 | 658.5 | 9.082 |

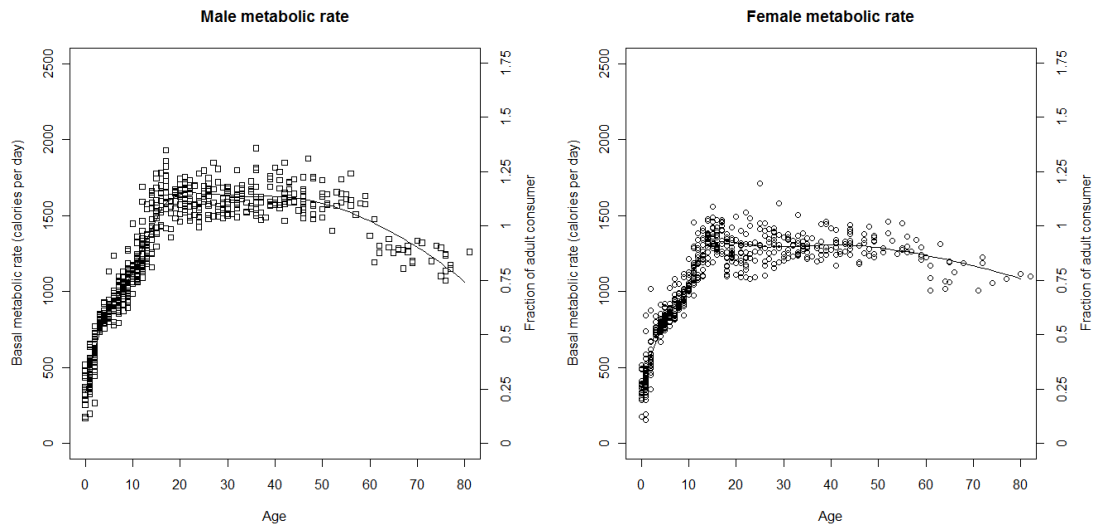


Fig. 2.2. BMR by age and sex (N= 680 males, 618 females; loess smoothing parameter = 0.5)

Consumption and net production estimates

Each individual's consumption rate was calculated as multiple of basal metabolic rate (BMR) estimated on the basis of age, sex, and body mass. BMR was estimated according to FAO formulae given in Table 2.2 (FAO 2001, Schofield 1985). For 47 individuals lacking body mass measures, BMR was imputed based on a loess curve predicting BMR as a function of age for each sex (Fig. 2.2). The BMR of an average adult (≥ 18 years) Tsimane' consumer was calculated at 1430.3 cal/day; BMR values of each individual were divided by this number to calculate the individual's 'fraction of adult consumer' (a.k.a. adult-consumer value).

For each region, total subsistence production per day (i.e. excluding sold rice) was summed, then divided by the sum total of adult-consumer values to yield the mean adult consumption rate. This value was multiplied by an individual's adult-consumer value to estimate individual consumption rate. The mean adult consumption rate for the full sample was estimated at 2558.8 calories per day.

Each individual's net production was calculated by subtracting their estimated consumption rate from measured gross production rate. The measured net production of each nuclear family was calculated by summing the measured net production of each family member. For the analyses of transfers between families in chapter five (Tables 5.1-5.3), an instrumental variable representing expected net family production was also calculated by summing the expected mean net production of each family member as predicted by age and sex (these values are plotted in Fig. 3.7b).

Transfer estimates

Daily caloric transfers between individuals co-resident in the same community were estimated on the basis of production events in the production and sharing dataset in the following way. Credit for caloric transfers in the form of raw gifts or prepared meals was attributed to producers using the same methods for attributing production credit above (i.e. it is split between acquirers in the case of game and fish, and between the harvester and field preparers in the case of horticultural products). The share received by gift recipients was determined by the specified quantity recorded for gifts; once gift quantities were subtracted, the product's remaining calories were divided among meal recipients in proportion to their relative metabolic rate (the mean adult metabolic rate was assumed for individuals outside the sample).

Sharing data were available for roughly 29,000,000 of 33,200,000 calories (87.3%) of game, 14,100,000 of 15,400,000 calories of fish (92.0%), and 59,200,000 of 361,200,000 calories (16.4%) of horticultural products in the production and sharing dataset. (This difference between game/fish and horticultural goods arises because the former are more likely to be shared out within 2-3 days of acquisition due to spoilability, whereas the latter are often saved for consumption weeks and months later.) Because these data were available on only a subset of subsistence products, quantitative estimates of calories transferred between individuals per unit time were calculated according to the following methods. The specific quantities estimated by these methods rely on two important assumptions: (1) that the observed *relative* amounts of calories of each type (game, fish, or horticulture) transferred to different individuals are

approximately proportional to the total absolute amounts transferred; and (2) that the calculated daily subsistence production rates in each economic domain (described above and reported in chapter three) are indeed representative of individuals' true subsistence production rates.

First, in order to estimate the mean calories of a certain type (game, fish, or horticulture) transferred *one category of individuals to another* (e.g. from males aged 20-29 to males aged 40-49, or from mothers aged 50-59 to offspring outside the nuclear family), the raw total of calories transferred from the donor category to the recipient category was summed, then divided by the raw total of calories transferred from the donor category to all recipients (within or outside the sample). This fraction of shared production received by the recipient category was then multiplied by the estimated mean daily production rate of the individuals in the donor category of calories of that type to estimate the mean number of calories transferred from the donor to the recipient category per day.

Second, to estimate mean calories transferred *one specific individual to another*, the raw total of calories transferred between from the donor to the recipient was summed, then divided by the raw total of calories transferred from the donor to all recipients. This fraction of the donor's shared production received by the recipient was then multiplied by the estimated mean daily production rate of the donor of calories of that type to estimate the mean number of calories transferred from the donor to the recipient per day. This second individual-dyad-level method can be expected to be more subject to individual-level sampling error than the aggregate category-based estimates described in the previous paragraph. Transfers from one nuclear family to another also were calculated from these individual-dyad-level measures by summing the estimated amounts transferred from each member of the donor family to each member of the recipient family.

Kinship

Consanguineous and affinal relationships between individuals residing in the same community were calculated on the basis of shared genetic ancestry and marriage according to a new algorithm programmed by the author. For any pair of individuals, A and B, this algorithm provides values of Wright's coefficient of relationship, summing across all independent pathways of genetic relatedness, as well as a verbal categorization of A's relationship to B, coded by sex, and vice versa (e.g. "female sibling", "male parent of female spouse"). A more detailed description of this algorithm is provided in appendix B.

CHAPTER 3. THE LIFE HISTORY OF TSIMANE' PRODUCTION AND CONSUMPTION

1. Introduction

The shape of the age-schedule of caloric production is crucial for understanding the life history of sociality in traditional human societies. One of the principal reasons for this is that—despite the fact that consumption and production must approximately balance each other over the long term in a population that is maintained at carrying capacity—characteristics of a population's ecological niche can affect the age-distribution of productivity in the population. That is, for a given level of production at the population level, there is variation in the relative degree to which different age- and sex-categories contribute to that total population production. Principles of life history, demography, and economics provide a guide for understanding and explaining this distribution of productivity across the life cycle and between sexes.

Theory developed by Kaplan, Bock, and Gurven has articulated how the importance of different determinants of efficiency across different productive domains is likely to affect age patterns of productivity in a society (Bock 2002a, Bock 2002b, Bock 2005, Bock and Johnson 2004, Gurven and Kaplan 2006, Kaplan 1997). This theory particularly takes into account the degree to which strength and/or skill are important determinants of efficiency within particular economic domains. The relative importance of these inputs has predictable effects on the patterning of efficiency (return-rates) by age and sex; these effects in turn impact the optimal allocations to productive effort across activities depending on age and sex. These optimal age-schedules of productive effort are also likely to depend on age-schedules of dependent need, in ways which depend on the key determinants (i.e. strength, skill) of efficiency across activities.

This chapter focuses on the empirical age-schedule of caloric return rates for both sexes among the Tsimane', and the roles of strength and skill in determining these return rates. It then examines the age-schedules of productive effort (i.e. time in production) and total daily productivity in light of these findings. In doing so, it discerns,

in part, the impact of ecological niche characteristics on the relative contribution of individuals by age and sex to the total amount of energy produced in society. The following chapter then goes on to explicitly examine the additional role of dependent need, as it interacts with the importance of different inputs into productivity across activity, in shaping the age-patterning of productivity.

Hypotheses and Predictions

Total daily production from each activity results from the interaction of the individual's efficiency (i.e. return rate) with the amount of time allocated to the activity. Embodied capital theory (particularly in its elaboration by Bock 2002a, 2002b, 2005 and Gurven & Kaplan 2006) provides a number of straight-forward hypotheses regarding the factors shaping the age-schedule of these two variables. First, it hypothesizes that the relationship between producer age/sex and **efficiency** in a particular domain of production depends on the degree to which (1) skill and experience, and (2) physical condition (i.e. strength, agility, robustness) are important determinants of productivity. Specifically:

- Peak efficiency in activities that require neither significant skill-development nor physical strength will be achieved relatively early in life and will not decline strongly with physical senescence.
- Efficiency in activities that depend on physical strength and agility but do not require high levels of skill development will increase with body growth, reach a maximum in early adulthood, and decline significantly with physical senescence.
- Efficiency in skill-intensive activities that do not require prime physical condition will begin low and increase for an extended period, and will not decline precipitously in old age.
- Efficiency in skill- and physical-condition-dependent activities will begin low and increase for an extended period, but will decline significantly with senescence.

Second, it hypothesizes that the optimal amount of **time allocated** to a particular domain of work effort should be sensitive to age- and sex-specific (1) return rates /

efficiency, (2) benefits from experience, (3) opportunity costs, (4) risks of injury, (5) familial need. Specifically:

- Other factors aside, individuals will put more effort toward activities yielding higher age-specific return rates.
- Time allocation to skill-intensive activities will precede attainment of high return rates.
- Older individuals will withdraw effort from more dangerous and strength- or physical-condition-dependent activities as they experience physical senescence.
- Time allocation of reproductive-age women will be depressed due to opportunities costs of withdrawn direct childcare; post-reproductive women on the other hand, will be released from this constraint.
- Effort will increase with the cumulative need of close kin; this and the preceding predictions are tested explicitly in chapter 4.

Finally, because **total production** is achieved through the allocation of effort yielding a particular return rate, total production is predicted to reflect the combined operation of those same causal forces affecting age-specific return rates and time allocation.

In the specific context of the Tsimane' subsistence economy, we expect hunting to be the domain of production most dependent on both skill and physical condition, creating the largest asymmetries in return rates and time allocation skewed toward adult men in the prime of life. While some forms of fishing may require higher levels of skill and/or strength, on the whole, we expect fewer biases by age and sex in return rates and time allocation. Similarly, as many forms of horticultural labor (i.e. weeding, harvesting) are neither skill- nor strength-intensive, we expect high horticultural production through most of life, especially as older individuals back off of other more physically demanding and dangerous activities. Those horticultural tasks requiring higher levels of strength (i.e. felling large trees), however, may be differentially undertaken by middle-age adult males.

Section II of this chapter presents a detailed analysis of the age-schedule of time allocation to, return rates from, and production from hunting, fishing, and horticulture

among the Tsimane'. Sources of variation in these variables across life are discussed in light of predictions derived from the theories of embodied capital investment and returns to specialization by age and sex. Section III of this chapter then evaluates the summed effect of this variation on the net caloric production of individuals and nuclear families, and its implications for intergenerational transfers.

II. Production by economic domain

Methods

The individual production data derived in chapter 2 were utilized to quantify age-trends in work effort and productivity. Linear regression was used to determine mean values of production variables (with 95% confidence intervals) across individuals within age-sex categories utilizing the `lm` function in R version 2.12. Individuals under 30 were grouped into 5-year age categories (0-4 ... 25-29), while those 30 and up were grouped into 10-year age categories (30-39 ... 70-79, 80+). The age- and sex-distribution of the sample is summarized in Table 3.1. Return rate data represent the subset of individuals in the sample who allocated a non-zero amount of time to the activity, and thus may tend to over-estimate the expected mean for the full sample, as low-productivity individuals are likely to self-select out of the sample. (The potential for self-selection bias is apparent in the table in appendix C, especially in hunting and, to a lesser extent, fishing.)

Table 3.1. Age- and sex-distribution of the production and sharing sample.

| <i>Age category</i> | <i>Males</i> | | <i>Females</i> | |
|---------------------|-------------------------------|-------------------------------------|-------------------------------|-------------------------------------|
| | <i>Full sample (N indivs)</i> | <i>Sample w. complete rice data</i> | <i>Full sample (N indivs)</i> | <i>Sample w. complete rice data</i> |
| 0-9 | 241 | 205 | 240 | 201 |
| 10-19 | 173 | 150 | 163 | 136 |
| 20-29 | 78 | 57 | 62 | 44 |
| 30-39 | 56 | 49 | 53 | 49 |
| 40-49 | 47 | 41 | 39 | 33 |
| 50-59 | 18 | 15 | 18 | 17 |
| 60-69 | 18 | 18 | 15 | 15 |
| 70-79 | 14 | 13 | 5 | 4 |
| 80+ | 1 | 1 | 4 | 4 |

Hunting

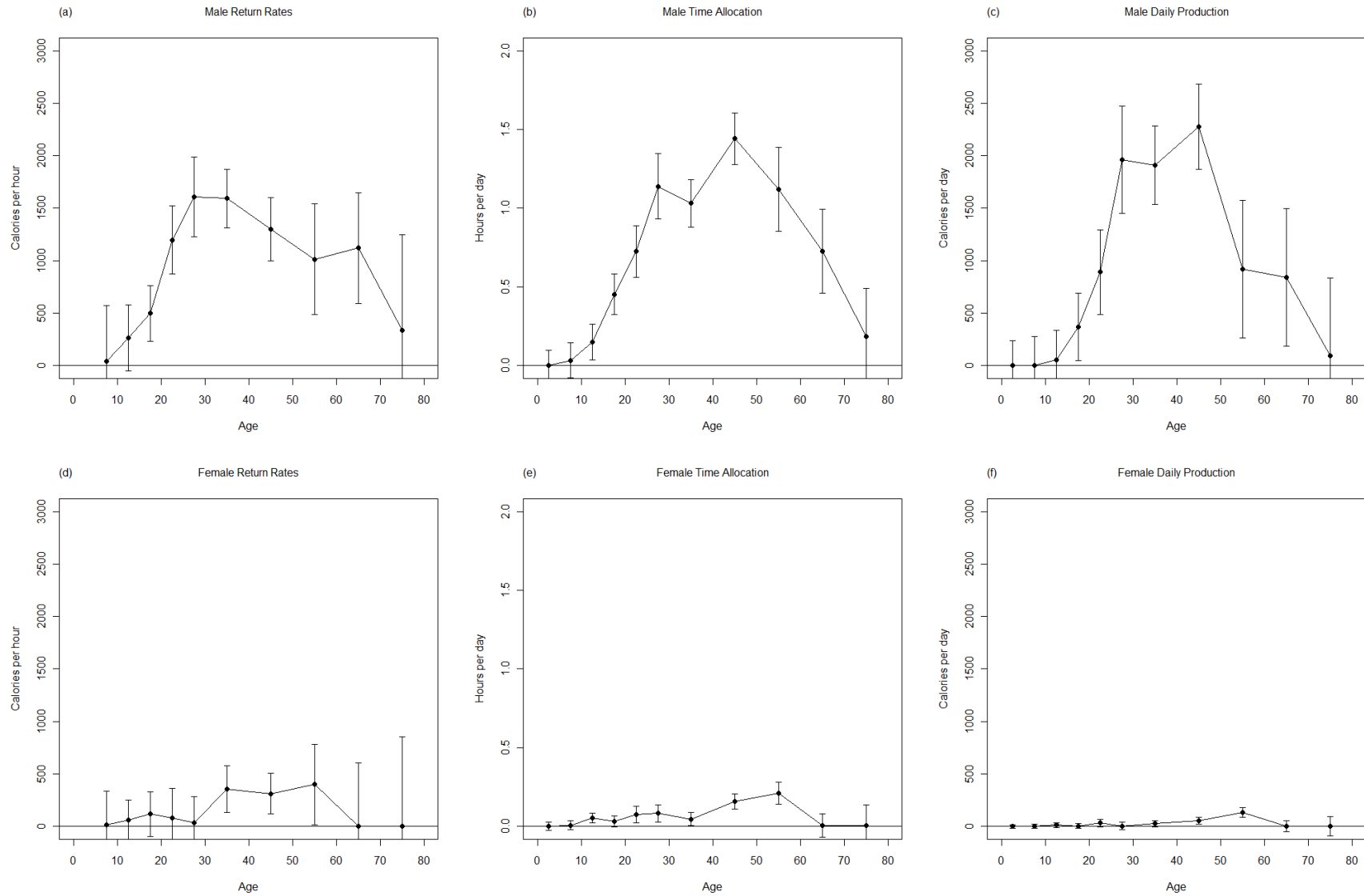


Fig. 3.1. Mean return rates from, time allocation to, and production from hunting by sex and age category. (Error bars indicate 95% confidence intervals.)

Fishing

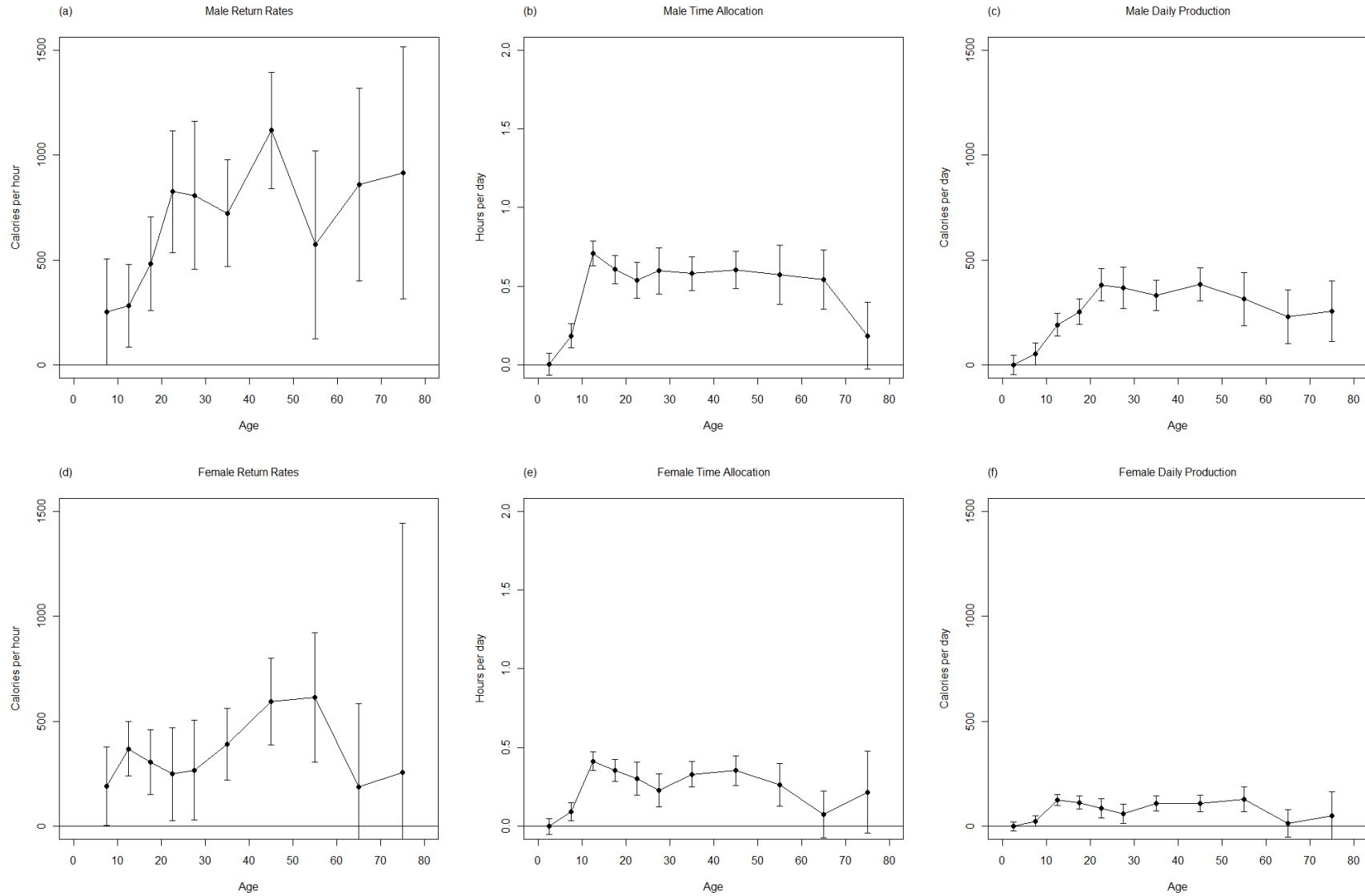


Fig. 3.2. Mean return rates from, time allocation to, and production from fishing by sex and age category. (Error bars indicate 95% confidence intervals.)

Horticultural Labor

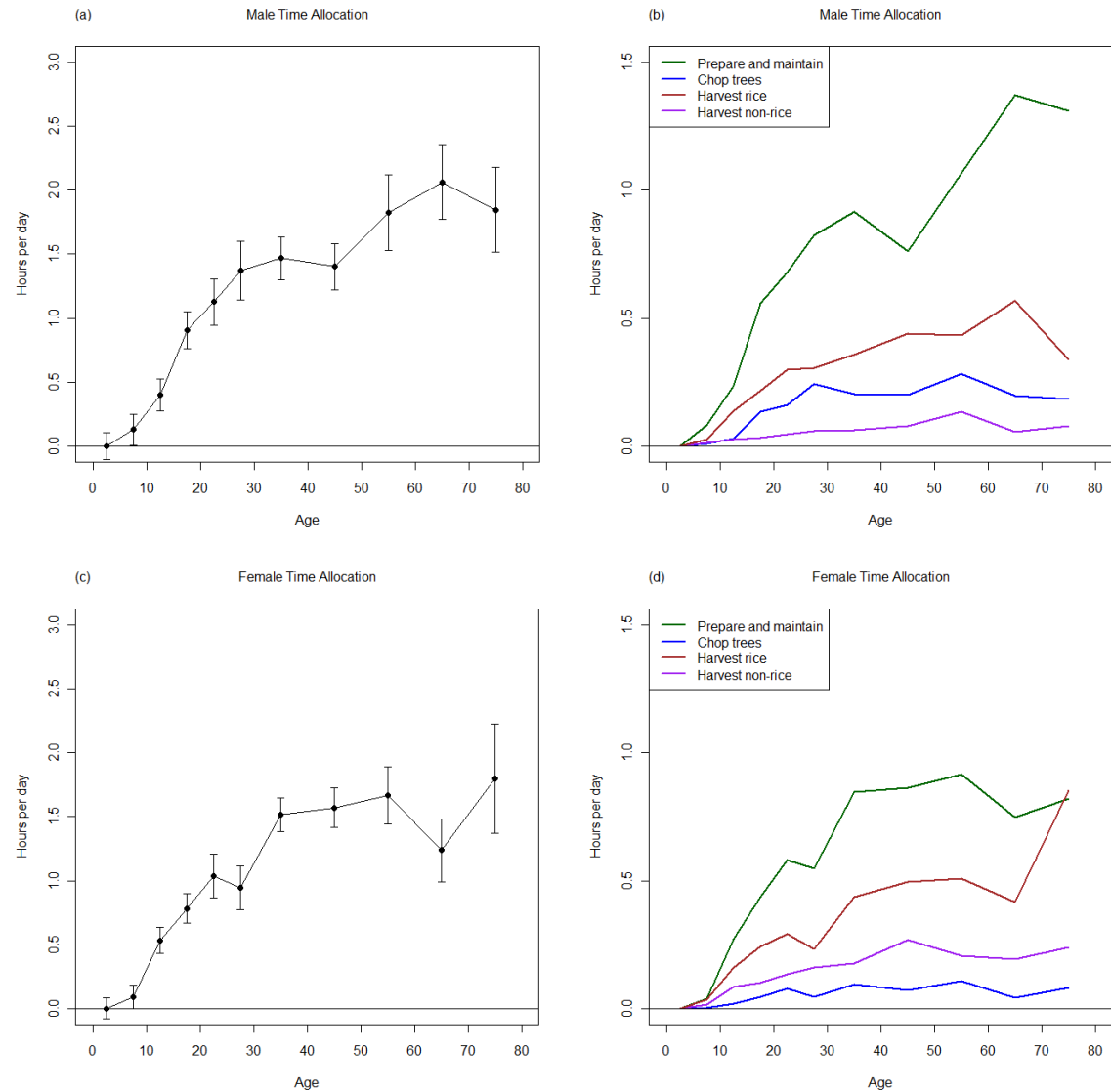


Fig. 3.3. Mean time allocation to horticultural labor by sex and age category. The left-hand panels (a) and (c) show total time allocation to horticultural labor, while the right-hand panels (b) and (d) disaggregate by activity type. (Error bars indicate 95% confidence intervals.)

Non-rice Horticultural Production

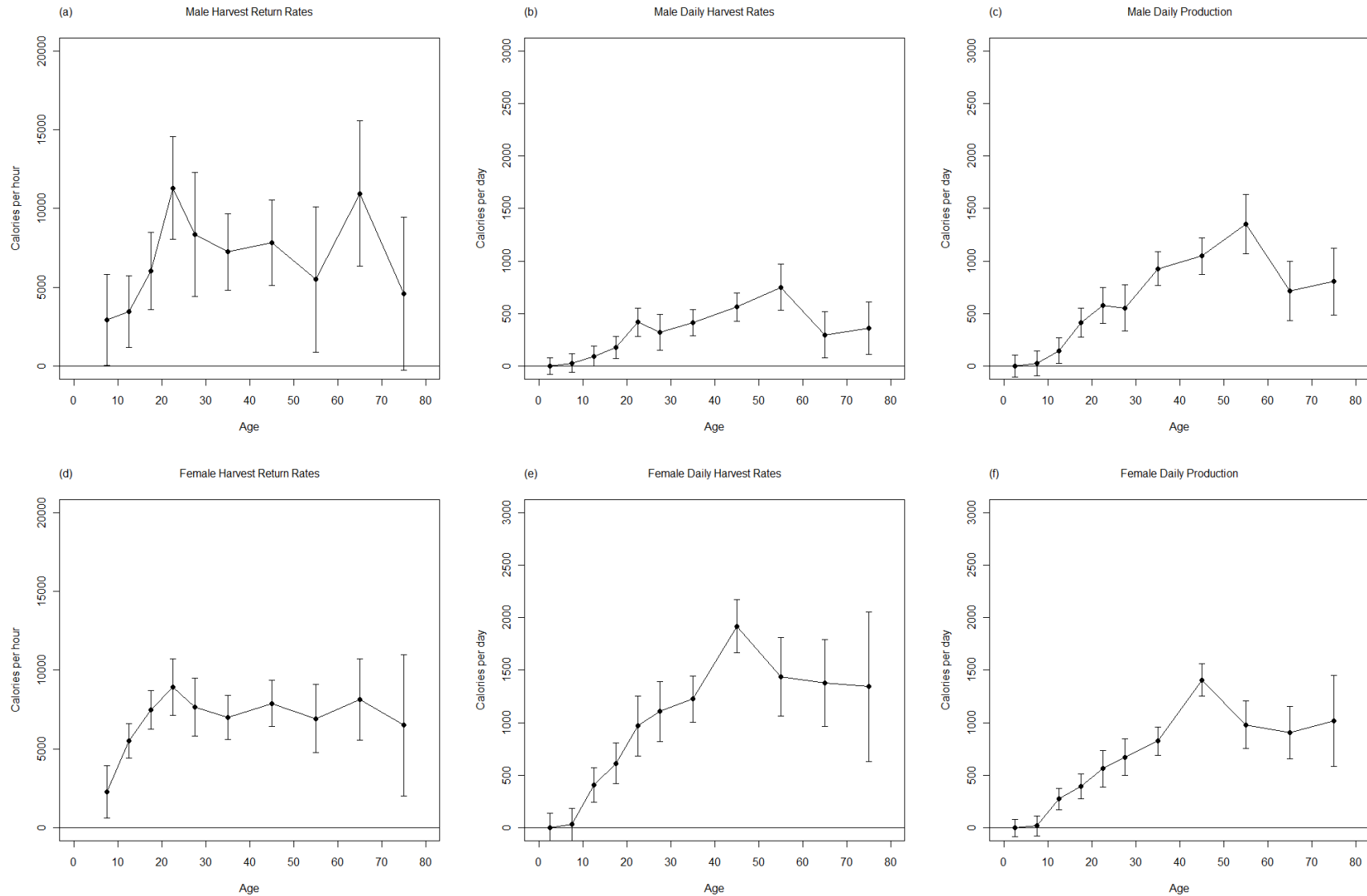


Fig. 3.4. Mean harvest return rates, daily harvest rates, and production of non-rice horticultural products by sex and age category. (Error bars indicate 95% confidence intervals.)

Rice Production

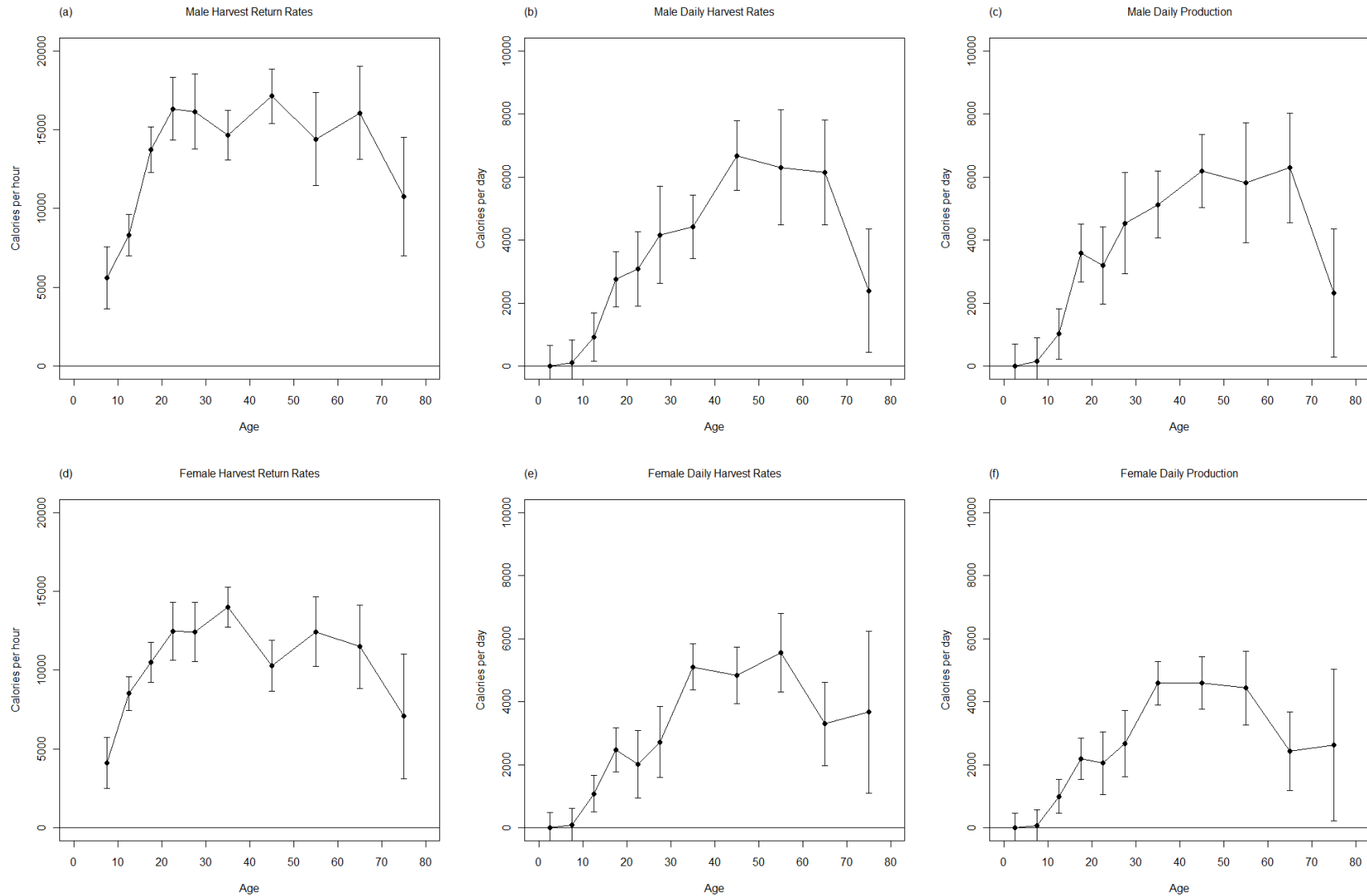


Fig. 3.5. Mean harvest return rates, daily harvest rates, and production of rice by sex and age category. (Error bars indicate 95% confidence intervals.)

Subsistence Rice Production

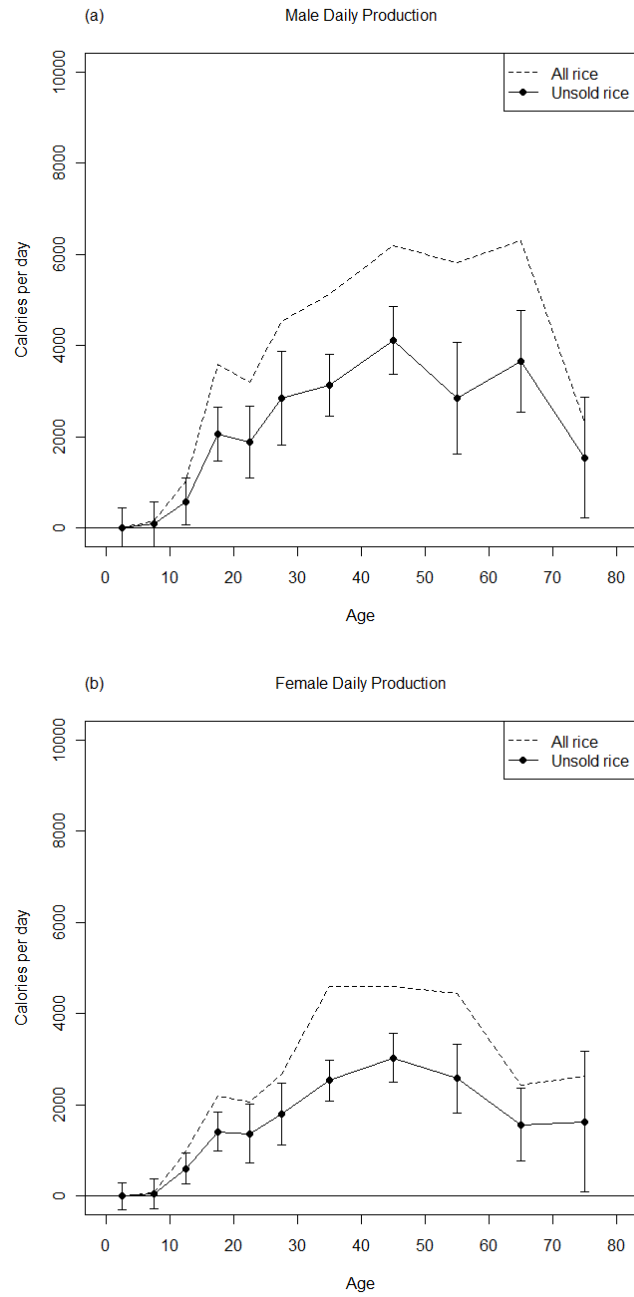


Fig. 3.6. Mean daily production of rice for subsistence by sex and age category. (Error bars indicate 95% confidence intervals.)

Results and discussion

Fig. 3.1 shows return rates from, time allocation to, and daily production from hunting for each sex across ages. Return rates begin very low for adolescent males and increase through the 20s, with a gain of about 90 calories per hour per year (Fig. 3.1a). Maximal return rates are attained in the late 20s and 30s; the mean return rate in this period is roughly 1600 calories per hour. Return rates begin to decline from the 40s onward, with men in their 70s producing at roughly the same level as teenagers. Male time allocation to hunting (Fig. 3.1b) increases steeply from about age 10 to age 30, reaching a peak in the 40s at about 90 minutes per day, then declines steeply across the 50s, 60s, and 70s. The high return rates and time allocation of men in their late 20s, 30s and 40s yield a high peak in total daily production across this period, around 2000 calories per day (Fig. 3.1c); men in their 50s and 60s are about half as productive, while the mean hunting production of men in their 70s is not significantly greater than zero.

The low hunting efficiency of males in their teens and early 20s is consistent with the skill-intensive nature of hunting in the South American tropics; maximal returns rates in this sample, however, are achieved somewhat earlier than has been found among the Tsimane' sample in Gurven et al. (2006), and among the Ache in Walker et al (2002). The mean adult return rates estimated from this large, interview-based sample (~1400-1600 calories per hour) are in close accordance with those estimated from the smaller, more precise sample examined in Gurven et al. (2006). Strong declines in hunting efficiency and effort also indicate the importance of physical condition for hunting; older men appear to adapt to their loss of efficiency and potentially increased risk of injury by shifting work effort to other, less physically demanding tasks. The role of dependent need in driving hunting effort in the middle of life is evaluated explicitly in chapter 4.

Hunting effort among the Tsimane is strongly sexually dimorphic, with mean female time allocation to hunting never exceeding 15 minutes per day, and mean production not exceeding 100 calories per day (Figs. 3.1d-f). Mean return rates for women aged 30-59 fall around 300 calories per hour. While this figure is likely to

underestimate women's potential as hunters, as most of women's hunting hours are spent accompanying men, not actively hunting, it may be that women's cumulative lifetime experience hunting is insufficient to reach the high return rates typical of adult men.

Mean return rates from fishing begin at around 250 calories per hour for males under 10, and increase to roughly 800 calories per hour by the early 20s; this return rate is more or less maintained across the rest of life, even into the 70s (Fig. 3.2a). Male time allocation to fishing increases to a shallow peak (~45 minutes per day) during the early teens, then remains stable at about 35 minutes per day from the 20s through the 60s, dropping only in the 70s (Fig. 3.2b). Men's daily production from fishing (around 400 calories per day) is well below that from hunting across adulthood, except in the 70s, where it is slightly higher (Fig. 3.2c). Return rates from fishing for females under 20 are similar to those of boys, but are lower than those of men during adulthood (Fig. 3.2d). Women's highest mean return rates, around 600 calories per hour, are attained in the 40s and 50s. Female time allocation to fishing (Fig. 3.2e) is about half that of males across life, also peaking in the early teens. Adult women's daily production of fish averages around 100 calories per day.

Importantly, the lack of decline in return rates at advanced ages suggests that fishing remains a viable means of protein production despite declining physical condition at least through the 60s. Fishing is the only economic activity in this study to show a peak in time allocation during adolescence. This is understandable given that during this period, fishing yields higher returns per hour of effort than hunting for boys; fishing is also relatively safe for children and adolescents, and (in contrast to hunting) can be undertaken in larger groups with mixed ages without sacrificing returns.

Fig. 3.3 shows time allocation to horticultural labor for both sexes across life. Remarkably, time expenditures increase nearly monotonically with age, and are relatively similar for both sexes (usually slightly higher for males). Figs. 3.3b and 3.3d break down this labor by activity type, showing that men tend to dedicate relatively more time felling trees, while women spend relatively more time harvesting non-rice

horticultural products (i.e. manioc, plantains). While men's absolute time allocation to tree felling is rather constant across life, men in the middle of life dedicate proportionally more of their horticultural labor to this task than older men, consistent with its more strength-intensive nature. This breakdown of labor by activity, however, is unable to show whether the nature of forest clearing effort may shift with age (e.g. with younger men differentially clearing larger trees in more virgin forest, and older men concentrating on less challenging patches); preliminary data drawn from focal follows and field interviews indicate that this may indeed be the case (Cummings, n.d.).

Harvest rates of non-rice horticultural products (per hour harvesting) are similar for both sexes, averaging around 7000 calories per hour from the 20s on, with no significant decline in old age (Figs. 3.4a and 3.4d). Men harvest significantly fewer calories of non-rice products per day than women (around 400 calories per day for men versus 1400 for women: Figs 3.4b and 3.4e), as expected from ethnographic observation. When credit for production is distributed according to field preparation and harvest, however, production of non-rice garden goods is relatively similar for the two sexes (Figs. 3.4c and 3.4f). This production increases steadily into adulthood, leveling off at about 1000 calories per day for women; men's production peaks in the 50s and declines somewhat in the 60s and 70s.

Rice harvest rates per hour harvesting also increase across adolescence and level off from age 20 onward, at about 16000 calories (~ 7 kg) per hour for men, and 13000 calories (~ 5 kg) per hour for women (Figs. 3.5a and 3.5d). These rates decline weakly in the 70s for both sexes. Daily harvest rates are highest for men in their 40s, 50s, and 60s, and for women in their 30s, 40s and 50s (Figs. 3.5b and 3.5e). Distributing rice production credit according to all labor inputs gives somewhat more credit to men in their 20s and 30s who contribute proportionally more labor to strength-intensive tasks such as tree-felling. Mean rice production peaks around 6000 calories per day for men, and 5000 calories for women (Figs. 3.5c and 3.5f). Clearly, horticulture with some division of labor by age and sex allows both men and women to be major producers of carbohydrates late into life in the Tsimane' ecology. Fig. 3.6 indicates the effect of

removing the production of rice for sale on the age curves of rice production, which yields a peak of around 4000 subsistence rice calories produced per day for men, and 3000 calories per day for women.

III. Net production and need of individuals and families

Methods

The subsistence production estimates for each economic domain were summed for each individual to obtain an estimate of total daily production for subsistence. As described in chapter 2, individual consumption was estimated by multiplying each individual's adult-consumer value (a scalar of BMR based on age, sex, and body mass) by total subsistence production per adult consumer day. Net production was then calculated by subtracting consumption rates from gross subsistence production rates. A loess curve of individual net production was fit as a function of age for each sex.

Next, the proportion of calories produced by each sex in each year of life relative to the total amount produced by both sexes across all ages was calculated, given the frequencies of males and females at each age in the population. For each sex in each year of life, gross production devalued by the probability of survival (l_x) to that age was divided by the sum of gross production devalued by the probability of survival for both sexes across all ages (assuming equal initial sex ratios). Tsimane' survivorship data for 1950-1989 were drawn from the life table in Gurven, Kaplan, and Zelada Supa (2007: Table 5). Finally, the net production of each nuclear family ($N = 195$ families with complete production data) was calculated by summing the net production of all family members. A loess curve of nuclear family net production was fit as a function of the mean age of the family's parents.

Chapter 3

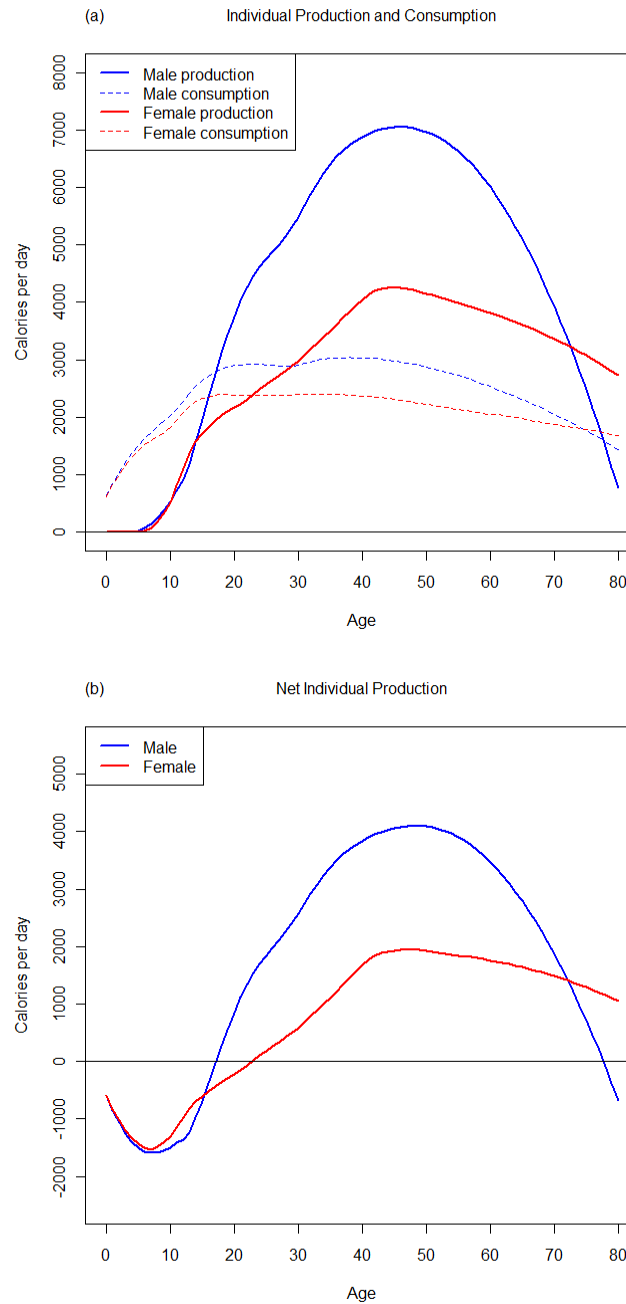


Fig. 3.7. Tsimane' mean daily production and consumption by age and sex. Panel (a) shows gross production and consumption rates, while panel (b) shows net production rates across the lifespan (i.e. production minus consumption). (Loess smoothing parameter = 0.5.)

Chapter 3

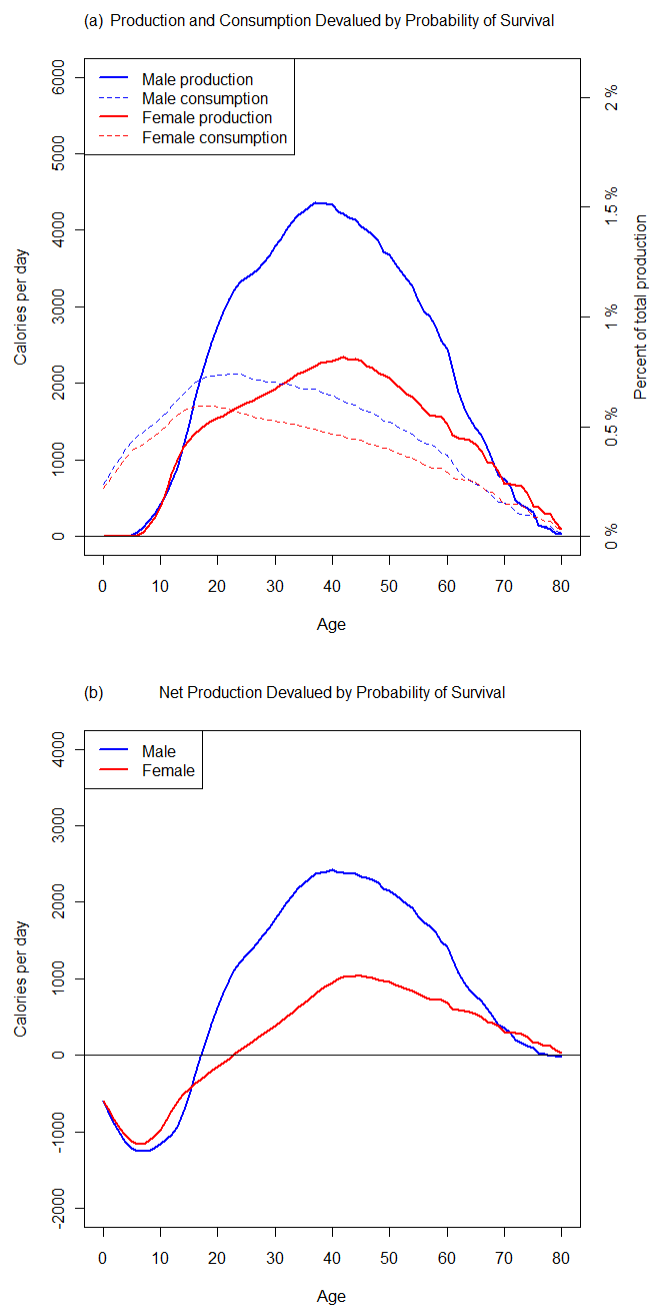


Fig. 3.8. Tsimane' daily production and consumption rates devalued by the probability of surviving to each age. Panel (a) shows expected gross production and consumption, while (b) shows net expected net production. The right-hand Y-axis in panel (a) indicates the percent contribution of each sex in each year of life to total subsistence production by all age and sex classes, given the traditional population age-structure documented in Gurven, Kaplan and Zelada Supa (2007). (Loess smoothing parameter = 0.5.)

Results and discussion

Fig. 3.7 plots Tsimane' gross and net production of energy across life. As in other traditional populations—the Ache, Hiwi, Machiguenga, Piro, Maya, Hadza, and !Kung—children consume more calories than they produce for most of the first two decades of life (Hill and Hurtado 2009, Howell 2010, Kaplan 1994, Kaplan et al. 2000, Kramer 2005b, Marlowe 2010).

Among the Tsimane' maximal net deficit (~ 1500 calories day) occurs around age 8 for both sexes, after which production begin to increase at a faster rate than consumption. Mean production matches mean consumption around age 17-18 for males, and around age 22-23 for females. Net production peaks in the late 40s for men at around 4000 calories per day, and in the early 40s for women at around 2000 calories per day. Declines in production with old age are more dramatic for men, with mean net production of men crossing zero in the later 70s. Women's mean net production, on the other hand, declines more slowly, surpassing that of men in the 70s, and remaining positive into the 80s (although the sample of women 80+ is limited to four women; one of these is in net deficit, while the other three are estimated to be net producers).

Fig. 3.8 plots daily production rates devalued by the probability of survival to each age. With their relative productivity and frequency given observed age-structure of the Tsimane' population, the age-sex classes estimated to contribute the greatest number of calories to the total gross subsistence energy pool are men and women in their late 30s and early 40s. Men aged 40-49 are estimated to produce roughly 14% of the total calories produced by all age-sex categories in the subsistence system, while women aged 40-49 contribute around 8%. Although attrition culls the ranks of individuals in their 50s and 60s, men in these age classes produce roughly 11 and 5% of total subsistence calories, respectively. Women in their 50s, on the other hand, produce around 6% of total subsistence calories, while those in their 60s produce around 5%. As evident in Fig. 3.7b, individuals in these age classes are consistent net producers; Fig. 3.8 confirms that when mortality is taken into account these net contributions are not insignificant relative to those of younger, larger generations. Men and women in their

70s, on the other hand, are responsible for roughly 1 and 2% of total production, respectively. Fig. 3.7.b informs us that for men of this age this amount is, on average, just barely sufficient to cover consumption; women, on the other hand, appear to maintain positive net production in their 70s, although their total contribution to the economy is small, given their small representation in the population. It is notable that the total gross production of men and women at age 70 is roughly equal to the gross total production of boys and girls at age 15; there are, however, many more mouths aged 15 than there are 70, meaning that total net productivity of the older age class is in fact significantly greater.

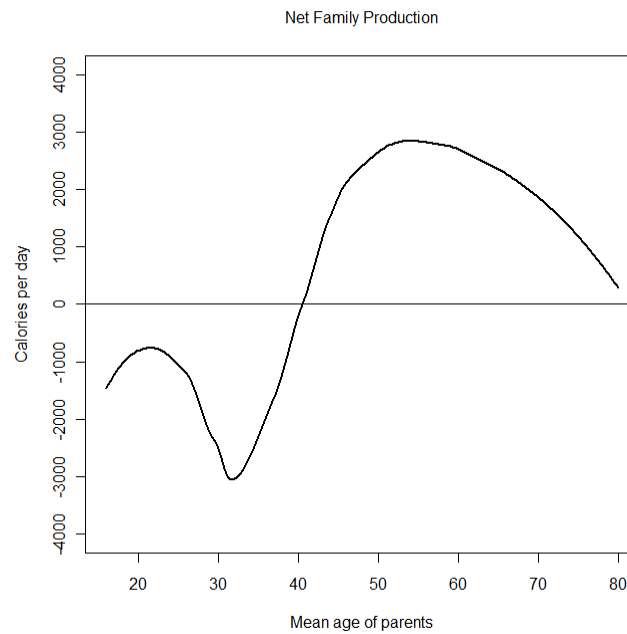


Fig. 3.9. Mean net daily subsistence production by age for Tsimane' nuclear families. (Loess smoothing parameter = 0.6.)

Fig. 3.9 plots the combined effect of the life history of net production and household demographics for the net production of families through time. The plot shows that despite the increasing productivity of young parents in their 20s and 30s, the accumulation of multiple non-productive offspring forces their mean net production below zero across this period. The mean net deficit reaches its maximum of roughly 3000 calories per day for families with parents in their early 30s. Mean net production begins to increase starting in the 30s and crosses the break-even point around age 40. The mean net surplus peaks for couples in their 50s, again at about 3000 calories per day. This surplus decreases past age 60, but is not fully exhausted in this sample until the early 80s.

IV. Conclusion

In this chapter, we have shown that increases in Tsimane' productive efficiency early in life and declines in efficiency later in life depend on the degree to which strength and skill are key determinants of productivity across different economic activities; that time allocated to production in different domains responds adaptively to variation in the costs and benefits of effort across life; and that these age patterns of efficiency and effort cause Tsimane' production rates to remain below consumption rates across the first two decades of life, and to peak remarkably late, in the 5th and 6th decades of life. Finally, we have examined the consequences of these age-patterns of production for the net productivity of Tsimane' families, showing that the high dependency but low productivity of young families result in net caloric deficits, while the low dependency but high productivity of older families yield net caloric surpluses. These results support the core hypothesis developed in chapter 1, that nature of production in traditional human subsistence economies yields large asymmetries in production and consumption across life that necessitate extensive caloric subsidization within and across nuclear families. We examine the specific patterning of these subsidies with respect to age, sex, and kinship explicitly in chapter 5 of this dissertation.

CHAPTER 4. EFFECTS OF DEPENDENT KIN ON TSIMANE' PRODUCTIVITY

I. Introduction

Energetic production rates depend on both the efficiency of productive labor as well as the level of effort dedicated to labor. While optimal productive effort levels are hypothesized to vary with the energetic need of one's immediate family (Chayanov 1966, Kramer and Lee 2002, Marlowe 2003, Turke 1988), it is unclear the extent to which the overall age-pattern of productivity is determined by variation in this need across life. With the aim of addressing this question, in this chapter we evaluate the impact of the need of close kin—siblings, children, and grandchildren—on the productive effort of Tsimane' producers across the lifespan. We do so by estimating the relationship between the presence of kin of different types and age categories on two individual-level economic variables in each domain of production: hours allocated per day to production, and total production of calories per day. As in chapter 3, our analyses focus on the three central domains of Tsimane' subsistence production: hunting, fishing, and horticulture.

Theory

The introductory chapter outlined a simple model for understanding the relationship between age-specific efficiency (i.e. return rates), costs of effort, kin need, and optimal effort levels across different activities (Chapter 1, section III). This model posits that individuals face a choice of how much effort to allocate to producing resources by each of the possible means of production. Since production effort entails costs to the producer—time, energy, risk of injury or death, and lost opportunities to pursue other fitness-enhancing activities (e.g. direct child care or mating effort)—effort levels should be optimized to balance these costs against the fitness benefits of the resources produced. Specifically, at the optimum, the marginal productivity of effort (i.e.

efficiency, return rate) multiplied by the marginal inclusive fitness benefits of the resources produced should equal the marginal cost of effort to produce them.

Within this framework (with some exceptions addressed below) producers who are surrounded by more close kin in need of resources face higher marginal fitness gains to producing and transferring resources to these kin. Thus, as reproductive-age individuals reproduce and gain more dependent offspring, they should be motivated to expend higher levels of effort to provision those offspring. Similarly, the effort of minors and grandparents should increase with the presence of more siblings and grandchildren in need, as long as their effort is sufficiently productive and not prohibitively costly.

Optimal effort levels in each activity should also be sensitive to variation in the efficiency and costs of effort in that particular activity. When the productivity of effort is higher, or the costs lower, producers will optimally expend more effort and produce more resources at the optimum. Conversely, if efficiency declines, or costs increase, optimal effort levels should drop. Because at the producer's optimum, the marginal cost of effort should equal the marginal productivity of effort multiplied by the marginal benefit of the resources, these three factors *interact* to determine optimal effort levels. That is, when a producer is more efficient (or faces lower costs) per unit of effort, an increase in dependent need (i.e. an increase in the marginal benefit of calories) should have a larger positive effect on optimal effort than when a producer is relatively less efficient (or faces higher costs).

When multiple productive activities are considered, differential efficiency and costs of effort across activities should impact the specific domain of production in which kin need registers its effects on producers. The effect of greater kin need on a hunting specialist, for example, should be manifest in hunting effort, while its effect on a horticultural specialist should be manifest in horticultural labor. The fact that lipids, proteins, and carbohydrates are complementary, rather than perfectly substitutable, elements of diet, furthermore means that optimal effort allocation across different activities should balance fulfilling the need for each of these calorie types (Hill 1988).

The presence of relatives should not always have positive effects on individuals' productive effort. If a relative is capable of producing sufficient resources for herself as well as other members of the focal individual's kin network, for example, her effect on the focal individual would be negative. That is, by alleviating the need of the focal individual's close kin, the marginal benefit of the focal individual's resource production is reduced, which decreases optimal effort levels. Even if the relative is not fully calorically self-sufficient, she can have negative effects on the focal producer's effort in particular domains of production, where her labor can substitute for that of the focal producer's, freeing up the focal producer to pursue other fitness-enhancing activities (Bock 2002b, Gurven and Kaplan 2006). In the case of mothers, young offspring require not only calories, but also direct care. The vital importance of this direct care means that the caloric need of a new infant (which would otherwise motivate greater productive effort) is likely to be accompanied by a more-than-counterbalancing increase in the opportunity costs of productive effort for mothers, leading to decreased production effort with the presence of infants and small children (Hurtado et al. 1985, Meehan 2009).

Predictions

We have seen in chapter 3 that minors of both sexes are able to achieve relatively high efficiency in both fishing and horticultural labor (at least as indexed by harvest rates) early in life. These observations suggest that household need would most likely register its effects for minors in fishing and horticulture, as the pursuit of these tasks are likely to be the most efficient means of subsistence production to contribute to the household economy.

We have also seen that men in mid-adulthood (from the later 20s through the 40s) are specialists in hunting - achieving not only the highest rates, but also expending the lion's share of effort. The decline in hunting return rates in older adulthood also indicated that hunting is strongly dependent on physical condition. These facts of high returns rates from hunting in middle adulthood, low return rates in older adulthood,

and (likely) increasing costs of hunting effort in older adulthood, lead to the prediction that dependent effects will be manifest in hunting for men in middle adulthood more than men later in life. The efficiency of old men in fishing and horticulture, on the other hand, does not show the same decline as in hunting, presumably because these production activities are less physically demanding than hunting. We may thus expect that effects of dependents on older men, if they exist, would be more likely to manifest themselves in fishing and horticultural effort than in hunting effort.

We are informed from studies in other traditional small-scale societies that human mothers experience a trade-off between direct care of young infants and children and (at least some forms of) productive work effort, and consistently favor the former at the expense of the latter (Hames 1991, Hurtado et al. 1985, Hurtado et al. 1992, Ivey 2000, Marlowe 2003, Meehan 2009). By examining whether there are negative relationships between the presence of young children and women's productivity, the current analysis serves as a test of this trade-off across the central productive activities of Tsimane' caloric economy. Post-reproductive women, on the other hand—released from the obligation of gestation and lactation—may be in a position to increase effort in a number of areas. Because, like older men, older women maintain relatively high efficiency in and time allocation to fishing and horticulture, that positive effects of offspring and grandoffspring need would most likely manifest themselves in these domains of the economy.

Because young children produce little, and are thus maximally in need, their effects on producers' effort are expected to be consistently positive (except for their hypothesized negative effect on mothers). Whether older siblings, children, and grandchildren have positive or negative effects, on the other hand, can give insight into their contributions to the household economy, or lack thereof.

II. Methods

The analyses in this chapter employ the same Tsimane' production dataset described and put to use in chapters 2 and 3. To estimate the effect of kin presence on the production of males and females across life, linear regression models were run predicting production hours spent and calories produced in each economic domain, utilizing the number of co-resident kin of different age classes and producer age as predictors. For each daily production variable—hunting hours, hunting calories, fishing hours, fishing calories, field hours, non-rice field calories, and rice calories—models were run to estimate the effect of siblings on dependent children, the effect of dependent children on adults, and the effect of grandchildren on older adults. These models were estimated separately for producers of each sex using the linear regression function (*lm*) in R version 2.12.

The sample of dependent children for the sibling-effect models was defined as all unmarried individuals under age 20 without children of their own who were co-resident with their parents or guardians. Sibling counts were composed of the number of ego's biological siblings within the family under 20, divided into two age categories: 0-12 and 13-19. To test for effects of siblings that vary by the life-stage of the producer, models were run including interactions between sibling counts and producer age category (0-12 or 13-19). Simpler models were also run in which the two sibling age categories were combined into a single variable, and with no interactions between sibling counts and producer age category. From these model permutations, the reported final model was selected on the basis of parsimony and goodness-of-fit as indicated by the Akaike information criterion (AIC; lower AIC values indicate better goodness-of-fit; Akaike 1974).

As the earliest age of first reproduction in this sample is 13 in both sexes, the sample of individuals for the child-effect models included all individuals from age 13 up. Dependent child counts were composed of the number of ego's unmarried, childless biological offspring under age 20 still living within the nuclear family. In order to

evaluate the specific effect of nursing-age children, for women offspring were divided into three age categories: 0-2, 3-12 and 13-19; for men they were divided into two categories: 0-12 and 13-19. To evaluate the effect of producer life-stage, models were run including interactions between dependent child counts and producer age category (under 50, over 50). Simplified models collapsing the offspring and producer age categories were also considered. Final models were again selected on the basis of parsimony and goodness-of-fit.

Relationships between number of grandchildren and older adults' productivity were also estimated utilizing the sample of adults age 40 and older. Grandchild counts represented the number of ego's biological grandoffspring under age 20 living within the community, divided into two age categories (0-12 and 13-19). To capture differences in production in early versus later grandparenthood, models were run including interactions between grandchild counts and producer age category (40-60, over 60). Final models were selected from among these and collapsed versions of these models according to their parsimony and goodness-of-fit.

For each model, linear, quadratic, or cubic age terms were included as predictors as appropriate to capture independent changes in productivity across producer age ranges. (The only model which utilized a cubic age term was that predicting fishing hours of males aged 13+, due to the pronounced peak in fishing hours during the teens.) To control for geographic variation in productivity, fixed effects of community membership were also included as predictors; the intercept estimates reported below reflect the intercept values for a baseline community, Tributary, which shows intermediate values across most of the economic variables. For models of daily field hours and rice production, the fraction of rice sold by the producer's family was included as an additional predictor. The sample sizes for these two variables are smaller than for other production variables, as data on rice production and sales were only available for a subset (80%) of families in the full sample.

Results from the best kin-effect model for each production variable for each sex in each stage of life (childhood, parenthood, and grandparenthood) are reported in

Tables 4.1 through 4.42 below. For comparison, these results are presented alongside estimates from 'age-only' models that only include terms for age and community (and, for field hours and rice calories, fraction of rice sold). The structure of these models, while good for being able to target age-specific effects, renders them vulnerable to problems of multicollinearity. The correlation between the number of dependent children aged 0-12 and the number aged 13-19 across the full sample, for example, is 0.55. While such multicollinearity is not expected to compromise overall model fit, it can sometimes distort parameter estimates and p-values in ways that make interpretation difficult (Gujarati 2002). In order to overcome this weakness, where the best-fit kin models included more than one kin term, separate models including each kin term in isolation (with controls for age, community, etc.) were also estimated; for comparison with the results from the full models, these 'isolated' parameter estimates and p-values are also reported in the tables below.

Finally, in order to evaluate the cumulative impact of dependent kin on the age-schedule of Tsimane' production, the final estimates these regressions were utilized to hypothetically 'remove' the effects of kin from observed work hours and caloric productivity. The results from the models predicting hours in production were used to adjust hours, while the results from the models predicting calories produced were used to adjust calories produced in each domain of production. Only the results from the kin effect models that yielded better fits (lower AIC values) than the 'age-only' models were considered. For each individual, for each production variable, for each kin model, the individual's number of kin in each relevant category (e.g. dependent siblings within the family aged 0-12, grandchildren 0-19, etc.) were multiplied by the relevant parameter estimate(s) to calculate the estimated effect of those kin on the individual's work hours or caloric output. These estimated effects were then subtracted from the individual's time allocation or caloric production to yield the adjusted values, which simulate the hypothetical effects of setting all individuals' kin counts (siblings, children, and grandchildren) to zero across life. Loess curves were fit to the observed and adjusted daily hours and production for each sex, as plotted in Figs. 1 and 2.

Sibling effect models for boys' hunting**Table 4.1. Regression models predicting dependent boys' hunting hours per day**

| Predictor | Age-only model | | | Best-fit sibling model | | |
|----------------|----------------|--------|------|------------------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | -0.0373110 | <0.001 | *** | -0.382189 | <0.001 | *** |
| Age | 0.035899 | <0.001 | *** | 0.035871 | <0.001 | *** |
| Sibs 0-19 | - | - | - | 0.001922 | 0.79 | ns |
| R ² | 0.4066 | | | 0.4067 | | |
| AIC | 102.4652 | | | 104.3920 | | |

N = 262 dependent males 6-19; models include fixed effects of community membership.

Table 4.2. Regression models predicting dependent boys' hunting calories per day

| Predictor | Age-only model | | | Best-fit sibling model | | |
|----------------|----------------|--------|------|------------------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | -177.607 | 0.001 | ** | -193.295 | 0.002 | ** |
| Age | 16.000 | <0.001 | *** | 15.952 | <0.001 | *** |
| Sibs 0-19 | - | - | - | 3.322 | 0.56 | ns |
| R ² | 0.1851 | | | 0.1863 | | |
| AIC | 3348.238 | | | 3349.873 | | |

N = 262 dependent males 6-19; models include fixed effects of community membership.

Child effect models for mens' hunting**Table 4.3. Regression models predicting men's hunting hours per day**

| Predictor | Age-only model | | | Child model | | |
|------------------|----------------|--------|------|-------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | -1.2317245 | <0.001 | *** | -0.7880887 | <0.001 | *** |
| Age | 0.0904280 | <0.001 | *** | 0.0552365 | <0.001 | *** |
| Age ² | -0.0010073 | <0.001 | *** | -0.0006124 | <0.001 | *** |
| Children 0-19 | - | - | - | 0.0753743 | <0.001 | *** |
| R ² | 0.4628 | | | 0.4889 | | |
| AIC | 698.6250 | | | 683.2978 | | |

N = 347 males ≥13; models include fixed effects of community membership.

Table 4.4. Regression models predicting men's hunting calories per day

| Predictor | Age-only model | | | Child model | | | Isolated estimates† | | |
|------------------------|----------------|--------|------|-------------|--------|------|---------------------|--------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -2831.2218 | <0.001 | *** | -1541.0443 | 0.006 | ** | - | - | - |
| Age | 182.9847 | <0.001 | *** | 75.9895 | 0.028 | * | - | - | - |
| Age ² | -2.0858 | <0.001 | *** | -0.08166 | 0.045 | * | - | - | - |
| Children 0-12 when <50 | - | - | - | 323.1854 | <0.001 | *** | 306.8106 | <0.001 | *** |
| Children 0-12 when ≥50 | - | - | - | 99.9917 | 0.54 | ns | -120.2892 | 0.46 | ns |
| Children 13-19 | - | - | - | -66.4965 | 0.64 | ns | 136.8285 | 0.34 | ns |
| R ² | 0.2928 | | | 0.3489 | | | - | | |
| AIC | 6195.87 | | | 6173.22 | | | - | | |

N = 347 males ≥13; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Grandchild effect models for older men' hunting**Table 4.5. Regression models predicting older men's hunting hours per day**

| Predictor | Age-only model | | | Grandchild model | | |
|--------------------|----------------|--------|------|------------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | 1.722177 | <0.001 | *** | 1.751379 | <0.001 | *** |
| Age | -0.025582 | 0.001 | ** | -0.026465 | 0.003 | ** |
| Grandchildren 0-19 | - | - | - | 0.003763 | 0.81 | ns |
| R ² | 0.4669 | | | 0.4673 | | |
| AIC | 257.5566 | | | 259.4870 | | |

N = 98 males ≥40; models include fixed effects of community membership.

Table 4.6. Regression models predicting older men's hunting calories per day

| Predictor | Age-only model | | | Grandchild model | | |
|--------------------|----------------|--------|------|------------------|-------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | 2959.91 | <0.001 | *** | 2896.854 | 0.002 | ** |
| Age | -48.37 | <0.001 | *** | -46.465 | 0.004 | ** |
| Grandchildren 0-19 | - | - | - | -8.125 | 0.77 | ns |
| R ² | 0.5471 | | | 0.5476 | | |
| AIC | 1728.655 | | | 1730.557 | | |

N = 98 males ≥40; models include fixed effects of community membership.

Sibling effect models for girls' hunting**Table 4.7. Regression models predicting dependent girls' hunting hours per day**

| Predictor | Age-only model | | | Sibling model | | |
|----------------|----------------|-------|------|---------------|-------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | -0.049042 | 0.083 | . | -0.0403534 | 0.21 | ns |
| Age | 0.005133 | 0.011 | * | 0.0049828 | 0.014 | * |
| Sibs 0-19 | - | - | - | -0.0015177 | 0.58 | ns |
| R ² | 0.2723 | | | 0.2735 | | |
| AIC | -355.6218 | | | -353.9445 | | |

N = 239 dependent females 6-19; models include fixed effects of community membership.

Table 4.8. Regression models predicting dependent girls' hunting calories per day

| Predictor | Age-only model | | | Sibling model | | |
|----------------|----------------|------|------|---------------|------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | -23.363 | 0.18 | ns | -13.3674 | 0.50 | ns |
| Age | 1.925 | 0.12 | ns | 1.7521 | 0.16 | ns |
| Sibs 0-19 | - | - | - | -1.7460 | 0.30 | ns |
| R ² | 0.1021 | | | 0.1073 | | |
| AIC | 2172.566 | | | 2173.424 | | |

N = 239 dependent females 6-19; models include fixed effects of community membership.

Child effect models for womens' hunting

Table 4.9. Regression models predicting women's hunting hours per day

| Predictor | Age-only model | | | Child model | | | Isolated estimates† | | |
|------------------------|----------------|------|------|-------------|-------|------|---------------------|--------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -0.02959 | 0.53 | ns | -0.03129 | 0.56 | ns | - | - | - |
| Age | 0.002984 | 0.24 | ns | 0.005204 | 0.13 | ns | - | - | - |
| Age ² | -0.00003382 | 0.28 | ns | -0.00007132 | 0.079 | . | - | - | - |
| Children 0-2 | - | - | - | -0.05253 | 0.002 | ** | -0.05693 | <0.001 | *** |
| Children 3-12 when <50 | - | - | - | -0.003274 | 0.70 | ns | -0.01418 | 0.067 | . |
| Children 3-12 when ≥50 | - | - | - | 0.03118 | 0.22 | ns | 0.04514 | 0.069 | . |
| Children 13-19 | - | - | - | 0.01020 | 0.50 | ns | 0.009151 | 0.55 | ns |
| R ² | 0.3734 | | | 0.4077 | | | - | | |
| AIC | -201.6519 | | | -210.6071 | | | - | | |

N = 301 females ≥13; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Table 4.10. Regression models predicting women's hunting calories per day

| Predictor | Age-only model | | | Child model | | | Isolated estimates† | | |
|------------------|----------------|------|------|-------------|-------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -17.848345 | 0.61 | ns | -8.95102 | 0.82 | ns | - | - | - |
| Age | 1.038436 | 0.58 | ns | 1.53096 | 0.55 | ns | - | - | - |
| Age ² | -0.009626 | 0.68 | ns | -0.02165 | 0.47 | ns | - | - | - |
| Children 0-2 | - | - | - | -38.96588 | 0.001 | ** | -35.82835 | 0.002 | ** |
| Children 3-19 | - | - | - | 4.29822 | 0.38 | ns | -0.52042 | 0.92 | ns |
| R ² | 0.3100 | | | 0.3348 | | | - | | |
| AIC | 3776.426 | | | 3769.393 | | | - | | |

N = 301 females ≥13; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Grandchild effect models for older womens' hunting

Table 4.11. Regression models predicting older women's hunting hours per day

| Predictor | Age-only model | | | Grandchild model | | | Isolated estimates† | | |
|-----------------------------|----------------|------|------|------------------|------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | 0.125901 | 0.37 | ns | 0.0143128 | 0.93 | ns | - | - | - |
| Age | -0.001912 | 0.41 | ns | -0.0002877 | 0.92 | ns | - | - | - |
| Grandchildren 0-19 when <60 | - | - | - | 0.0099869 | 0.10 | ns | 0.010509 | 0.066 | . |
| Grandchildren 0-19 when ≥60 | - | - | - | -0.0009406 | 0.80 | ns | -0.0029927 | 0.39 | ns |
| R ² | 0.5214 | | | 0.5452 | | | - | | |
| AIC | 1.227363 | | | 1.090553 | | | - | | |

N = 81 females ≥40; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Table 4.12. Regression models predicting older women's hunting calories per day

| Predictor | Age-only model | | | Grandchild model | | | Isolated estimates† | | |
|-----------------------------|----------------|------|------|------------------|-------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | 18.4742 | 0.86 | ns | -58.8978 | 0.62 | ns | - | - | - |
| Age | -0.3336 | 0.85 | ns | 0.6290 | 0.76 | ns | - | - | - |
| Grandchildren 0-19 when <60 | - | - | - | 8.5020 | 0.061 | . | 8.4406 | 0.046 | * |
| Grandchildren 0-19 when ≥60 | - | - | - | 0.1106 | 0.97 | ns | -1.6363 | 0.53 | ns |
| R ² | 0.5523 | | | 0.5779 | | | - | | |
| AIC | 1072.156 | | | 1071.392 | | | - | | |

N = 81 females ≥40; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Sibling effect models for boys' fishing**Table 4.13. Regression models predicting dependent boys' fishing hours per day**

| Predictor | Age-only model | | | Sibling model | | | Isolated estimates† | | |
|--------------------|----------------|--------|------|---------------|--------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -1.81583 | <0.001 | *** | -1.599470 | <0.001 | *** | - | - | - |
| Age | 0.36494 | <0.001 | *** | 0.330292 | <0.001 | *** | - | - | - |
| Age ² | -0.01301 | <0.001 | *** | -0.012256 | <0.001 | *** | - | - | - |
| Sibs 0-12 when <13 | - | - | - | 0.008339 | 0.63 | ns | -0.009464 | 0.56 | ns |
| Sibs 0-12 when ≥13 | - | - | - | 0.051739 | 0.002 | ** | 0.048616 | 0.001 | ** |
| Sibs 13-19 | - | - | - | -0.008799 | 0.75 | ns | 0.004774 | 0.86 | ns |
| R ² | 0.3563 | | | 0.3848 | | | - | | |
| AIC | 292.2030 | | | 287.1666 | | | - | | |

N = 262 dependent males 6-19; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Table 4.14. Regression models predicting dependent boys' fishing calories per day

| Predictor | Age-only model | | | Sibling model | | | Isolated estimates† | | |
|------------------|----------------|-------|------|---------------|-------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -438.179 | 0.002 | ** | -420.0484 | 0.003 | ** | - | - | - |
| Age | 78.062 | 0.001 | ** | 79.0266 | 0.001 | ** | - | - | - |
| Age ² | -2.414 | 0.016 | * | -2.4460 | 0.015 | * | - | - | - |
| Sibs 0-12 | - | - | - | 5.9003 | 0.38 | ns | 1.763 | 0.79 | ns |
| Sibs 13-19 | - | - | - | -30.4046 | 0.022 | * | -27.2492 | 0.033 | * |
| R ² | 0.2631 | | | 0.2799 | | | - | | |
| AIC | 3307.985 | | | 3306.332 | | | - | | |

N = 262 dependent males 6-19; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Child effect models for men's fishing**Table 4.15. Regression models predicting men's fish hours per day**

| Predictor | Age-only model | | | Child model | | |
|------------------|----------------|--------|------|-------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | 1.544 | <0.001 | *** | 1.566 | <0.001 | *** |
| Age | -0.08305 | <0.001 | *** | -0.08482 | <0.001 | *** |
| Age ² | 0.002019 | 0.002 | ** | 0.002044 | 0.002 | ** |
| Age ³ | -0.00001508 | 0.002 | ** | -0.00001514 | 0.002 | ** |
| Children 0-19 | - | - | - | 0.003146 | 0.81 | ns |
| R ² | 0.2131 | | | 0.2132 | | |
| AIC | 442.5369 | | | 444.4752 | | |

N = 347 males ≥13; models include fixed effects of community membership.

Table 4.16. Regression models predicting men's fishing calories per day

| Predictor | Age-only model | | | Child model | | |
|------------------|----------------|-------|------|-------------|-------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | 88.02863 | 0.32 | ns | 102.31091 | 0.32 | ns |
| Age | 14.75955 | 0.002 | ** | 13.62661 | 0.035 | * |
| Age ² | -0.18669 | 0.001 | ** | -0.17398 | 0.023 | * |
| Children 0-19 | - | - | - | 2.42658 | 0.80 | ns |
| R ² | 0.1369 | | | 0.1370 | | |
| AIC | 5010.364 | | | 5012.294 | | |

N = 347 males ≥13; models include fixed effects of community membership.

Grandchild effect models for older men's fishing**Table 4.17. Regression models predicting older men's fishing hours per day**

| Predictor | Age-only model | | | Grandchild model | | |
|--------------------|----------------|-------|------|------------------|-------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | 0.757920 | 0.002 | ** | 0.742281 | 0.003 | ** |
| Age | -0.004782 | 0.22 | ns | -0.004309 | 0.31 | ns |
| Grandchildren 0-19 | - | - | - | -0.002015 | 0.79 | ns |
| R ² | 0.2354 | | | 0.2361 | | |
| AIC | 119.0965 | | | 121.0145 | | |

N = 98 males ≥40; models include fixed effects of community membership.

Table 4.18. Regression models predicting older men's fishing calories per day

| Predictor | Age-only model | | | Grandchild model | | | Isolated estimates† | | |
|---------------------|----------------|--------|------|------------------|--------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | 930.746 | <0.001 | *** | 993.189 | <0.001 | *** | - | - | - |
| Age | -9.829 | 0.003 | ** | -11.818 | 0.001 | ** | - | - | - |
| Grandchildren 0-12 | - | - | - | 24.989 | 0.009 | ** | 16.736 | 0.022 | * |
| Grandchildren 13-19 | - | - | - | -52.368 | 0.17 | ns | 12.855 | 0.67 | ns |
| R ² | 0.2646 | | | 0.3239 | | | - | | |
| AIC | 1438.293 | | | 1434.055 | | | - | | |

N = 98 males ≥40; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Sibling effect models for girls' fishing**Table 4.19. Regression models predicting dependent girls' fishing hours per day**

| Predictor | Age-only model | | | Sibling model | | | Isolated estimates† | | |
|------------------|----------------|--------|------|---------------|--------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -1.057882 | <0.001 | *** | -1.142116 | <0.001 | *** | - | - | - |
| Age | 0.181425 | <0.001 | *** | 0.175428 | <0.001 | *** | - | - | - |
| Age ² | -0.005992 | 0.001 | ** | -0.005638 | 0.002 | ** | - | - | - |
| Sibs 0-12 | - | - | - | 0.022156 | 0.067 | . | 0.024825 | 0.036 | * |
| Sibs 13-19 | - | - | - | 0.021731 | 0.32 | ns | 0.030795 | 0.15 | ns |
| R ² | 0.3371 | | | 0.3564 | | | - | | |
| AIC | 132.1880 | | | 130.3675 | | | - | | |

N = 239 dependent females 6-19; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Table 4.20. Regression models predicting dependent girls' fishing calories per day

| Predictor | Age-only model | | | Sibling model | | | Isolated estimates† | | |
|------------------|----------------|-------|------|---------------|-------|------|---------------------|------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -332.2545 | 0.002 | ** | -322.1919 | 0.003 | ** | - | - | - |
| Age | 51.4796 | 0.007 | ** | 51.5001 | 0.007 | ** | - | - | - |
| Age ² | -1.5191 | 0.063 | . | -1.5226 | 0.063 | . | - | - | - |
| Sibs 0-12 | - | - | - | 2.6574 | 0.62 | ns | 0.9561 | 0.85 | ns |
| Sibs 13-19 | - | - | - | -13.8521 | 0.16 | ns | -12.7650 | 0.18 | ns |
| R ² | 0.2750 | | | 0.2832 | | | - | | |
| AIC | 2529.231 | | | 2531.011 | | | - | | |

N = 239 dependent females 6-19; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Child effect models for women's fishing

Table 4.21. Regression models predicting women's fishing hours per day

| Predictor | Age-only model | | | Child model | | | Isolated estimates† | | |
|-------------------------|----------------|--------|------|-------------|--------|------|---------------------|------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | 0.303446 | <0.001 | *** | 0.313461 | <0.001 | *** | - | - | - |
| Age | -0.003249 | 0.006 | ** | -0.003535 | 0.011 | * | - | - | - |
| Children 0-2 | - | - | - | -0.014333 | 0.66 | ns | -0.01801 | 0.52 | ns |
| Children 3-12 | - | - | - | -0.023371 | 0.13 | ns | -0.009691 | 0.42 | ns |
| Children 13-19 when <50 | - | - | - | 0.065207 | 0.037 | * | 0.035419 | 0.17 | ns |
| Children 13-19 when ≥50 | - | - | - | -0.007156 | 0.89 | ns | -0.017479 | 0.72 | ns |
| R ² | 0.2434 | | | 0.2575 | | | - | | |
| AIC | 193.1114 | | | 195.4572 | | | - | | |

N = 301 females ≥13; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Table 4.22. Regression models predicting women's fishing calories per day

| Predictor | Age-only model | | | Child model | | | Isolated estimates† | | |
|----------------|----------------|-------|------|-------------|--------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | 82.2270 | 0.001 | ** | 105.5924 | <0.001 | *** | - | - | - |
| Age | -0.8783 | 0.11 | ns | -1.3820 | 0.022 | * | - | - | - |
| Children 0-2 | - | - | - | -39.8236 | 0.006 | ** | -32.8494 | 0.011 | * |
| Children 3-19 | - | - | - | 5.2485 | 0.28 | ns | -0.07025 | 0.87 | ns |
| R ² | 0.1664 | | | 0.1880 | | | - | | |
| AIC | 3889.559 | | | 3885.640 | | | - | | |

N = 301 females ≥13; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Grandchild effect models for older women's fishing

Table 4.23. Regression models predicting older women's fishing hours per day

| Predictor | Age-only model | | | Grandchild model | | | Isolated estimates† | | |
|------------------------------|----------------|-------|------|------------------|-------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | 0.452962 | 0.016 | * | 0.402471 | 0.052 | . | - | - | - |
| Age | -0.005383 | 0.082 | . | -0.004355 | 0.24 | ns | - | - | - |
| Grandchildren 0-12 | - | - | - | -0.008541 | 0.23 | ns | -0.005909 | 0.32 | ns |
| Grandchildren 13-19 when <60 | - | - | - | 0.099735 | 0.038 | * | 0.088919 | 0.046 | * |
| Grandchildren 13-19 when ≥60 | - | - | - | 0.010078 | 0.58 | ns | -0.010456 | 0.48 | ns |
| R ² | 0.3861 | | | 0.4341 | | | - | | |
| AIC | 45.0778 | | | 44.48612 | | | - | | |

N = 81 females ≥40; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Table 4.24. Regression models predicting older women's fishing calories per day

| Predictor | Age-only model | | | Grandchild model | | | Isolated estimates† | | |
|-----------------------------|----------------|-------|------|------------------|-------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | 218.578 | 0.010 | * | 126.0752 | 0.17 | ns | - | - | - |
| Age | -2.457 | 0.078 | . | -0.9269 | 0.57 | ns | - | - | - |
| Grandchildren 0-19 when <60 | - | - | - | 6.5113 | 0.067 | . | 7.418 | 0.027 | * |
| Grandchildren 0-19 when ≥60 | - | - | - | -1.6346 | 0.44 | ns | -2.972 | 0.15 | ns |
| R ² | 0.3214 | | | 0.3744 | | | - | | |
| AIC | 1034.673 | | | 1032.080 | | | - | | |

N = 81 females ≥40; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age and community.

Sibling effect models for boys' horticulture**Table 4.25. Regression models predicting dependent boys' field hours per day**

| Predictor | Age-only model | | | Sibling model | | |
|-----------------------|----------------|--------|------|---------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | -0.485363 | <0.001 | *** | -0.42494 | <0.001 | *** |
| Age | 0.070635 | <0.001 | *** | 0.07081 | <0.001 | *** |
| Fraction of rice sold | 0.334736 | 0.018 | * | 0.31943 | 0.024 | * |
| Sibs 0-19 | - | - | - | -0.01235 | 0.25 | ns |
| R ² | 0.3687 | | | 0.3728 | | |
| AIC | 246.0243 | | | 246.5956 | | |

N = 228 dependent males 6-19; models include fixed effects of community membership.

Table 4.26. Regression models predicting dependent boys' non-rice field calories per day

| Predictor | Age-only model | | | Sibling model | | | Isolated estimates [†] | | |
|---------------------|----------------|-------|------|---------------|-------|------|---------------------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | 300.340 | 0.17 | ns | 250.943 | 0.26 | ns | - | - | - |
| Age | -71.584 | 0.061 | . | -67.963 | 0.075 | . | - | - | - |
| Age ² | 4.815 | 0.002 | ** | 5.136 | 0.001 | ** | - | - | - |
| Sibs 0-12 | - | - | - | -1.806 | 0.87 | ns | -11.208 | 0.27 | ns |
| Sibs 13-19 when <13 | - | - | - | -1.693 | 0.94 | ns | 9.960 | 0.66 | ns |
| Sibs 13-19 when ≥13 | - | - | - | -87.266 | 0.008 | ** | -88.608 | 0.004 | ** |
| R ² | 0.2674 | | | 0.2941 | | | - | | |
| AIC | 3528.713 | | | 3525.67 | | | - | | |

N = 262 dependent males 6-19; models include fixed effects of community membership.

[†] From models evaluating each kin predictor in isolation, with controls for age and community.

Table 4.27. Regression models predicting dependent boys' rice calories per day

| Predictor | Age-only model | | | Sibling model | | |
|-----------------------|----------------|--------|------|---------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | 4835.68 | 0.042 | * | 4816.29 | 0.044 | * |
| Age | -1108.77 | 0.007 | ** | -1125.59 | 0.007 | ** |
| Age ² | 62.23 | <0.001 | *** | 62.90 | <0.001 | *** |
| Fraction of rice sold | 1689.07 | 0.13 | ns | 1718.25 | 0.13 | ns |
| Sibs 0-19 | - | - | - | 22.23 | 0.80 | ns |
| R ² | 0.2799 | | | 0.2802 | | |
| AIC | 4180.247 | | | 4182.175 | | |

N = 228 dependent males 6-19; models include fixed effects of community membership.

Child effect models for men's horticulture

Table 4.28. Regression models predicting men's field hours per day

| Predictor | Age-only model | | | Child model | | | Isolated estimates† | | |
|-------------------------|----------------|--------|------|-------------|--------|------|---------------------|--------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -0.3008377 | 0.19 | ns | -0.5644966 | 0.037 | * | - | - | - |
| Age | 0.0586039 | <0.001 | *** | 0.0834943 | <0.001 | *** | - | - | - |
| Age ² | -0.0004377 | 0.005 | ** | -0.0007414 | <0.001 | *** | - | - | - |
| Fraction of rice sold | 0.6687425 | 0.006 | ** | 0.5773529 | 0.016 | * | - | - | - |
| Children 0-12 | - | - | - | -0.0125776 | 0.70 | ns | -0.0550742 | 0.075 | . |
| Children 13-19 when <50 | - | - | - | -0.2083272 | 0.006 | ** | -0.2421495 | <0.001 | *** |
| Children 13-19 when ≥50 | - | - | - | 0.1982307 | 0.12 | ns | 0.2863281 | 0.024 | * |
| R ² | 0.3172 | | | 0.3532 | | | - | | |
| AIC | 728.3364 | | | 718.3967 | | | - | | |

N = 295 males ≥13; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age, community, and fraction of rice sold.

Table 4.29. Regression models predicting men's non-rice field calories per day

| Predictor | Age-only model | | | Child model | | |
|------------------|----------------|--------|------|-------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | -601.8162 | 0.005 | ** | -657.705 | 0.010 | ** |
| Age | 68.4886 | <0.001 | *** | 72.9220 | <0.001 | *** |
| Age ² | -0.7189 | <0.001 | *** | -0.7687 | <0.001 | *** |
| Children 0-19 | - | - | - | -9.4956 | 0.68 | ns |
| R ² | 0.2206 | | | 0.2210 | | |
| AIC | 5629.103 | | | 5630.922 | | |

N = 347 males ≥13; models include fixed effects of community membership.

Table 4.30. Regression models predicting men's rice calories per day

| Predictor | Age-only model | | | Child model | | |
|-----------------------|----------------|--------|------|-------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | -2051.1541 | 0.12 | ns | -2766.833 | 0.080 | . |
| Age | 321.4057 | <0.001 | *** | 378.248 | <0.001 | *** |
| Age ² | -3.1842 | <0.001 | *** | -3.823 | 0.001 | ** |
| Fraction of rice sold | 2341.7552 | 0.091 | . | 2345.559 | 0.090 | . |
| Children 0-19 | - | - | - | -121.297 | 0.40 | ns |
| R ² | 0.2582 | | | 0.2601 | | |
| AIC | 5834.830 | | | 5836.095 | | |

N = 295 males ≥13; models include fixed effects of community membership.

Grandchild effect models for older men's horticulture**Table 4.31. Regression models predicting older men's field hours per day**

| Predictor | Age-only model | | | Grandchild model | | | Isolated estimates† | | |
|-----------------------------|----------------|-------|------|------------------|-------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | 0.51703 | 0.40 | ns | 0.80268 | 0.22 | ns | - | - | - |
| Age | 0.01766 | 0.11 | ns | 0.01220 | 0.29 | ns | - | - | - |
| Fraction of rice sold | 1.07532 | 0.051 | . | 1.05241 | 0.056 | . | - | - | - |
| Grandchildren 0-19 when <60 | - | - | - | 0.00388 | 0.89 | ns | -0.00630 | 0.82 | ns |
| Grandchildren 0-19 when ≥60 | - | - | - | 0.03459 | 0.095 | . | 0.03400 | 0.091 | . |
| R ² | 0.2778 | | | 0.2821 | | | - | | |
| AIC | 262.0027 | | | 261.4738 | | | - | | |

N = 88 males ≥40; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age, community, and fraction of rice sold.

Table 4.32. Regression models predicting older men's non-rice field calories per day

| Predictor | Age-only model | | | Grandchild model | | |
|--------------------|----------------|--------|------|------------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | 2193.614 | <0.001 | *** | 2442.726 | <0.001 | *** |
| Age | -21.187 | 0.014 | * | -28.715 | 0.002 | ** |
| Grandchildren 0-19 | - | - | - | 32.100 | 0.051 | . |
| R ² | 0.2639 | | | 0.2962 | | |
| AIC | 1627.323 | | | 1624.918 | | |

N = 98 males ≥40; models include fixed effects of community membership.

Table 4.33. Regression models predicting older men's rice calories per day

| Predictor | Age-only model | | | Grandchild model | | |
|-----------------------|----------------|-------|------|------------------|-------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | 7362.82 | 0.012 | * | 7774.49 | 0.011 | * |
| Age | -30.42 | 0.52 | ns | -41.71 | 0.43 | ns |
| Fraction of rice sold | 4515.04 | 0.090 | . | 4367.70 | 0.10 | ns |
| Grandchildren 0-19 | - | - | - | 44.96 | 0.62 | ns |
| R ² | 0.3072 | | | 0.3095 | | |
| AIC | 1756.559 | | | 1758.263 | | |

N = 88 males ≥40; models include fixed effects of community membership.

Sibling effect models for girls' horticulture**Table 4.34. Regression models predicting dependent girls' field hours per day**

| Predictor | Age-only model | | | Sibling model | | | Isolated estimates† | | |
|-----------------------|----------------|--------|------|---------------|--------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -0.527738 | <0.001 | *** | -0.35313 | 0.021 | * | - | - | - |
| Age | 0.087048 | <0.001 | *** | 0.07117 | <0.001 | *** | - | - | - |
| Fraction of rice sold | 0.209413 | 0.15 | ns | 0.20436 | 0.15 | ns | - | - | - |
| Sibs 0-19 when <13 | - | - | - | -0.01148 | 0.34 | ns | 0.192471 | 0.18 | ns |
| Sibs 0-19 when ≥13 | - | - | - | 0.02133 | 0.15 | ns | 0.025929 | 0.062 | . |
| R ² | 0.4703 | | | 0.4843 | | | - | | |
| AIC | 137.9222 | | | 137.1394 | | | - | | |

N = 202 dependent females 6-19; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age, community, and fraction of rice sold.

Table 4.35. Regression models predicting dependent girls' non-rice field calories per day

| Predictor | Age-only model | | | Sibling model | | |
|----------------|----------------|--------|------|---------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | -376.647 | <0.001 | *** | -314.993 | 0.007 | ** |
| Age | 52.450 | <0.001 | *** | 51.424 | <0.001 | *** |
| Sibs 0-19 | - | - | - | -10.770 | 0.27 | ns |
| R ² | 0.2898 | | | 0.2945 | | |
| AIC | 2865.165 | | | 2865.782 | | |

N = 239 dependent females 6-19; models include fixed effects of community membership.

Table 4.36. Regression models predicting dependent girls' rice calories per day

| Predictor | Age-only model | | | Sibling model | | | Isolated estimates† | | |
|-----------------------|----------------|--------|------|---------------|--------|------|---------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -1492.28 | 0.002 | ** | -1129.944 | 0.087 | . | - | - | - |
| Age | 221.21 | <0.001 | *** | 173.960 | <0.001 | *** | - | - | - |
| Fraction of rice sold | 171.31 | 0.78 | ns | 195.236 | 0.75 | ns | - | - | - |
| Sibs 0-19 when <13 | - | - | - | -4.980 | 0.92 | ns | -30.860 | 0.53 | ns |
| Sibs 0-19 when ≥13 | - | - | - | 97.619 | 0.13 | ns | 99.578 | 0.097 | . |
| R ² | 0.2694 | | | 0.2816 | | | - | | |
| AIC | 3116.658 | | | 3117.65 | | | - | | |

N = 202 dependent females 6-19; models include fixed effects of community membership.

† From models evaluating each kin predictor in isolation, with controls for age, community, and fraction of rice sold.

Child effect models for women's horticulture

Table 4.37. Regression models predicting women's field hours per day

| Predictor | Age-only model | | | Child model | | | Isolated estimates [†] | | |
|------------------------|----------------|--------|------|-------------|--------|------|---------------------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -0.0306268 | 0.87 | ns | 0.1874049 | 0.40 | ns | - | - | - |
| Age | 0.0631825 | <0.001 | *** | 0.0533492 | <0.001 | *** | - | - | - |
| Age ² | -0.0005719 | <0.001 | *** | -0.0005103 | 0.002 | ** | - | - | - |
| Fraction of rice sold | 0.6083539 | 0.004 | ** | 0.5125049 | 0.014 | * | - | - | - |
| Children 0-2 | - | - | - | -0.1602313 | 0.016 | * | -0.1599624 | 0.008 | ** |
| Children 3-19 when <50 | - | - | - | 0.0449053 | 0.099 | . | -0.0016365 | 0.95 | ns |
| Children 3-19 when ≥50 | - | - | - | 0.1551895 | 0.011 | * | 0.1429331 | 0.012 | * |
| R ² | 0.3385 | | | 0.3744 | | | - | | |
| AIC | 491.4763 | | | 483.6241 | | | - | | |

N = 248 females ≥13; models include fixed effects of community membership.

[†] From models evaluating each kin predictor in isolation, with controls for age, community, and fraction of rice sold.

Table 4.38. Regression models predicting women's non-rice field calories per day

| Predictor | Age-only model | | | Child model | | | Isolated estimates [†] | | |
|------------------|----------------|--------|------|-------------|--------|------|---------------------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -144.0045 | 0.42 | ns | -47.8918 | 0.82 | ns | - | - | - |
| Age | 54.2285 | <0.001 | *** | 50.3537 | <0.001 | *** | - | - | - |
| Age ² | -0.4925 | <0.001 | *** | -0.4710 | 0.002 | ** | - | - | - |
| Children 0-2 | - | - | - | -32.9549 | 0.031 | * | -111.2312 | 0.058 | . |
| Children 3-19 | - | - | - | 29.7601 | 0.24 | ns | 13.3185 | 0.58 | ns |
| R ² | 0.3297 | | | 0.3413 | | | - | | |
| AIC | 4755.584 | | | 4754.351 | | | - | | |

N = 301 females ≥13; models include fixed effects of community membership.

[†] From models evaluating each kin predictor in isolation, with controls for age and community.

Table 4.39. Regression models predicting women's rice calories per day

| Predictor | Age-only model | | | Child model | | | Isolated estimates [†] | | |
|-----------------------|----------------|--------|------|-------------|-------|------|---------------------------------|-------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | -1455.2779 | 0.13 | ns | -37.5191 | 0.97 | ns | - | - | - |
| Age | 243.1098 | <0.001 | *** | 147.3429 | 0.039 | * | - | - | - |
| Age ² | -2.3404 | <0.001 | *** | -1.3788 | 0.10 | ns | - | - | - |
| Fraction of rice sold | 2504.2832 | 0.018 | * | 2267.3677 | 0.030 | * | - | - | - |
| Children 0-2 | - | - | - | -654.2680 | 0.045 | * | -406.1721 | 0.20 | ns |
| Children 3-19 | - | - | - | 354.5647 | 0.009 | ** | 275.270 | 0.036 | * |
| R ² | 0.2882 | | | 0.3136 | | | - | | |
| AIC | 4714.888 | | | 4709.891 | | | - | | |

N = 248 females ≥13; models include fixed effects of community membership.

[†] From models evaluating each kin predictor in isolation, with controls for age, community, and fraction of rice sold.

Grandchild effect models for older women's horticulture**Table 4.40. Regression models predicting older women's field hours per day**

| Predictor | Age-only model | | | Grandchild model | | |
|-----------------------|----------------|--------|------|------------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | 2.189186 | <0.001 | *** | 2.316751 | <0.001 | *** |
| Age | -0.011596 | 0.16 | ns | -0.015455 | 0.100 | . |
| Fraction of rice sold | 1.177760 | 0.011 | * | 1.111659 | 0.018 | * |
| Grandchildren 0-19 | - | - | - | 0.010881 | 0.37 | ns |
| R ² | 0.3144 | | | 0.3238 | | |
| AIC | 177.2047 | | | 178.1937 | | |

N = 73 females ≥40; models include fixed effects of community membership.

Table 4.41. Regression models predicting older women's non-rice field calories per day

| Predictor | Age-only model | | | Grandchild model | | |
|--------------------|----------------|--------|------|------------------|--------|------|
| | B | p | sig. | B | p | sig. |
| (Intercept) | 2279.738 | <0.001 | *** | 2436.837 | <0.001 | *** |
| Age | -16.968 | 0.028 | * | -22.340 | 0.010 | * |
| Grandchildren 0-19 | - | - | - | 15.733 | 0.17 | ns |
| R ² | 0.4045 | | | 0.4207 | | |
| AIC | 1310.425 | | | 1310.198 | | |

N = 81 females ≥40; models include fixed effects of community membership.

Table 4.42. Regression models predicting older women's rice calories per day

| Predictor | Age-only model | | | Grandchild model | | | Isolated estimates [†] | | |
|-----------------------------|----------------|-------|------|------------------|-------|------|---------------------------------|------|------|
| | B | p | sig. | B | p | sig. | B | p | sig. |
| (Intercept) | 7492.49 | 0.006 | ** | 5897.60 | 0.052 | . | - | - | - |
| Age | -56.93 | 0.18 | ns | -33.67 | 0.51 | ns | - | - | - |
| Fraction of rice sold | 3491.57 | 0.13 | ns | 3503.11 | 0.14 | ns | - | - | - |
| Grandchildren 0-19 when <60 | - | - | - | 135.28 | 0.21 | ns | 142.01 | 0.16 | ns |
| Grandchildren 0-19 when ≥60 | - | - | - | -11.70 | 0.85 | ns | -39.33 | 0.51 | ns |
| R ² | 0.3072 | | | 0.3310 | | | - | | |
| AIC | 1423.302 | | | 1424.741 | | | - | | |

N = 73 females ≥40; models include fixed effects of community membership.

[†] From models evaluating each kin predictor in isolation, with controls for age, community, and fraction of rice sold.

Chapter 4

Table 4.43. Significant relationships between Tsimane' male production and the presence of siblings, children, and grandchildren across life

| Domain | Variable | Boys | Fathers | Grandfathers |
|--------------|----------------------------|---|--|--|
| Hunting | Hours spent | none | positive relationship with # of children 0-19 | none |
| | Calories produced | none | positive relationship with # of children 0-12 for men <50 | none |
| Fishing | Hours spent | positive relationship with # of young sibs for teenage boys | none | none |
| | Calories produced | negative relationship with # of teenage sibs | none | positive relationship with # of grandchildren 0-12 |
| Horticulture | Hours spent | none | negative relationship with # of teenage children for men <50 | marginal positive relationship with # of grandchildren for men ≥60 |
| | Non-rice calories produced | negative relationship with # of teenage sibs for teenage boys | none | marginal positive relationship with # of grandchildren |
| | Rice calories produced | none | none | none |

Reference guide for tables of males' model results

| Domain | Variable | Boys | Fathers | Grandfathers |
|--------------|--------------|------------|------------|--------------|
| Hunting | Hours | Table 4.1 | Table 4.3 | Table 4.5 |
| | Calories | Table 4.2 | Table 4.4 | Table 4.6 |
| Fishing | Hours | Table 4.13 | Table 4.15 | Table 4.17 |
| | Calories | Table 4.14 | Table 4.16 | Table 4.18 |
| Horticulture | Hours | Table 4.25 | Table 4.28 | Table 4.31 |
| | No-rice cals | Table 4.26 | Table 4.29 | Table 4.32 |
| | Rice cals | Table 4.27 | Table 4.30 | Table 4.33 |

Table 4.44. Significant relationships between Tsimane' female production and the presence of siblings, children, and grandchildren across life

| Domain | Variable | Girls | Mothers | Grandmothers |
|--------------|----------------------------|---|---|--|
| Hunting | Hours spent | none | negative relationship with # of children 0-2 | marginal positive relationship with # of grandchildren for women <60 |
| | Calories produced | none | negative relationship with # of children 0-2 | marginal positive relationship with # of grandchildren for women <60 |
| Fishing | Hours spent | positive relationship with # of young sibs | marginal positive relationship with # of teenage children for women <50 | positive relationship with # of teenage grandchildren for women <60 |
| | Calories produced | none | negative relationship with # of children 0-2 | positive relationship with # of grandchildren for women <60 |
| Horticulture | Hours spent | marginal positive relationship with # of sibs for teenage girls | negative relationship with # of children 0-2; positive relationship with # of children 3-19 for women ≥50 | none |
| | Non-rice calories produced | none | negative relationship with # of children 0-2 | none |
| | Rice calories produced | marginal positive relationship with # of sibs for teenage girls | negative relationship with # of children 0-2; positive relationship with # of children 3-19 | none |

Reference guide for tables of females' model results

| Domain | Variable | Girls | Mothers | Grandmothers |
|--------------|--------------|------------|------------|--------------|
| Hunting | Hours | Table 4.7 | Table 4.9 | Table 4.11 |
| | Calories | Table 4.8 | Table 4.10 | Table 4.12 |
| Fishing | Hours | Table 4.19 | Table 4.21 | Table 4.23 |
| | Calories | Table 4.20 | Table 4.22 | Table 4.24 |
| Horticulture | Hours | Table 4.34 | Table 4.37 | Table 4.40 |
| | No-rice cals | Table 4.35 | Table 4.38 | Table 4.41 |
| | Rice cals | Table 4.36 | Table 4.39 | Table 4.42 |

III. Results

Tables 4.1 through 4.42 report the regression results estimating relationships between the presence of siblings, children, and grandchildren and the production rates of males and females across the lifespan. The results for each domain of the subsistence economy are described in turn.

Hunting

No significant relationships were found between number of siblings within the family and boys' time allocation to hunting, nor boys' caloric production from hunting (Tables 4.1 and 4.2). For adult men, however, number of dependent children within the family is significantly predictive of time spent hunting per day (Table 4.3). The best-fit model suggests that this effect—an additional 5 minutes of hunting per day for each additional child—is general to all children under 20, and is stable across men's ages. As men in middle adulthood spend roughly 70 minutes hunting per day (see Fig. 3.1b), this represents a 7% increase in hunting time for each additional dependent child. Analysis of men's daily caloric production from hunting also shows a significant effect of children, which is concentrated for children age 0-12, for fathers under 50; the models in Table 4.4 estimate that men under 50 produce roughly 300 additional calories per day for each additional child under 13. No significant relationships were found between number of grandchildren and older men's time allocation to or production from hunting (Table 4.5 and 4.5).

No relationships were detected between number of siblings within the family and girls' time allocation to or production from hunting (Tables 4.7 and 4.8). For women, a significant negative effect of having children aged 0-2 was manifest in both hunting daily hours and calories (Tables 4.9 and 4.10). There were non-significant trends ($p = X$) detected for mothers under 50 to produce fewer hunting calories with more children aged 3-12, and for mothers over 50 to produce more calories with more children aged 3-12 (Table 4.10). For grandmothers under 60, there is a slight positive relationship

between number of grandchildren and hunting, in terms of both hours and calories (Tables 4.11 and 4.12). It should be noted, however, that the age term reverses direction when grandchildren are added to the age-only model of grandmothers' hunting calories (see Table 4.12), indicating some instability in the relationships, which is understandable given the relative paucity of women with non-zero production from hunting (14.8% of women aged 40+).

Fishing

The fishing hours of males aged 13-19 were positively predicted by the total number of siblings in the family aged 0-12 (Table 4.13). In the best-fit model for boys' production from fishing in terms of calories, in contrast, production is negatively related to the number siblings aged 13-19 (Table 4.14). The output of a model that breaks up the effect of siblings 13-19 by the producer's age category (not shown) suggests that this effect is manifest for both boys under and over 13, but is greater for boys over 13 (-18 cal/day/sib for boys ≤ 12 versus -31 cal/day/sib for teenage boys). There were no significant relationships detected between number of dependent children and men's time allocation or production in fishing (Tables 4.15 and 4.16). While grandfathers' daily fishing hours are statistically unrelated to number of grandchildren (Table 4.17), their daily caloric production from fishing is positively predicted by the number of grandchildren aged 0-12 (Table 4.18). The size of this effect in the grandchild model (25 calories per day per grandchild ≤ 12) appears to be somewhat exaggerated due to co-linearity between the grandchild variables, and is more modest when evaluated in a reduced model (17 calories per day per grandchild ≤ 12).

Girls' time allocated to fishing is significantly positively related to the number of siblings age 0-12 in the family (Table 4.19). The best-fit model for girls' fishing calories, however, does not show significant relationships between production from fishing with sibling counts (Table 4.20); it may in fact show a slight negative relationship with number of teenage sibs, as was the case for boys (refer back to Table 4.14). Mothers' time allocation to fishing positively related to overall number of children under age 20 in

the full kin model, but the parameter estimate is not significant when considered in a model isolating the effect (Table 4.21). The negative effect of children age 0-2 is again apparent in the best-fit model for women's caloric production from fishing (4.22). Grandmothers under age 60 appear to show higher time allocation to fishing with more teenage grandchildren (4.23) and greater daily production from fishing with more total grandchildren (Table 4.24).

Horticulture

Boys' time allocation to horticultural labor shows no significant relationship with the number of siblings in the household (Table 4.25). The best-fit model for boys' production of non-rice field calories (i.e. manioc, plantains, corn, etc.) estimates a significant negative relationship between teenage boys' number of siblings aged 13-19 and production of non-rice field calories (Table 4.26). Boys' rice production shows no significant relationships with number of siblings (Table 4.27). For fathers under age 50, there is a significant negative relationship between number of teenage children and daily time allocation to horticultural labor (Table 4.28). A model disaggregating these children by sex shows that this relationship is stronger for number of male teenagers ($B = -0.285$ hours/day/son; $p < 0.001$) than for number of female teenagers ($B = -0.154$ hours/day/daughter; $p = 0.20$). Men's achieved production of non-rice and rice field calories, however, appears to be unrelated to number of dependent children (Tables 4.29 and 4.30). For grandfathers over age 60 there is a slight relationship approaching significance ($p = X$) between number of grandchildren under age 20 and time allocation to field labor (Table 4.31). Grandfathers' production of non-rice field calories is also marginally positively related to number of grandchildren under age 20 (Table 4.32); the results of a different model specification with inferior goodness-of-fit (not shown) suggests that this effect is stronger for grandfathers over 60, consistent with the result for field hours. There is, however, no significant relationship between grandchildren and grandfathers' rice production (Table 4.33).

For dependent teenage girls aged 13-20, there is a slight positive relationship between number of siblings in the family and hours worked in horticultural labor that approaches significance (Table 4.34). There are significant relationships between number of sibs and girls' non-rice field production (Table 4.35). For girls aged 13-20, there is again a slight positive relationship between number of siblings and rice calorie production that approaches significance (Table 4.36). The negative effect of children aged 0-2 on mothers' horticultural production is manifest in women's horticultural time allocation, non-rice field production, and rice production (Table 4.37-4.29). Mothers also show higher time allocation to horticulture with more dependent children aged 3 and up, particularly after age 50 (Table 4.37). While women's non-rice field production is negatively related to the number of children 0-2, there is no significant relationship with the number of children aged 3-19 (Table 4.38). Women's rice production is negatively related to children aged 0-2, but positively related to the number of children 3-19 (Table 4.39). Although there are slight positive trends between number of grandchildren and grandmothers' horticultural variables, none are statistically significant (Tables 4.40, 4.41, and 4.42).

Sum of kin effects on the life history of production.

To give a sense of the cumulative impact of the effects estimated in Tables 4.1 through 4.42 on mean time allocation and production rates across life, the age-schedules of time allocation and production were recalculated hypothetically 'removing' the estimated effects of dependent kin (as described in methods). Figs. 4.1 and 4.2 compare the results of this exercise against the observed life history of productive effort and output. For males, the estimated cumulative effect of dependents on total daily work hours is modest, but consistently positive across life (Fig 4.1). These effects become apparent starting in the teens, and are at their highest toward the tail end of life (from the 50s onward). The estimated effect of dependent kin on total male productive output is also consistently positive, but is relatively larger and concentrated in middle adulthood (Fig. 4.2). The divergence between the observed curve (with

dependent effects) and the adjusted curve (with dependent effects removed) begins in the late teens, is greatest in the 30s and 40s, and declines into old age.

The effect of removing the estimated effect of dependents from time allocated to production is qualitatively different for females than males (Fig. 4.1). While there is a slight positive effect of siblings on girls time allocation in the early teens, starting around age 17 the net effect of dependent kin is negative, due to the effect of nursing-age children. In hours, this depressing effect of very young children yields a net negative effect for all children through the 30s, after which the net effect of all dependents (children and, increasingly, grandchildren) becomes positive for the remainder of life. The effect of dependents on female caloric output similarly shows a net negative effect of children on production early in the reproductive period (Fig. 4.2). Although the negative effect of nursing-age children remains consistent across life, countervailing positive effects of older children means that the net effect of all children on women's caloric production goes from negative to positive rather quickly, in the mid 20s. Similar to males, the greatest positive effect of dependent children on female productivity occurs around age 40, and declines slowly into old age.

IV. Discussion and conclusion

The pattern of relationships discerned in this chapter give insight into individuals' motives for food production, and the nature of the division of labor within human families. Tables 4.43 and 4.44 summarize these relationships for male and female Tsimane' producers across three generations.

To begin with the clearest effect: Tsimane' mothers show reductions in effort across all domains of production with the presence of very young offspring (under 3 years old: essentially, the nursing period). This finding confirms the maternal commitment to nursing and direct care of very young children at the expense of productive effort for the Tsimane', as has been found among the Ache, Hiwi, Ye'kwana,

Efe, Aka, Ngandu, and Hadza (Hames 1991, Hurtado et al. 1985, Hurtado et al. 1992, Ivey 2000, Marlowe 2003, Meehan 2009).

In contrast to the negative response to very young children, mothers show greater work effort in horticultural production with more dependent children aged 3 to 19. For one measure (daily horticultural hours) this relationship was strongest for women over 50, while for another (rice production) it was more consistent across maternal ages. These findings indicate that, except when caring for nursing-age children, women who have more dependent children work significantly harder than those with fewer. This effect has also been found for the Ache and Hiwi (Hurtado et al. 1985, Hurtado et al. 1992). Tsimane' women also show marginally significant positive relationships between number of children over 3 and hours spent fishing (when under 50) and hunting (when over 50).

Men's hunting effort and returns are also strongly related to the number of children in the nuclear family, particularly younger children when men are still under 50 years old. This finding supports the hypothesis that men's hunting effort is motivated by the consumer demand of their children, which has been frequently debated (Gurven and Hill 2009, Hawkes 2004, Wood 2006). The age-specificity of this effect is also consistent with the importance of prime physical condition for hunting ability, as observed in the age-curve of hunting return rates in chapter 3.

Men under 50 appear to decrease horticultural effort with more teenage children (especially boys) in the household (Table 4.28). This could be interpreted as a simple effect of reduced need, as older children can begin shouldering some of the burden of family production. Alternatively, this may be interpreted as an effect of labor substitution within a household division of labor (Gurven and Kaplan 2006). Given that meat and horticultural carbohydrates are complements, not substitutes, the ability of older children to shoulder a heavier burden of field labor may free up fathers to devote more time to meat acquisition through hunting. It is worth noting that the outcome of the best-fit model predicting men's hunting hours, where men's hunting time is best

predicted by the total number of children 0-19, not just younger dependents, is consistent with this interpretation (see Table 4.3).

Tsimane' grandparents' production is positively related with number of grandchildren in multiple domains. The strongest domain in which this is true for both grandmothers and grandfathers is fishing. Interestingly, both the hunting effort and caloric returns of grandmothers under 60 is also predicted by number of grandchildren, although the relationships only approach significance. Grandfathers also trend toward greater horticultural effort and non-rice horticultural production with a higher number of grandchildren. These positive effects of dependency on adult work effort are broadly consistent with findings by other behavioral ecologists. Turke, for instance, found that on Ifaluk the more offspring of any age an individual had, the harder they worked both before and after age 60 (citing Turke 1985, Turke 1988).

Tsimane' girls, especially teenage girls, still living as dependents within their parents' family show positive relationships between the number of siblings in the family and work effort in fishing and horticulture; for fishing, this relationship is primarily with number of young siblings (under 13), while for horticulture it is with total number of siblings. These findings are consistent with the proposal that the economic effort of older children in human families is motivated in part to fulfill the caloric need of the household (Kramer 2005a, Kramer 2005b).

Like girls, teenage boys show greater fishing hours with more siblings under age 13. In contrast, however, they also show lower production from fishing with more teenage siblings. A similar trend appears in non-rice horticultural production: teenage boys with more teenage siblings appear to produce fewer calories of garden products per day. The fact that these negative effects register clearly for males but not for females is interesting, and may suggest greater opportunity costs of horticultural and fishing effort for males relative to females. It is plausible that male adolescents may benefit from diverting effort to hunting, as significant time investments are necessary to gain expertise, and hunting provides valuable fat and protein. The lack of sibling effects for dependent males' hunting, however, does not bolster this interpretation.

Chapter 4

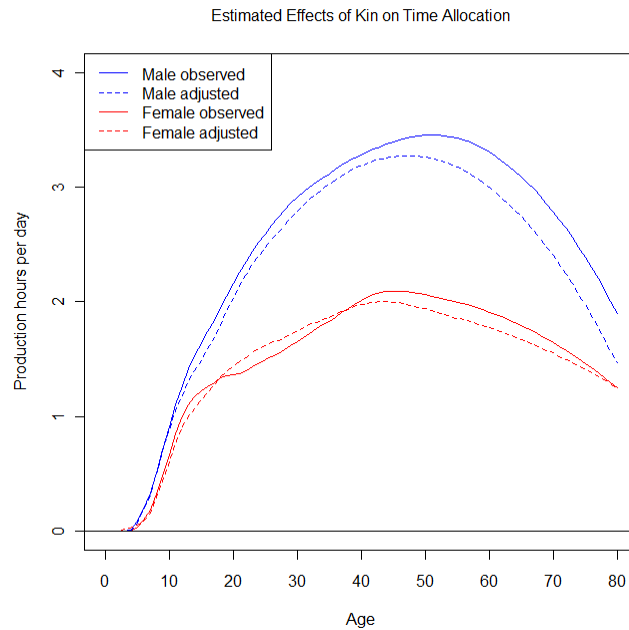


Fig. 4.1. The effect of removing the estimated effects of siblings, children, and grandchildren from the age-schedule of Tsimane' time allocation to production. The solid lines show the observed age-schedule of Tsimane' time allocation (from chapter 3); the dashed lines, on the other hand, show the adjusted age-schedule of time allocation, removing the effects of close kin estimated in the preceding models of work hours (loess smoothing parameter = 0.5).

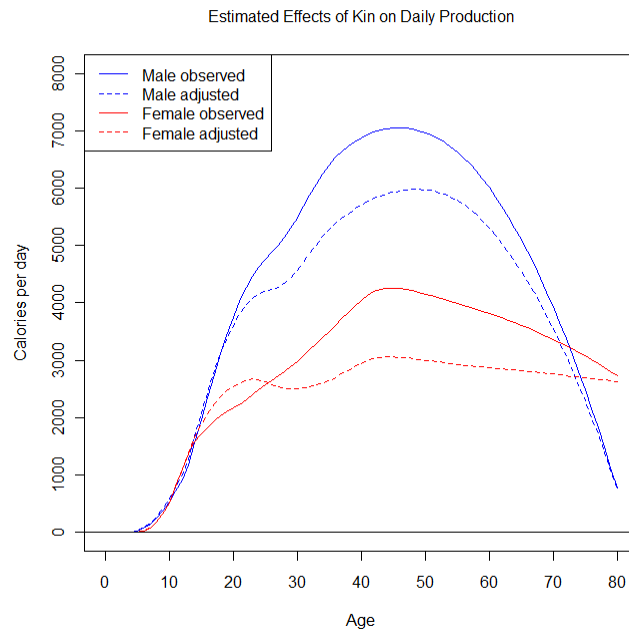


Fig. 4.2. The effect of removing the estimated effects of siblings, children, and grandchildren from the age-schedule of Tsimane' daily caloric production. The solid lines show the observed age-schedule of Tsimane' caloric production (from chapter 3); the dashed lines show the adjusted age-schedule of production, removing effects of close kin estimated in the preceding models of caloric production (loess smoothing parameter = 0.5).

These findings are generally consistent with and complement the results of Stieglitz's analysis of Tsimane' children's time allocation (Stieglitz 2009). Analyzing both sexes together, Stieglitz found that the number of younger co-resident siblings positively predicted children's field labor and family-directed work (combining field labor, sibcare, and housework); the number of older siblings, on the other hand, positively predicted children's field labor, but negatively predicted time spent hunting, fishing, and collecting fruit. The results here and in Stieglitz (2009) suggest that the intra-familial division of labor is complexly structured according to producer sex, age, and macronutrient need within the family.

Figs. 4.1 and 4.2 illustrate how the life history of Tsimane' production would be affected in a hypothetical (and counterfactual) world in which individuals had no siblings, offspring, or grandoffspring affecting their productive effort and output, given the direction and size of the effects estimated in this chapter. The effect of dependent kin on the productive effort and output of men estimated in this chapter is clear: if all men had no offspring or grandoffspring, they would work and produce less than they in fact do. In terms of time (Fig. 4.1), these effects are modest but consistent. In terms of calories (Fig. 4.2), however, the effects are greater. For women, in contrast, the net effect of dependents in the early reproductive period on productive effort is negative, due primarily to the demand of nursing-age children. In terms of time (Fig. 4.1), this net effect remains negative across the majority of the reproductive period, then crosses to become a net positive effect in the later 30s. In terms of calories (Fig. 4.2), the period in which nursing-age children make the net effect of dependents on maternal production negative is shorter, from the mid-teens to the mid-20s; after this period, although nursing-age children continue to exert a negative effect on maternal production, the positive effect of older dependent children is more than counterbalancing. Like men, from the 30s onward, women produce significantly more calories than they would if they had no dependent offspring or grandoffspring.

One should note that both of these curves include (what are presumably) substitution effects on male and female production: that is, negative effects of the

presence of sibs, children, or grandchildren on individuals' production not explained by the competing demands of direct childcare. The strongest of these is the negative relationship between teenagers (particularly male teenagers) and men's horticultural hours. Thus in the adjusted age-curves of male time allocation to production, the cumulative effect of removing children (though consistently in the negative direction of dependency effects) is not large (compare relative proximity of blue curves in Fig. 4.1 to their greater differentiation in Fig. 4.2). This occurs for the following reason: While men increase effort in some areas with any dependent offspring, they simultaneously decrease effort in other areas with more older dependent offspring, at least in terms of hours. Interestingly, while these strong negative effects do show up for men's hours, they do not show up in achieved caloric production for adults of either sex. Some relatively small negative responses to the presence of teenagers were registered for boys in caloric production; the estimated net effect of siblings on male adolescent production is essentially nil as a result (compare overlap of blue curves until age 18, Fig. 4.2).

To summarize, this chapter has evaluated the relationship between the presence of young kin and variation in productive effort among the Tsimane' across the lifespan. The results support the proposition that the productive effort of parents and grandparents of both sexes is motivated in part by the caloric need of their descendent offspring. The work effort of dependent children was also shown to respond to the need of young siblings in the household. The results also strongly support the hypothesis that reproductive age women sacrifice productivity in order to care for nursing-age children. Finally, these analyses inform us that while dependent need does have a measureable impact on the age-schedules of productivity, the general shape of this curve remains robust even if the effect of dependent need is removed. This analysis thus reaffirms the validity of the embodied capital model of human life history evolution, while adding new insight into the processes shaping the demographic structure of production in small-scale human societies.

CHAPTER 5. THE DEMOGRAPHIC STRUCTURE OF TSIMANE' ENERGY TRANSFERS

I. Introduction

To this point this dissertation has examined the demographic structure of energy production within the Tsimane' subsistence economy. By examining variation in productive ability, effort, and output due to sex, age, and kin dependency, it has addressed the questions of who is responsible for contributing what types of calories to the total subsistence energy pool, and (in part) for what reasons. This chapter now analyzes the demographic structure of the redistribution of that energy within Tsimane' communities by examining gross and net caloric flows within and between families. These energetic transfers are analyzed with respect to sex, age, kinship, dependency, and energy type (i.e. carbohydrate vs. lipids and proteins), and discussed in the context of the theory of human life history evolution laid out in the first chapter of this dissertation.

Theory and predictions

In the introductory chapter, we hypothesized that energy transfers in traditional small-scale social networks such as those of the Tsimane' can be understood on the basis of three principal theoretical rationale: (1) nepotistic provisioning; (2) sex- and age-specific specialization and exchange; and (3) inter-temporal variance reduction.

(1) Hamilton's theory of kin selection informs us that the benefits of transfers to kin are registered in the fitness function of producers by virtue of genetic relatedness (Hamilton 1964). We have seen in chapter 3 that the age pattern of production in traditional human economies generates systematic variance in the benefits and costs of energetic transfers across life. As humans remain in a stage of no or low productivity for an extended period of time relative to other primates and mammals, the benefit of subsidization by individuals in later, more productive phases of life remains high across childhood and adolescence. As demonstrated in chapter 4, Tsimane' parents respond to

this benefit of energetic investment by producing for and provisioning their offspring. We have also seen that grandparents are motivated to help underwrite the growth of their grandoffspring, while older children in families are motivated to provision their younger siblings. This principal of provisioning kin in need should generalize beyond children, grandchildren, and siblings as well: when families sustain periods of particularly low productivity or high consumer need, close kin with relatively more to spare should similarly be motivated to help make energetic ends meet on the basis of inclusive fitness benefits.

(2) Additional energetic flows arise as a component of the system of sex- and age-specific division of labor. This division of labor takes advantage of gains to specialization due to differential efficiency in and costs of production across different economic activities (Gurven and Kaplan 2006; chapter 3). We have seen that Tsimane' men in middle adulthood produce the bulk of protein and fat in the economy through hunting, but that return rates and time allocation decline with physiological aging in older adulthood. This old-age decline in hunting is accompanied by simultaneous increases in effort in horticultural production—which depends less stringently on prime physical condition—resulting in very high output of carbohydrates by men in their 50s, 60s, and 70s. Women—particularly when released from the demand of young infants—and older children are also in a position to contribute carbohydrates through horticulture. As we have also seen, both sexes are capable of producing lipid and protein resources through fishing from adolescence onward, though at lower return rates than middle-aged men achieve through hunting. Within residential clusters, individuals thus differentially contribute fat and protein (from meat) or carbohydrates (from horticulture) depending on their differential efficiency/costs of effort. Between producers, this is expected to result in patterns of bidirectional exchange of the two complementary energetic resources. The domain of economic specialization should likewise determine the primary currency by which producers subsidize the energy budgets of less productive kin. As reproductive-age women specialize in enhancing household fitness through activities outside of primary energy production—i.e.

gestation, lactation, direct childcare, food preparation, etc.—they may appear as net receivers in the currency of calories alone; the same logic applies to any individuals that provide differentially greater inputs to household well-being outside primary production (Kramer and Lee 2002).

(3) Variance in returns to productive effort across time also generates gains to reciprocal food sharing between both kin and non-kin. These gains are expected to be the greatest for foods characterized by large package sizes and high variance in return rates, particularly hunted game (Kaplan and Hill 1985, Winterhalder 1986). Such reciprocal sharing for consumption-smoothing is expected to generate fairly balanced bidirectional caloric flows between individuals. Because cooperative risk-reduction is hypothesized to be most stable within the context of enduring relationships with specific trusted individuals, our analysis is also expected to show evidence of contingency: that is, how much individual A gives to individual B depends positively on the amount that B gives to A (Gurven 2004, Gurven 2006).

Two additional aspects of Tsimane' socioecology are worth consideration in dissecting the structure of caloric flows documented in this chapter. The first of these is the informal pattern of bride service typical of the Tsimane' and many other small-scale egalitarian societies: in the first few years of marriage, young couples often co-reside with the wife's kin, during which period the young husband is expected to contribute food and labor to his wife's family. Human behavioral ecologists have theorized this phenomenon in terms of an informal contract negotiated between husband, wife, and kin, whereby the young husband's labor is contributed in return for access to the young woman's fertility; the magnitude and duration of these contributions presumably depends on local dynamics of the mating/marriage market (Lancaster 1981, Lancaster and Kaplan 1992).

Finally, the patterning of gross and net caloric transfers is also affected by the collective nature of Tsimane' horticultural production. The present methods of accounting for producer credit for horticultural production based on relative labor inputs (see chapter 2, section III) yield a pattern of energetic flows from each laborer to

each consumer of the fruits of that labor. As an appropriate result of this method, two individuals who contributed to and consumed equally from the family's field production, for example, will show equal bidirectional transfers of horticultural calories (with zero net transfer); if one individual contributes or consumes proportionally more than the other, this will appropriately be reflected in the magnitude of the transfers in each direction (with positive net transfer in one direction or the other).

II. Methods

This chapter employs the caloric transfer estimates calculated from the production and sharing dataset according to the procedures described in chapter 2, section III. It treats the transfer of calories from hunting and fishing (which are together termed 'meat' throughout this chapter) and from horticulture separately, and in combination.

Proportions of production received by different categories of individuals—represented in Figs. 5.1, 5.2, and 5.3—were established utilizing the category-based estimation methods described in chapter 2, section III: for producers of each sex in each decade of life, the raw total calories transferred to each recipient category (grandchildren, children within family, children outside family, etc.) from that producer category were summed, then divided by the total number of calories transferred to all recipients (both within and outside the sample) from that producer category. Fig. 5.1 represents the proportional amounts received by each recipient category in equally sized pie charts. To give a sense of the relative scale of the amounts transferred, Fig. 5.2 scales the size of each pie by the estimated daily production rates of each age-sex producer category. Finally, to give a sense of the proportional contribution of each age-sex category to the overall Tsimane' subsistence economy, Fig. 5.3 scales the size of each pie by the estimated daily production rates of each age category devalued by the probability of survival to the middle of the age category (i.e. age 5 for age category 0-10; age 15 for age category 10-20, etc.). Survivorship numbers are drawn

from the life table for the period 1950-89 (Table 5) in Gurven, Kaplan, and Zelada Supa (2007).

Representations of gross and net caloric transfers per day between individuals within the extended family—the diagrams represented in Figs. 5.4, 5.5, and 5.6—were constructed in the following way. The diagrams posit the existence of six focal individuals: a married father and mother approximately of age 30, and their respective post-reproductive parents approximately of age 60. The number and age of the focal parents' children correspond to the rounded mean values for married individuals of those aged 25-34 in this sample; Fig. 5.6 additionally shows the grandparental generation's expected number of additional children, children-in-law, and grandchildren within the community, which are representative of the rounded mean counts for married individuals aged 55-64. Reported transfers between each parent and offspring represent the category-based transfer estimates between parents in the age range 20-39 and offspring in the age ranges 8-10, 6-8, 4-6, and 2-4. Reported transfers within couples represent transfer estimates between spouses aged 20-39 for the parental generation, and 50-69 for the grandparental generation. Reported transfers between the parental and grandparental generation represent transfer estimates between fathers aged 50-69 and sons aged 20-39; between fathers-in law aged 50-69 and daughters-in-law aged 20-39; and so on. In Fig. 5.6, net transfers to the grandparents' other children, their spouses, and grandchildren were estimated by summing the mean net transfers from grandparents aged 50-69 to all children, their spouses, and grandchildren, then subtracting the total expected net flow from those grandparents to the focal father, mother, and offspring. To reduce clutter, the figures do not illustrate flows between the focal parents' family and their siblings' families, nor between offspring within the nuclear family. The numeric values in the plots indicate calories transferred per day. The widths of the directed arrows are proportional to the square root of calories transferred per day; thus, if the arrows are conceptualized as 3-dimensional cylinders, the number of calories transferred per day is linearly proportional to the cross-sectional area of the cylinder.

Finally, caloric transfers between nuclear families were analyzed in linear mixed-effect regression models utilizing the `lmer` function in R version 2.12. Pairs of families with complete production data co-residing in the same community served as the units of analysis. Separate models were run predicting gross meat calories, horticultural calories, and total subsistence calories transferred from family A to family B per day. Quantities transferred from family A to B per day were calculated by summing the amounts transferred from each member of family A to each member of family B according to the individual-dyad-level transfer estimation method described in chapter 2, section III. The mean age of the parents in each family, the mean genetic relatedness between the two families, the net production of family A, the net need of family B (calculated simply as negative net production), and the number of calories transferred from family B to family A were included as predictors in the models. For the total caloric transfer model, instrumental variables were computed to represent the expected net production/need of each family by summing the expected net production of each family member according to age and sex from the age-curves of net production derived in chapter 3 (see Fig. 3.7b). For the meat and horticultural transfer models, additional instrumental variables were computed to represent expected net production/need of each family for meat and horticultural calories separately. Meat and horticultural calories transferred from family B to family A were also treated separately in the meat and horticultural transfer models, but combined in the total transfer model. Quadratic age terms, interactions between age and relatedness, and interactions between net production/need and relatedness were included as appropriate to capture to the curvature of the relationships. The identities of each family and community were included as random effects in all three models.

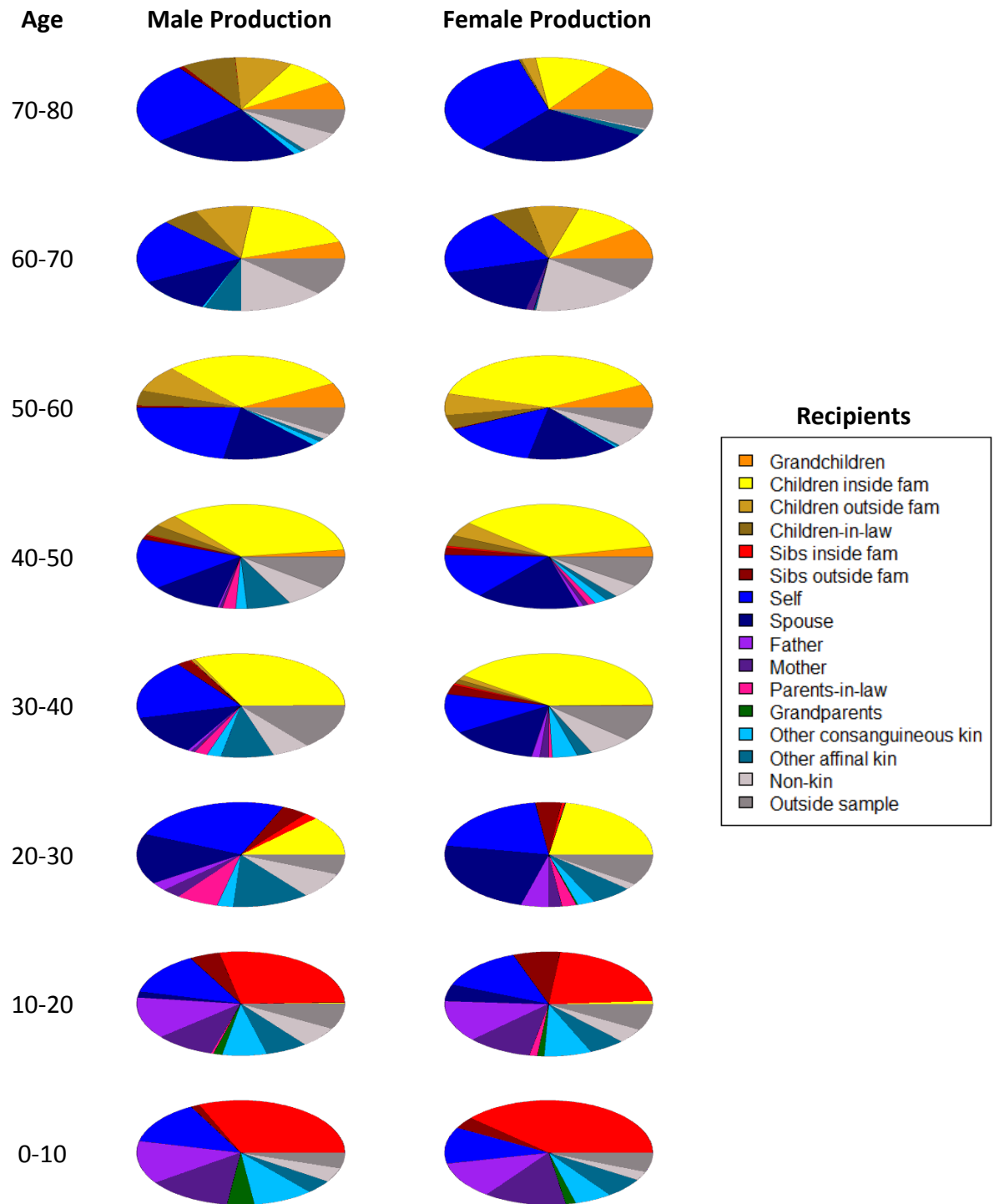


Fig. 5.1. Proportions of production received by recipient categories, by producer age and sex.

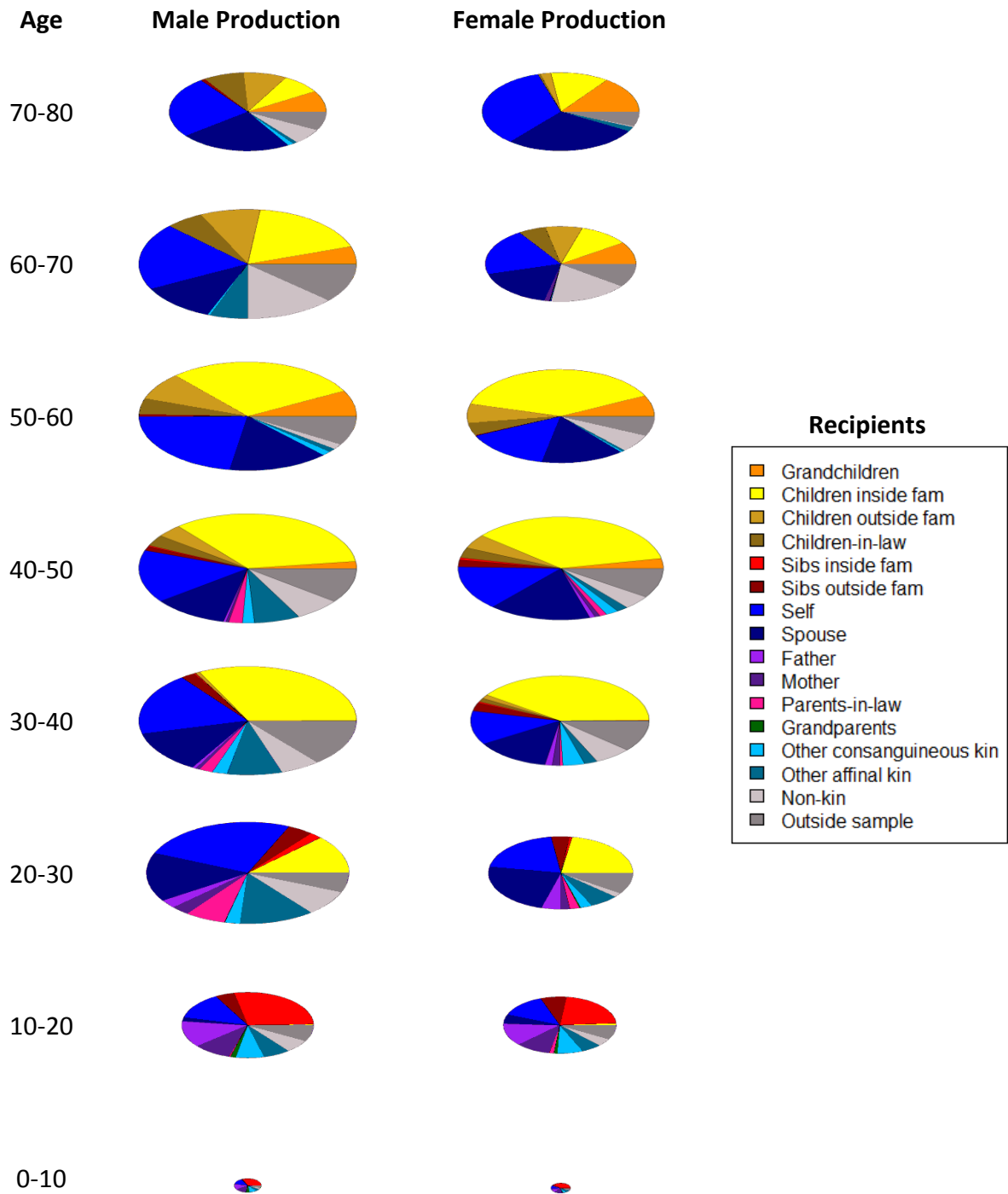


Fig. 5.2. Relative magnitude of caloric transfers to recipients, by producer sex and age. The size of pies reflect mean daily caloric production rates of males and females in each age category (see Fig. 3.7 in chapter 3).

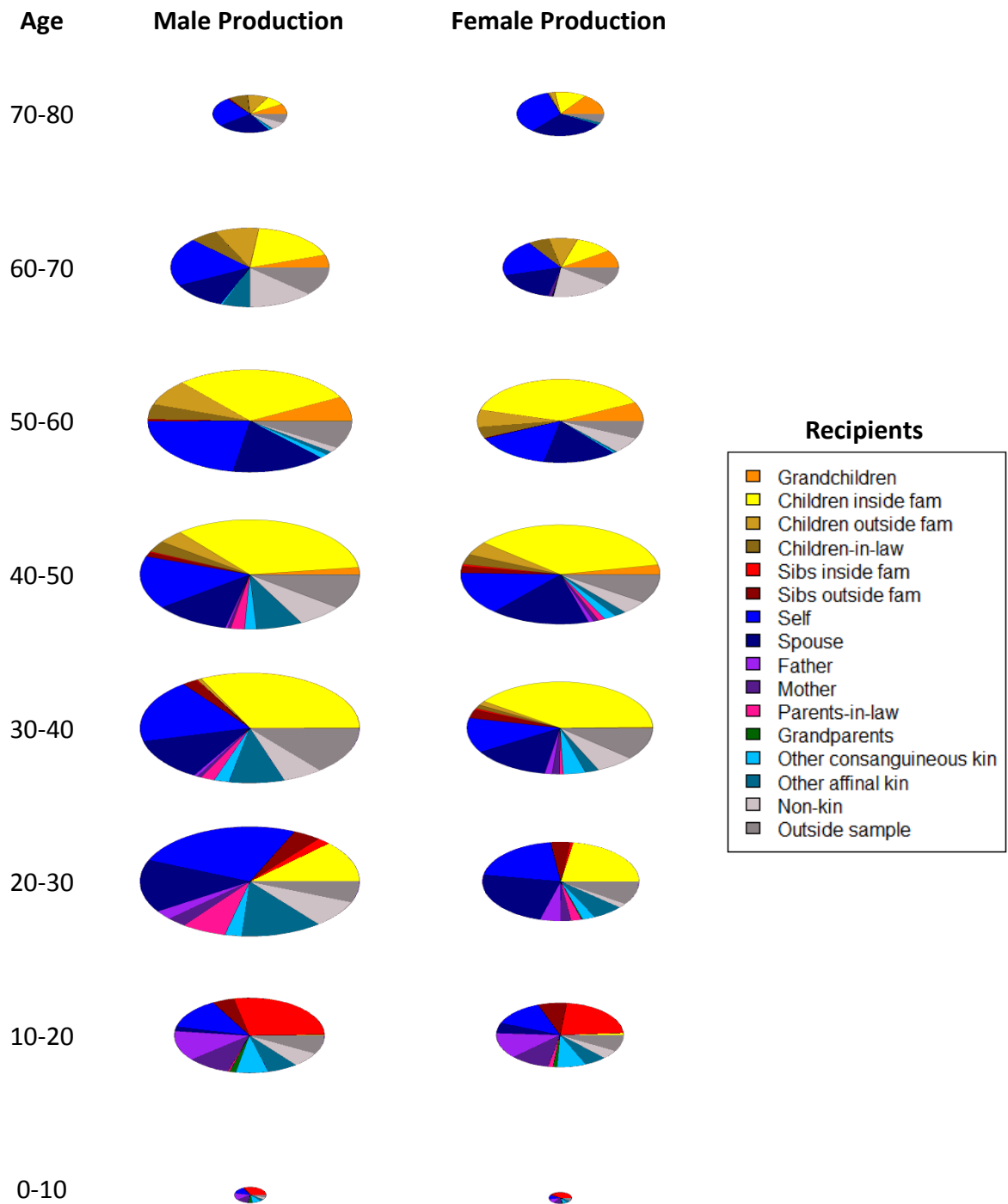


Fig. 5.3. Proportional contributions of producers toward recipient categories, by producer age and sex, based on productivity rates, redistribution profiles, and demographic age structure. The size of pies reflect mean daily caloric production rates devalued by the probability of survival to each age (from Gurven et al. 2007; see methods).

III. Results

The changing profile of recipients of Tsimane' subsistence production across life is illustrated by the pie charts in Fig. 5.1. Fig. 5.2 gives a sense of the scale of the transfers to these recipients by weighting the size of each pie by the total subsistence productivity of each sex in each decade of life. Fig. 5.3 in turn indicates the relative contribution of each sex at each age to the total Tsimane' subsistence economy by weighting the size of each pie by the productivity of each age-sex class devalued by the probability of survival to that age.

Tsimane' children and adolescents of both sexes give the majority of their production to members of their immediate nuclear family. In the first two decades of life, mothers, fathers, and the child itself each consume roughly 10-13% of the child's production, while siblings consume 30-42%. For males aged 10-19, this leads to an estimate of 250 calories produced for personal consumption per day (80 calories of meat, primarily fish, and 170 calories of horticultural goods), 215 calories for each parent, and 87 calories for each sibling. The pattern of distribution for females aged 10-19 is similar but slightly scaled down, with 190 calories (25 meat, 165 horticulture) produced for personal consumption, 160 for each parent, and 74 calories for each sibling.

The transition from adolescence to adulthood is marked by major shifts in patterns of caloric redistribution in both sexes, with declines in shares to parents and siblings, and increases in shares to spouses and children. In the 20s and 30s men are estimated to produce roughly 1200 calories for personal consumption, 800 calories for their wife's consumption, and 400 calories for the consumption of each child in the family per day. Women during this period are estimated to produce approximately 500-some calories each for their own consumption and that of their husbands, and roughly 200 calories per day for each child. As reproduction continues and family size grows, the total volume of production channeled to children continues to increase across the 30s, 40s, and 50s for both sexes. Across this period, the fraction of calories produced by

parents that are consumed by the parents and children within the nuclear family remains fairly constant at about 2/3rds of total production. For parents in their 40s and 50s, the mean amount received by each child within the nuclear family is approximately 450 calories per day from fathers, and 400 calories per day from mothers.

By the 40s onward, a significant proportion of production begins to be channeled to adult offspring who have left the immediate nuclear family, as well as children-in-law and grandchildren. Men in their 50s and 60s are estimated to provide 25% of their production to children still within the nuclear family (~ 1300 calories), and 20% to their adult children, children-in-law, and grandchildren outside the family, roughly 1100 calories per day. Grandchildren are estimated to consume around 1/3rd of these calories, or about 325 calories per day. Women in their 50s and 60s are similarly estimated to provide 30% of their production to children within the nuclear family (~ 750 calories), and 20% of their production to their children, children-in-law, and grandchildren outside the nuclear family, around 500 calories per day. Despite declining productivity in the 70s, both sexes continue to provide a non-negligible amount of food for their descendent kin. As both sexes show nearly equal productivity at this age, both men and women in their 70s are estimated to provide roughly 300 calories per day for co-resident offspring (~ 10% of production), and 500 calories per day for children, children-in-law, and grandchildren outside the immediate household (~ 20% of production).

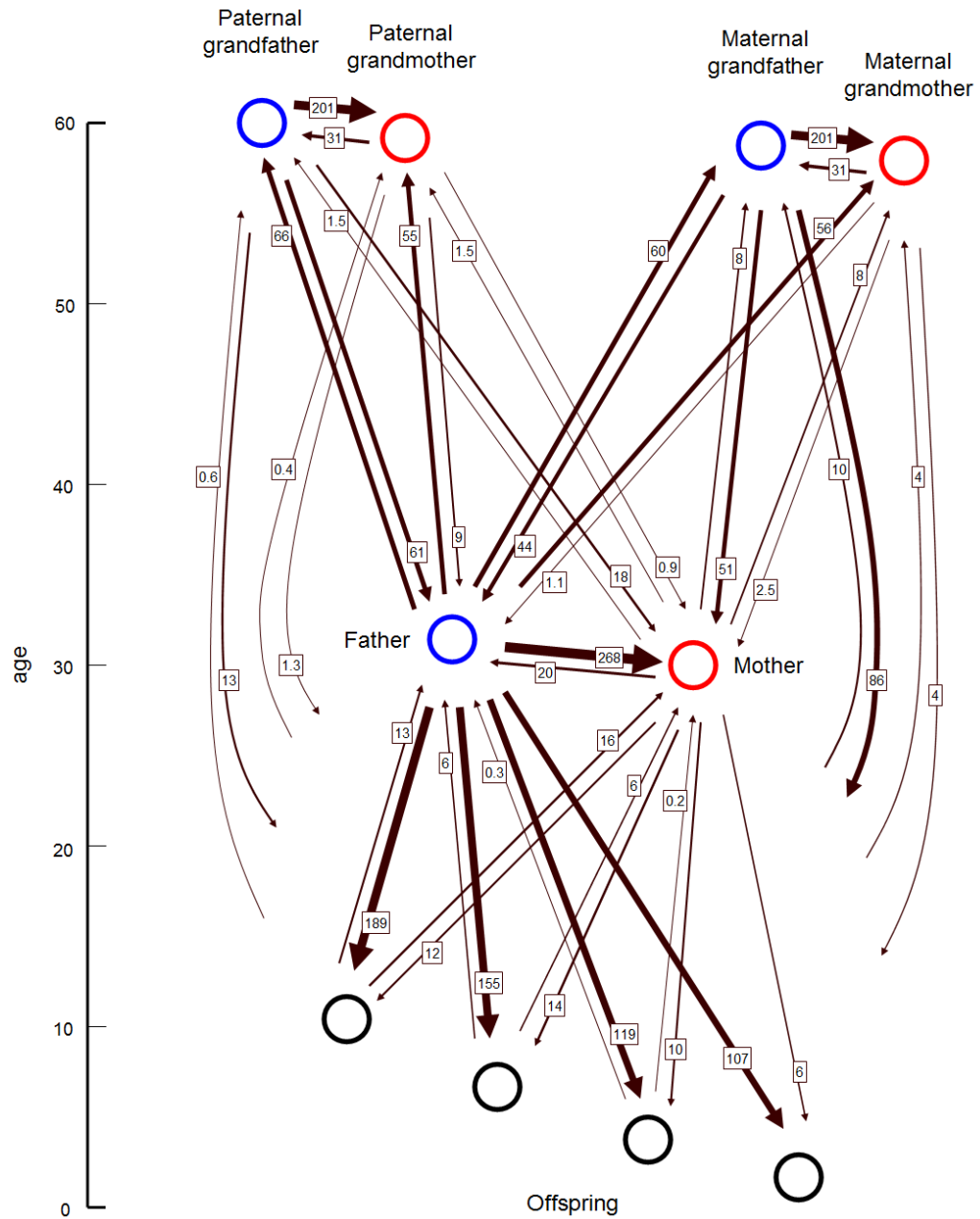


Fig. 5.4. Bidirectional transfers of calories from game and fish within the extended family. Arrow values indicate mean calories transferred per day.

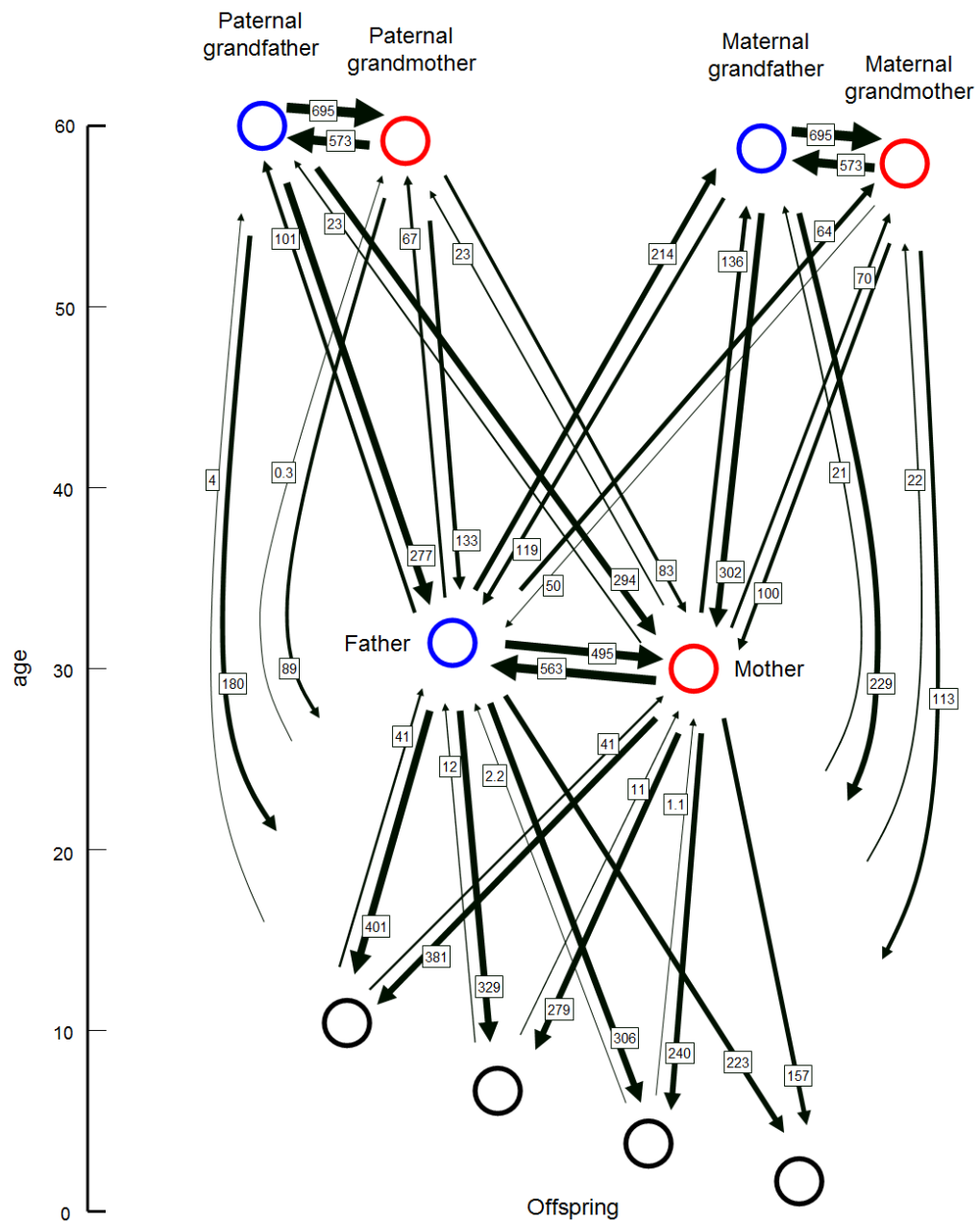


Fig. 5.5. Bidirectional transfers of horticultural calories within the extended family. Arrow values indicate mean calories transferred per day.

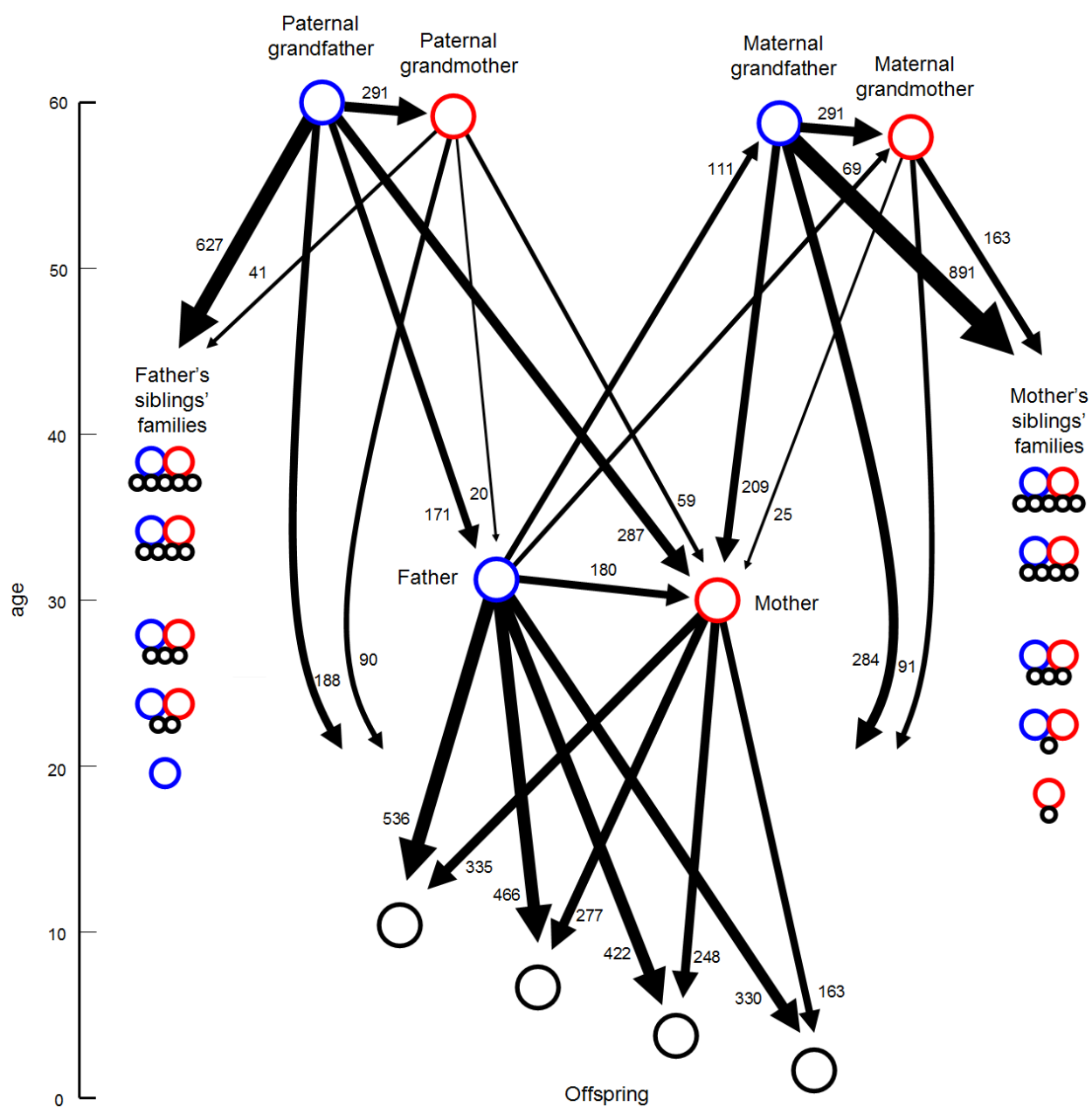


Fig. 5.6. Net caloric transfers within the extended family. Arrow values indicate mean net calories transferred per day (game, fish and horticulture combined).

In order to understand patterns of *net* energetic investment, it is necessary to consider the bidirectional nature of energetic transfers in Tsimane' social networks. Figs. 5.4 and 5.5 represent the pattern of gross bi-directional transfers of meat (5.4) and horticultural products (5.5) across a composite three-generational Tsimane' family (see methods). Fig. 5.6 shows the resulting direction and magnitude of net caloric transfers that result from these bidirectional flows.

Adult men clearly play a dominant role in provisioning game and fish to their families (Fig. 5.4). Mean net flows of meat from fathers to children are consistently downward across childhood and adolescence. As fathers age and sons mature, the direction of mean net meat transfers between the two reverses by the time that sons reach their mid-20s. For female offspring, on the other hand, net meat transfers between fathers and daughters remain downward across life. Although dependent children's production of meat is an order of magnitude less than that of fathers, children of both sexes are estimated to become net suppliers of meat (especially fish) to their mothers around age 10-12. This reversal coincides with the boom in time spent fishing during adolescence for both boys and girls observed in chapter 3 (Fig. 3.2).

We have seen that while meat production shows a strong peak for men in middle adulthood, horticultural production continues to increase into older ages for both sexes, with greater production rates in the 50s and 60s than in the 20s and 30s. As a result, the pattern of horticultural sharing within Tsimane' extended families show greater balance between the sexes, and more consistent downward directionality than that of meat (Fig. 5.5). Mean net horticultural transfers from parents to children are consistently downward across most of life, at least into the early 70s. Grandparents are estimated to be net providers of horticultural calories to grandchildren across all ages.

The current sample shows asymmetries between the contributions of maternal versus paternal kin. While sons in their 20s and 30s are net receivers from their own parents (when both meat and horticulture are taken into account), they are estimated to be net contributors to their parents-in-law, likely reflecting the custom of bride

service. This tendency is also manifest in the Fig. 5.1: the age-sex class that shows the greatest proportion of production routed to parents-in-law (around 7% of total production) is men in their 20s; women, in contrast, give only 3% of their production to their parents-in-law in this period. Interestingly, while mothers aged 20-39 receive more gross calories from their own parents than parents-in-law, when transfers in both directions are taken into account, parents-in-law appear to provide the greater net contribution. It is maternal grandparents, however that appear to provide more net calories to directly to grandchildren. For the prototypical family represented in Fig. 5.6, when the net contributions of paternal versus maternal kin are summed (i.e. net flows from the 3rd generation downward to the 2nd and 1st generation), paternal kin appear to provide substantially more calories to young nuclear families than do maternal kin. Whether this result depends on the specific composition of the current sample, or is a more robust feature of Tsimane' social organization requires further investigation.

Table 5.1. Linear mixed model predicting gross meat calories transferred from family A to family B per day

| Predictor | B | p | sig. |
|--------------------------------------|----------|--------|------|
| (Intercept) | 21.521 | 0.14 | ns |
| [Meat calories from B to A] | 0.443 | <0.001 | *** |
| [Horticultural calories from B to A] | 0.013 | <0.001 | *** |
| [Age of A] | 0.049 | 0.52 | ns |
| [Age of B] | 0.107 | 0.061 | . |
| [Net meat production of A] | -0.002 | 0.18 | ns |
| [Net meat need of B] | -0.002 | 0.18 | ns |
| [R] | -226.134 | 0.14 | ns |
| [R] × [Age of A] | 19.461 | <0.001 | *** |
| [R] × [Age of A] ² | -0.202 | <0.001 | *** |
| [R] × [Age of B] | 10.963 | 0.010 | * |
| [R] × [Age of B] ² | -0.107 | 0.014 | * |
| [R] × [Age of A] × [Age of B] | -0.102 | 0.024 | * |
| [R] × [Net meat production of A] | 0.075 | <0.001 | *** |
| [R] × [Net meat need of B] | 0.043 | 0.006 | ** |

N = 6558 family dyads (194 families); model includes random effects for community and the identities of family A and family B; AIC = 73600.

The final analyses of this chapter turn our focus from transfers between individuals to those between nuclear families. Tables 5.1, 5.2, and 5.3 display the results for regression models of meat sharing, horticultural sharing, and total sharing between nuclear families, respectively. First off, there is clear evidence of reciprocity between families in all three models: how many calories family A gives to family B is highly dependent on how many calories B gives to A over the sample period. In models 5.1 and 5.2, there is evidence of cross-currency reciprocity; that is, how much meat A gives to B depends not only on how much meat, but also how much horticultural production B gives to A (and vice versa: how much horticultural production A gives to B depends on how much meat and horticultural production B gives to A).

Independent of relatedness, family age and estimated net need do little to predict transfers between families in any of the three models. When interacted with relatedness, however, these life-historical variables become significantly predictive of inter-family sharing. That is: family age and need strongly affect sharing patterns between closely related families, but not between unrelated families. While the parameter estimate for the independent relatedness term is negative in all three models, the summed effect of relatedness for the relevant age ranges is substantially positive.¹

In the inter-family meat-sharing model (Table 5.1), the ages of each family, the net meat production (surplus) of the donor family, and the net meat need (negative net production, or deficit) all independently predict the volume of gross meat transfers between related families. The non-linear $R \times \text{age}$ interactions in this model yield a nuanced picture of directional meat transfers between closely related families at different stages of life (see Fig. D.1 in the appendix). When nuclear families are young, with parents in their teens and 20s, gross meat transfers are directed primarily upward, to closely related families with parents aged 40-60, primarily representing transfers to the couples' parents and in-laws. As the donor family matures into the 30s, 40s, and 50s,

¹ For two families with 40-year-old parents and zero net meat production, for example, the effect of a 0.1 increase in relatedness on the gross number of meat calories shared from one family to the other is $0.1 \times (-226.134 + 19.461 \times 40 - 0.202 \times 40^2 + 10.963 \times 40 - 0.107 \times 40^2 - 0.102 \times 40 \times 40) = 33.3$ calories per day.

the age of the families who receive the greatest quantity of meat from that family declines, indicating a transition from predominantly upward to predominantly lateral and downward provisioning of meat. Intuitively, by the 50s, the primary kin recipients of gross meat transfers are families in their mid-20s. Consistent with the age-schedule of meat production observed in chapter 3, the peak in gross outflow of meat to relatives occurs for families with parents in their 30s and 40s. The age-independent interactions of relatedness with net meat production and need in this model reinforce this peak in giving in middle adulthood, with positive net flows to both younger and older relatives. A plot of the mean net transfer of meat between closely related families ($r \geq 0.1$) in Fig. 5.7 shows that families with parents from the mid-20s to the mid-40s tend to have zero or positive net outflow of meat, while teenage and older families tend to be net recipients. (The fluctuation in net meat transfers in this figure in the 20s and 30s can be understood as a function of both changing production rates as well as changing dependency levels within the family in this period.)

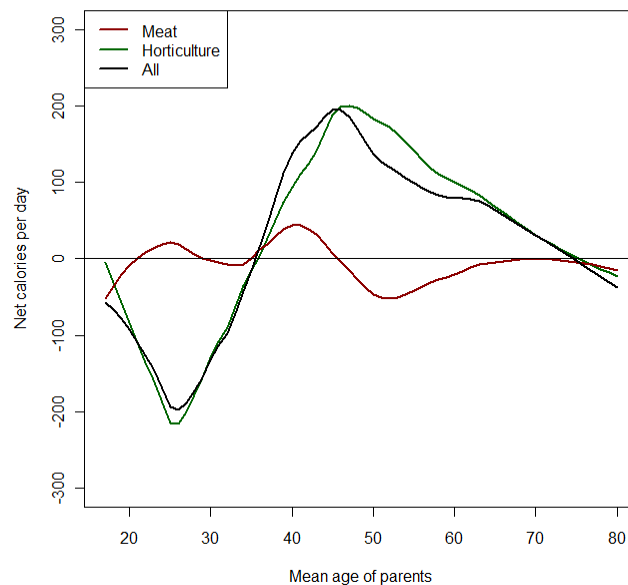


Fig. 5.7. Mean net transfers of meat, horticulture, and all calories to closely related families as a function of family age. (N = 886 family dyads where mean $r \geq 0.1$; smoothing parameter = 0.4)

Table 5.2. Linear mixed model predicting gross horticultural calories transferred from family A to family B per day

| Predictor | B | p | sig. |
|---|----------|--------|------|
| (Intercept) | -5.5998 | 0.99 | ns |
| [Meat calories from B to A] | 0.5701 | <0.001 | *** |
| [Horticultural calories from B to A] | 0.1603 | <0.001 | *** |
| [Age of A] | 0.0441 | 0.97 | ns |
| [Age of B] | 0.2234 | 0.70 | ns |
| [Net horticultural production of A] | -0.0003 | 0.90 | ns |
| [Net horticultural need of B] | 0.0027 | 0.39 | ns |
| [R] | -536.339 | 0.43 | ns |
| [R] × [Age of A] | 90.6068 | <0.001 | *** |
| [R] × [Age of A] ² | -0.7785 | <0.001 | *** |
| [R] × [Age of B] | 22.8446 | 0.038 | * |
| [R] × [Age of A] × [Age of B] | -0.8728 | <0.001 | *** |
| [R] × [Net horticultural production of A] | 0.2731 | <0.001 | *** |
| [R] × [Net horticultural need of B] | 0.0436 | 0.20 | ns |

N = 6558 family dyads (194 families); model includes random effects for community and the identities of family A and family B; AIC = 97078.

The between-family horticultural sharing model (Table 5.2) presents a similar, but somewhat simpler, pattern of intergenerational resource flows. The $R \times \text{age}$ interactions in this model (plotted in Fig. D.2 in the appendix) indicate that for families in their teens, gross horticultural transfers to related families are directed primarily upward; for those in their 20s and 30s, transfers to relatives are rather equally upward and downward; for those in their 40s and above, however, horticultural calories become strongly directed toward younger related families, especially those in their teens and early 20s. Consistent with the findings in Fig. 5.5, as the gross volume of transfers from younger families is less than that of older families, the net direction of horticultural transfers between older and younger related families is consistently downward. In the horticultural model, the $R \times \text{donor surplus}$ term is a significant positive predictor of transfers, while the $R \times \text{recipient need}$ term is positive, but not fully significant. These effects serve to reinforce the downward directionality of net horticultural transfers between families. Fig. 5.7 shows that families tend to be consistent net receivers of horticultural products from closely related families until the mid-30s, but tend to be net donors across the 40s, 50s, and 60s.

Table 5.3. Linear mixed model predicting gross total calories transferred from family A to family B per day

| Predictor | B | p | sig. |
|-------------------------------|----------|--------|------|
| (Intercept) | 50.270 | 0.39 | ns |
| [Calories from B to A] | 0.220 | <0.001 | *** |
| [Age of A] | 0.147 | 0.74 | ns |
| [Age of B] | 0.361 | 0.45 | ns |
| [Net production of A] | 0.000 | 0.99 | ns |
| [Net need of B] | 0.002 | 0.51 | ns |
| [R] | -222.972 | 0.76 | ns |
| [R] × [Age of A] | 113.940 | <0.001 | *** |
| [R] × [Age of A] ² | -0.992 | <0.001 | *** |
| [R] × [Age of B] | 22.827 | 0.062 | . |
| [R] × [Age of A] × [Age of B] | -1.052 | <0.001 | *** |
| [R] × [Net production of A] | 0.219 | <0.001 | *** |
| [R] × [Net need of B] | 0.060 | 0.042 | * |

N = 6558 family dyads (194 families); model includes random effects for community and the identities of family A and family B; AIC = 97595.

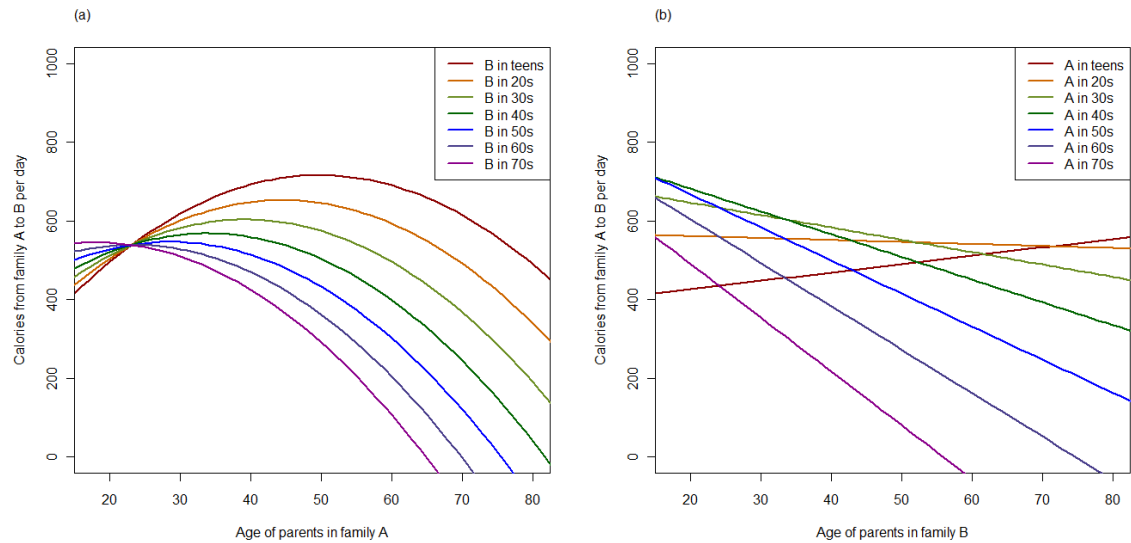


Fig. 5.8. Predicted independent effects of the ages of donor family A and recipient family B on gross calories transferred between closely related ($r = 0.25$) nuclear families (based on model estimates in table 5.3).

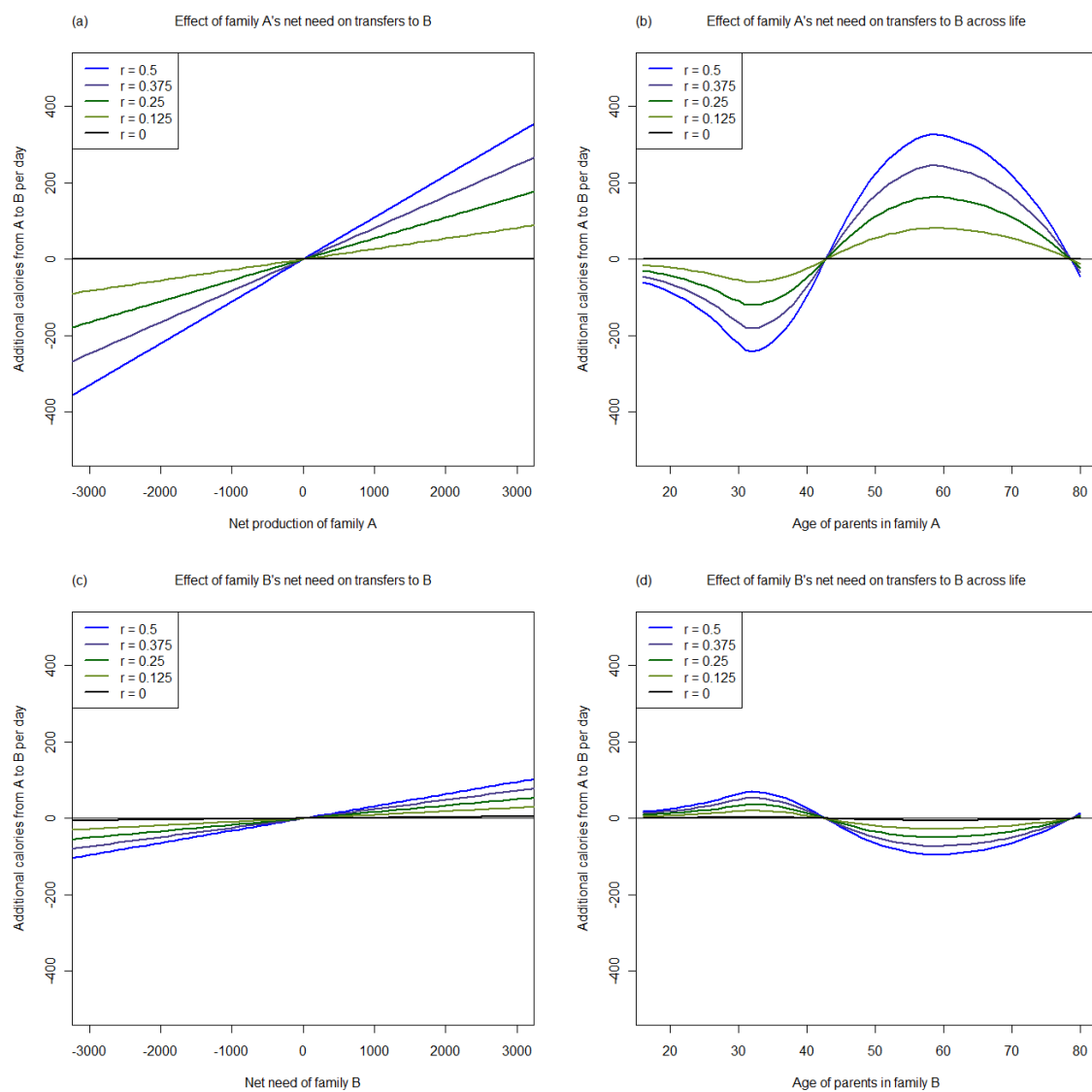


Fig. 5.9. Predicted effects of donor (family A) and recipient (family B) net need on gross calories transferred between families as a function of relatedness (based on model estimates in table 5.3).

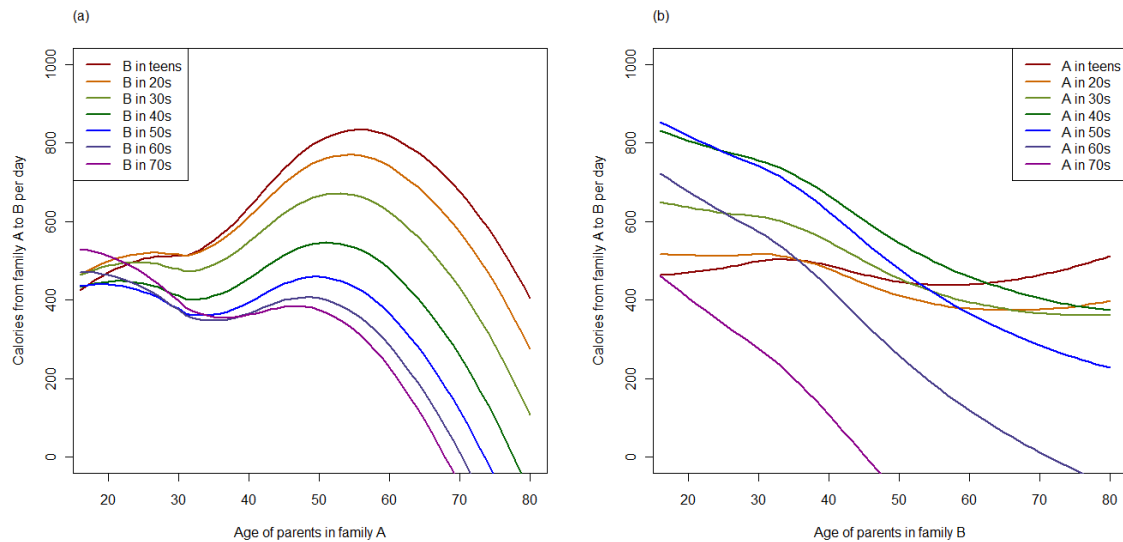


Fig. 5.10. Predicted combined effects of age and need on gross caloric transfers between closely related ($r = 0.25$) families (based on model estimates in table 5.3).

The full model of gross caloric transfers between families, which combines game, fish, and horticulture, is presented in Table 5.3. The $R \times \text{age}$ interactions in this model, illustrated in Fig. 5.8, yield predictions which are qualitatively very similar to those of the horticultural model. Panel (a) in this figure shows the age of maximal giving to related families in different stages of life, while panel (b) indicates the age of maximal receiving from related families of different ages. It can be seen that, by the $R \times \text{age}$ terms alone, very young families tend to direct gross transfers upward, but that by middle age, transfers are directed primarily downward. The highest predicted gross transfer rates are appropriately from families around age 50 to close relatives in their teens and early 20s (witness the red line in panel a, and blue line in panel b of Fig. 5.8).

The predicted independent effects of family need on total caloric transfers between families are illustrated in Fig. 5.9. It can be seen that the age-schedule of net need/surplus additionally reinforces the pattern of transfers from older kin with high total productivity but fewer needy dependents, to younger kin with lower productivity but more dependents, above and beyond the effect of the $R \times \text{age}$ terms alone.

The summed effects of the $R \times \text{age}$ and $R \times \text{need}$ interactions on patterns of caloric transfers between kin across life are illustrated in Fig. 5.10. When all the terms of the model are taken into account, the tendency for aging families to differentially direct resources toward the families of younger kin is once again evident. Maximal gross transfers are again predicted to occur from families in their 50s to related families in their teens and 20s.

IV. Discussion and conclusion

The analyses in this chapter together provide a coherent picture of the pattern of energetic flows within and between Tsimane' families. Far from showing generalized resource pooling within communities, Tsimane' transfers show strong biases toward close kin, especially directly dependent siblings, offspring, and grandoffspring (Fig. 5.1). Reproductive-age mothers and fathers work to provision their dependent offspring, while post-reproductive grandparents work to provision their adult children, children-in-law, and grandchildren (Fig. 5.6).

The regression models summarized in Tables 5.1-5.3 confirm that nepotistic flows between nuclear families are also structured by the life history of net caloric production and need: between relatives, families with higher productivity but lower consumer need give more and receive fewer calories per day than those families with lower productivity but higher consumer need. These models also provide evidence for an interaction between relatedness and age that is independent of estimated net need, which further reinforces the net downward directionality of resource flows between kin. It is unclear to what extent these age \times relatedness effects may be capturing life-historical variation in the benefits of caloric investment which are not captured in the current measures of net caloric need (e.g. reproductive value, or higher benefits of embodied capital investment early in life).

By examining the redistribution of resources rich in fat and protein (from hunting and fishing) and carbohydrates (from horticulture) separately, we have found evidence

of age- and sex-specific economic specialization and exchange. Men in middle adulthood are the predominant net providers of meat to all classes of individuals, including older kin (Fig. 5.4). Older men and women, at least into their 60s, serve as powerhouses of carbohydrate production that flows downward to complete the diets of young and middle-aged families (Fig. 5.5). Our analyses of caloric transfers between adults aged 20-39 and their older parents and in parents-in-law (Figs. 5.4-5.5) also show signatures of bride service by young men to the apparent net benefit of their wife's kin.

Reciprocal provisioning of game and fish is evident in the bidirectional nature of transfers within extended families (Fig. 5.4) and in regression models of transfers between families (Tables 5.1-5.3). These models show higher estimates of contingency for meat than for horticultural products, suggesting that bidirectional food sharing for the purpose of variance reduction is more common for meat than horticulture, at least at the time-scales captured in this sample. These models also support the hypothesis of specialization and exchange by demonstrating cross-currency reciprocity: meat sharing in one direction is predicted by horticultural sharing in the other, and vice versa. Caloric interdependence within extended families is deepened by the collective nature of horticultural production, and is manifest in the bi-directional flow of horticultural calories observed in Fig. 5.5.

Detailed quantitative data on food transfers in traditional societies are difficult to acquire. While the Tsimane' production and sharing dataset provides greater detail for a larger sample than has previously been available for perhaps any other ethnographic population, it is constrained by the methodological limitation of incomplete sharing information for all products produced, especially horticultural products (see data preparation section III in chapter 2). While we feel that the methods employed here to overcome this shortcoming are well justified, there is no doubt that the quantitative estimates derived in these analyses would benefit from cross-validation with estimates derived from complementary datasets, particularly direct observational data on consumption rates.

It would be inappropriate to assume that the exact patterns observed for the Tsimane' immediately generalize to all other traditional small-scale human societies. It is worth noting, however, that the theoretical and empirical bases for the predictions laid out in this dissertation—most importantly, the logic of inclusive fitness and the old-age-biased age-schedule of human caloric production—are shared across all traditional human societies in which they have been evaluated (Hill and Hurtado 2009, Howell 2010, Marlowe 2010, Gurven and Kaplan 2006, Kaplan et al. 2000). As such, it may be argued that many of the empirical regularities uncovered here and in the preceding two chapters are instantiations in one particular socioecological context of more deeply fundamental features of traditional human social organization.

CHAPTER 6. SUMMARY AND CONCLUSION

This dissertation constitutes an integrated analysis of the Tsimane' economic subsistence system. Its analyses were guided by a body of evolutionary theory which posits that life history traits, the structure of social relationships, and nature of economic production co-evolve in patterned and predictable ways. This theory gives particular causal imperative to the constraints imposed by the age-schedule of productive efficiency on a species' equilibrium life history and social structure. The studies in this dissertation have evaluated predictions from this theory from a number of angles, and found that it performs remarkably well across the multiple domains to which it was applied. The principal findings of the dissertation can be summarized as follows.

- (1) Mean Tsimane' return rates do not reach their peak until after age 20 across all economic domains. Peak productive efficiency per unit time is achieved earlier in fishing and harvesting than in hunting, likely due to the greater importance of skill-acquisition in determining returns from hunting. Declines in physical condition with aging also hit return rates from hunting earlier and harder than those from fishing or harvesting.
- (2) As return rates from hunting far outpace those from fishing for men in their later 20s, 30s, and 40s, men in this period of life specialize in hunting and produce the bulk of fat and protein consumed in the Tsimane' diet. Male time allocation to hunting then declines in parallel with declining efficiency across the 50s, 60s, and 70s. Time allocation to horticulture, on the other hand, increases nearly monotonically across life for both sexes, resulting in peak horticultural production in the 40s, 50s, and 60s. These contributions of men and women aged 40-70 to total productivity within the population are substantial even when mortality is taken into account, due to the relatively high adult survival rates across these ages typical of the Tsimane' and other traditional human populations (Gurven and

Kaplan 2007). Adolescents contribute calories to the household economy principally through fishing and horticulture, though at lower mean return rates than those of adults.

- (3) The age-schedule of production was shown to be sensitive not only to changes in the efficiency and cost of productive effort, but also to changes in the consumption requirements of dependent kin through time. These estimated effects of dependent need on producer effort are patterned in accordance with a specialized division of labor within families:
 - a) In the earliest period of productivity, adolescents of both sexes dedicate more time to fishing when they have more young siblings in the household.
 - b) Later, reproductive-age couples respond to offspring need in a coordinated, complementary manner. Mothers decrease production rates across all production activities when nursing-age children are present; controlling for this effect, they increase horticultural production when there are more weaned dependent offspring in the household. Fathers under age 50, on the other hand, significantly increase their hunting effort and output with each additional dependent offspring.
 - c) At the tail end of life, grandparents of both sexes show greater productivity from fishing when more grandchildren are present in the community.
(Marginal positive relationships were also found between number of grandchildren and grandfathers' horticultural productivity and, somewhat surprisingly, grandmothers' hunting effort.)
- (4) As a consequence of the observed age-schedules of productive efficiency and effort across life, males and females are estimated to remain in net caloric deficit until around ages 17 and 23, respectively, confirming the remarkably long duration of human dependency during which energy must be supplied by older, more productive individuals, primarily kin. From the 20s onward, both sexes produce a substantial net surplus, which is channeled to support the growth and development of these younger dependents. Men are estimated to remain positive

net producers until their mid-70s, while women in this sample continue to produce a net surplus even into their 80s.

- (5) Our investigation of the effects of dependent need on producer effort informs us that while the consumption requirements of dependent kin do motivate higher levels of productivity in adulthood than would be achieved in their absence, they are not primarily responsible for the dominant late-age-biased shape of the production curve that requires such substantial intergenerational subsidization. These analyses do suggest, however, that if not for the depressing effect of small infants on young mothers' productivity, Tsimane' females would likely become net producers in their late teens, around the same age as males, rather than at the observed cross-over point in the early 20s.
- (6) A direct analysis of the recipients of Tsimane' subsistence productivity confirms that calories are produced primarily to the benefit of close dependent kin, with adolescents supplying calories to their siblings, mothers and fathers supplying calories to their offspring, and grandparents supplying calories to their adult offspring and grandoffspring. Within Tsimane' extended families, the net flow of calories is consistently downward across generations with two exceptions: men in middle adulthood (from the mid-20s through the 40s) provide a net surplus of meat to both their descendent and ancestral kin; young husbands also provide a net surplus of calories to their parents-in-law, presumably as a manifestation of bride service. Bride service aside, the high productivity of parents and grandparents in their 40s, 50s, and 60s ensures a strong downward flow of carbohydrate calories that help fulfill the dietary need of descendent kin.
- (7) Further examination of production in light of Tsimane' demography and familial structure shows that the individual-level pattern of net need early in life and net surplus later in life recapitulates itself at the level of the nuclear family: because young families grow at a rate that outpaces the productivity of parents in their teens, 20s, and 30s, families of young parents tend to sit in a state of net caloric deficit; families of older parents (especially in the range 50-70), on the other hand,

are highly productive, yet have fewer directly dependent offspring. These older families are thus in a prime position to help supply younger families in need.

- (8) Finally, our analysis of transfers between families confirm that this pattern of net subsidization does in fact occur at the family level: older families with higher productivity and fewer dependents provide a net surplus to younger, closely related families with lower productivity and more dependents. This is accomplished predominantly through the high horticultural production levels of older families. Since the lion's share of meat, on the other hand, is produced by men in middle adulthood, there is a tendency for net upward flows of meat from middle-aged families to the families of younger and older kin; the older generation, complementarily, provides the bulk of carbohydrates downward. The analysis of inter-family transfers also reveals strong signatures of reciprocity, both in-kind (meat for meat, horticulture for horticulture) and cross-currency (meat for horticulture, and vice versa). We suggest that these results indicate the importance of (a) reciprocal consumption-smoothing and (b) specialization and exchange in the Tsimane' economic system, across and within generations.

These studies constitute an important step forward in human life history research by demonstrating the ways in which the life history of energy production, demography, and social structure are linked in one traditional human society, the Tsimane'. Its synthesis of inclusive fitness theory and embodied capital theory has proven particularly productive in understanding the equilibrium structure of energy flows between individuals in society, and the effects of close kin on optimal age-schedules of productive effort across life.

The success of this type of life history model in explaining patterns of human cooperative reproduction may also prove useful in understanding some forms of cooperative breeding in non-human animals. Empirical associations between cooperative breeding, extended development, and longevity (Arnold and Owens 1998, Covas and Griesser 2007, Hatchwell and Komdeur 2000), for example, could potentially

be explained in part by the logic of embodied capital investment. The simultaneous consideration of the age-schedules of productive efficiency on the one hand, and reproductive efficiency on the other (as in section II of chapter 1), may prove useful in understanding why some species exhibit patterns of direct reproduction by older adults supported by pre-reproductive sub-adults, while others exhibit patterns of younger adult reproduction supported by (potentially post-reproductive) older adults, as in traditional human societies.

This headway appropriately brings our attention to a new set of questions for further investigation. The current analysis has set aside, for example, the endogenous nature of residence choices, which are likely to be optimized across the life course in ways that maximize the gains and minimize the costs of the kind of social investments we have observed here (Gurven n.d., Hill et al. 2011). Variation in energy expenditure across the life course could also be more fully integrated into estimates of consumption rates. The ability to make quantitative estimates of caloric transfers also opens the possibility of quantifying the ultimate demographic benefits of older individuals' energetic investments, for example in terms of number of additional surviving grandoffspring.

The energetic approach taken in this dissertation complements existing demographic methods of evaluating the effects of kin on fertility and survival (e.g. Lahdenperä et al. 2007, Sear and Mace 2008, Willfür 2009, for the Tsimane' see: Winking et al. 2011a, Winking et al. 2011b) by putting a spotlight on the actual material means of investment in kin. It also serves to flesh out in greater detail the internal structure of relationships that constitute the human pattern of cooperative reproduction. This adds importantly to studies of residential group composition (Hill et al. 2011) and current conceptualizations of resource pooling and redistribution in humans (Kramer and Ellison 2010). We hope that the content of this dissertation stands as an argument for the utility of this approach.

APPENDIX A

Supplementary materials on rice sales data

I. Correction of rice sales figures in the field interview

In the field interview, interviewees report how much rice from this year's harvest they have already sold, and how much they additionally plan to sell. Because interviewees may ultimately be unable to sell as much as they originally expect, a 'devaluation' factor D was calculated for each region in order to discount the amount planned for sale. The final estimate for the amount sold was then calculated as:

$$[\text{Rice ultimately sold}] = [\text{Rice already sold}] + D \times [\text{Rice planned to sell}]$$

To estimate the devaluation factor D, it was assumed that the ultimate total amount sold is roughly a function of the total amount harvested, such that:

$$[\text{Rice ultimately sold}] = B \times [\text{Rice harvested}] + C \times [\text{Rice harvested}]^2$$

Substituting the right side of the first equation into the left side of the second gives:

$$[\text{Rice already sold}] + D \times [\text{Rice planned to sell}] = B \times [\text{Rice harvested}] + C \times [\text{Rice harvested}]^2$$

Rearranging:

$$[\text{Rice already sold}] = B \times [\text{Rice harvested}] + C \times [\text{Rice harvested}]^2 - D \times [\text{Rice planned to sell}]$$

The values of the coefficients B, C, and D in this equation were then estimated for each region using the model represented in Table A.1.

Table A.1. Regression model predicting amount of rice already sold based on amount harvested and amount planned to sell in the future (in units of arrobas of rice per year)

| Predictor | B | p | sig. |
|---|---------|--------|------|
| [Downriver] × [Rice harvested] (B) | 0.3996 | <0.001 | *** |
| [Forest] × [Rice harvested] (B) | 0.2160 | <0.001 | *** |
| [Tributary] × [Rice harvested] (B) | 0.0910 | 0.026 | * |
| [Ton'tumsi] × [Rice harvested] (B) | 0.2359 | <0.001 | *** |
| [Rice harvested] ² (C) | 0.0009 | <0.001 | *** |
| [Downriver] × [Rice planned to sell] (-D) | -0.4613 | 0.31 | ns |
| [Forest] × [Rice planned to sell] (-D) | -0.4968 | 0.011 | * |
| [Tributary] × [Rice planned to sell] (-D) | -0.2551 | 0.19 | ns |
| [Ton'tumsi] × [Rice planned to sell] (-D) | -0.7189 | <0.001 | *** |

N = 283 field interviews; R² = 0.771.

Appendices

Based on the values of D estimated for each region in this model, the corrected amount sold was calculated according to the following equations:

For Downriver: [Corrected amount sold] = [Rice already sold] + 0.4613 × [Rice planned to sell]

For Forest: [Corrected amount sold] = [Rice already sold] + 0.4968 × [Rice planned to sell]

For Tributary: [Corrected amount sold] = [Rice already sold] + 0.2551 × [Rice planned to sell]

For Ton'tumsi: [Corrected amount sold] = [Rice already sold] + 0.7189 × [Rice planned to sell]

II. Correction of rice sales figures in the field interview

To predict the amount of rice sold by families for whom sales data were unavailable, a regression model was run on the sample of families for whom sales data were available. The estimates from this model, given in Table A.2. were used to predict the missing amounts sold.

Table A.2. Regression model predicting amount of rice sold on the basis of amount of rice harvested (in units of kg per day) and region

| Predictor | B | p | sig. |
|---|---------|---------|------|
| [Downriver] × [Rice harvested] | 0.3760 | < 0.001 | *** |
| [Downriver] × [Rice harvested] ² | 0.0281 | 0.014 | * |
| [Forest] × [Rice harvested] | 0.4364 | <0.001 | *** |
| [Forest] × [Rice harvested] ² | -0.0164 | <0.001 | *** |
| [Tributary] × [Rice harvested] | 0.2841 | <0.001 | *** |
| [Tributary] × [Rice harvested] ² | -0.0014 | 0.42 | ns |
| [Ton'tumsi] × [Rice harvested] | 0.5090 | <0.001 | *** |
| [Ton'tumsi] × [Rice harvested] ² | 0.0015 | 0.49 | ns |

N = 184 families; R² = 0.865.

The predicted amount sold was calculated based on the amount harvested and region:

For Downriver: [Amount sold] = 0.3760 × [Rice harvested] + 0.0281 × [Rice harvested]²

For Forest: [Amount sold] = 0.4364 × [Rice harvested] - 0.0164 × [Rice harvested]²

For Tributary: [Amount sold] = 0.2841 × [Rice harvested] - 0.0014 × [Rice harvested]²

For Ton'tumsi: [Amount sold] = 0.5090 × [Rice harvested] + 0.0015 × [Rice harvested]²

APPENDIX B

Description of kinship algorithm

For the analyses in chapters 4 and 5 of this dissertation, a kinship algorithm was developed to identify consanguineous and affinal relationships between all pairs of individuals in the sample. The algorithm takes as its inputs the identities of each individual's vertically ancestral kin (i.e. parents, grandparents, great grandparents), as well as the identity of each individual's spouse(s). In the Tsimane' case, a maximum of three generations of ancestral genealogy were available; the algorithm, however, may be generalized to identify relationships rooted any number of generations back from the focal generation(s). The algorithm's output provides the following for each pair of individuals in the sample:

- coefficient of genetic relatedness, summed across all independent pathways of relatedness;
- primary consanguineous relationship (e.g. mother, grand nephew, 2nd cousin);
- generational difference between the two individuals (e.g. -1 if A is 1 generation below than B, 0 if they are members of the same generation, 2 if A is 2 generations above B);
- primary affinal relationship (e.g. brother of spouse, spouse of 1st cousin); and
- affinal coefficient of relatedness, defined as the coefficient of relatedness between individual A and B's spouse, or between individual A's spouse and B (as in Hill and Dunbar 2003).

Object definitions

Individual dyads table: A summary table in which each entry (a.k.a. record, row) corresponds to one pair of individuals in the sample. (Each dyad is represented twice: once for A and B, and once for B and A). The entries in this table are created for each

pair of individuals in the sample prior to running the algorithm. The algorithm's final output is recorded in this summary table.

Kinship pathway table: A table which is filled in the course of running the algorithm in which each entry corresponds to one independent pathway of genetic relatedness between two individuals. Each pair of individuals in the individual dyads table may have 0, 1, or several entries in the kinship pathway table. See pseudo-code below for more details on the function of this table.

Pedigree vector: Each individual in the sample has a pedigree vector filled with the identities of the 15 individuals indicated in Table B.1. The identities of these ancestral kin are drawn from the Tsimane' census and demography datasets.

Table B.1. Definition of pedigree vector for individual A

| <i>Index</i> | <i>Relationship to ego</i> | <i>Ancestor code</i> | <i>Vector entries</i> |
|--------------|--------------------------------|----------------------|-----------------------|
| 0 | Ego | null | (ID) |
| 1 | Father | P | (ID) |
| 2 | Paternal grandfather | PP | (ID) |
| 3 | Maternal grandfather | MP | (ID) |
| 4 | Father of paternal grandfather | PPP | (ID) |
| 5 | Father of paternal grandmother | PMP | (ID) |
| 6 | Father of maternal grandfather | MPP | (ID) |
| 7 | Father of maternal grandmother | MMP | (ID) |
| 8 | Mother | M | (ID) |
| 9 | Paternal grandmother | PM | (ID) |
| 10 | Maternal grandmother | MM | (ID) |
| 11 | Mother of paternal grandfather | PPM | (ID) |
| 12 | Mother of paternal grandmother | PMM | (ID) |
| 13 | Mother of maternal grandfather | MPM | (ID) |
| 14 | Mother of maternal grandmother | MMM | (ID) |

Appendices

Match matrix: A match matrix is constructed for each pair of individuals, A and B, in order to compare the identities of the individuals in A's pedigree vector with those in B's pedigree vector (Table B.2). As the algorithm is run, the elements of this matrix are filled with one of three values: 'primary common ancestor', 'secondary common ancestor', or 'no match'. Primary common ancestors represent recent common ancestors through which paths of independent blood relatedness are traced. Secondary common ancestors are implied by the existence of (younger) primary common ancestors, and do not contribute additional independent paths of blood relatedness, above and beyond those of primary common ancestors. The elements in Table C.2 marked 'na' are irrelevant, as they imply a cross-sex match.

Table B.2. Definition of kinship match matrix for individuals A and B

| | | | B's Ancestors | | | | | | | | | | | | | | |
|---------------|--------------------------------|--------------------------------|---------------|--------|----------------------|----------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------|----------------------|----------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|
| | | | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| | | | Ego | Father | Paternal grandfather | Maternal grandfather | Father of paternal grandfather | Father of paternal grandmother | Father of maternal grandfather | Father of maternal grandmother | Mother | Paternal grandmother | Maternal grandmother | Mother of paternal grandfather | Mother of paternal grandmother | Mother of maternal grandfather | Mother of maternal grandmother |
| A's Ancestors | Index | Ancestor | | | | | | | | | | | | | | | |
| | 0 | Ego | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 1 | Father | . | . | . | . | . | . | . | . | na | na | na | na | na | na | na |
| | 2 | Paternal grandfather | . | . | . | . | . | . | . | . | na | na | na | na | na | na | na |
| | 3 | Maternal grandfather | . | . | . | . | . | . | . | . | na | na | na | na | na | na | na |
| | 4 | Father of paternal grandfather | . | . | . | . | . | . | . | . | na | na | na | na | na | na | na |
| | 5 | Father of paternal grandmother | . | . | . | . | . | . | . | . | na | na | na | na | na | na | na |
| | 6 | Father of maternal grandfather | . | . | . | . | . | . | . | . | na | na | na | na | na | na | na |
| | 7 | Father of maternal grandmother | . | . | . | . | . | . | . | . | na | na | na | na | na | na | na |
| | 8 | Mother | . | na | na | na | na | na | na | na | . | . | . | . | . | . | . |
| | 9 | Paternal grandmother | . | na | na | na | na | na | na | na | . | . | . | . | . | . | . |
| | 10 | Maternal grandmother | . | na | na | na | na | na | na | na | . | . | . | . | . | . | . |
| | 11 | Mother of paternal grandfather | . | na | na | na | na | na | na | na | . | . | . | . | . | . | . |
| | 12 | Mother of paternal grandmother | . | na | na | na | na | na | na | na | . | . | . | . | . | . | . |
| | 13 | Mother of maternal grandfather | . | na | na | na | na | na | na | na | . | . | . | . | . | . | . |
| 14 | Mother of maternal grandmother | . | na | na | na | na | na | na | na | . | . | . | . | . | . | . | |

Kinship algorithm pseudo-code

Part I. Consanguineous relationships

- For each pair of individuals A and B:
 - For each individual i in A's pedigree vector:
 - For each individual j in B's pedigree vector:
 - If identity of i = identity of j (i.e. if i is a common ancestor of both A and B):
 - If element (i,j) in the match matrix is marked 'secondary common ancestor' (i.e. if this match was already known as a consequence of a younger primary common ancestor), do nothing.
 - If element (i,j) is not marked 'secondary common ancestor':
 - Mark element (i,j) in the match matrix 'primary common ancestor'.
 - Mark each element in the match matrix corresponding to the father, mother, and grandparents of individual i as 'secondary common ancestor's (Note: this may overwrite elements previously marked as 'primary common ancestor' if a more proximate common relative has been found.)
 - If identity of i ≠ identity of j, mark element (i,j) in the match matrix 'no match'.
 - For each element in the match matrix marked 'primary common ancestor', which corresponds to A and B's identified common ancestor Z:
 - Create a new entry in the kinship pathway table representing the blood relationship between A and B through individual Z.
 - Record identity of A, B, and Z.
 - Record Z's relationship to A, as derived from the location of Z in A's pedigree vector (e.g. 'maternal grandmother').
 - Record Z's relationship to B, as derived from the location of Z in B's pedigree vector (e.g. 'mother').
 - Record A's relationship to B through Z, as derived from location of Z in the match matrix (e.g. 'half niece' if A is female, 'half nephew' if male). See Table C.2 for these relationship definitions. Note: each relationship between A and B through a single primary common ancestor is a half relationship, unless it is a directly vertical relationship, i.e. parent-child, grandparent-grandchild, or great-grandparent-great-grandchild relationship.
 - Record the number of generations A is above B according to their relationship through Z (e.g. if A is B's niece, record -1). This is given by [# of generations A is above B] = [# of generations Z is above B] - [# generations Z is above A]. (Note: The

Appendices

character length of the ancestor codes for the entries in A and B's pedigree vectors--see Table C.1--yield the number of generations Z is above A or B, and can thus be utilized to calculate generational distances.)

- Calculate and record the partial coefficient of relatedness (partial r) between A and B through Z. This is given by $[\text{partial } r] = 0.5^{([\# \text{ of generations Z is above A}] + [\# \text{ of generations Z is above B}])}$.
- Open the entry in the individual dyads table corresponding to A and B to record the following consanguineous relationship data:
 - Record the full coefficient of relatedness. To calculate the full relatedness between A and B through all independent pathways, sum the partial r of all entries in the kinship pathway table corresponding to the pair A and B.
 - Record the mean number of generations A is above B, determined by averaging across the entries in the kinship pathway table corresponding to the pair A and B.
 - Record the principal blood relationship label for the relationship between A and B. To determine this relationship label, create a collapsed version of the kinship pathway table, which collapses any pathway entries in the kinship pathway table corresponding to the pair A and B that are of the same relationship type, and sums the partial r's of the collapsed entries. For example, if A and B share both a grandfather and a grandmother, they are 'half' cousins through two independent pathways (each with partial r = 0.0625), and thus, collapsing these two pathways, full cousins (with a combined partial r = 0.125). From among these collapsed relatedness pathway entries, record the relationship label from the entry with the highest partial r as the principal blood relationship label.

Part II. Affinal relationships

- For each pair of individuals A and B:
 - If A is married to some individual C:
 - Find the entry in the individual dyads table corresponding to the dyad B and C.
 - If B and C are blood relatives (as determined in part I above), store the fact that B is the [blood relationship of B to C] of A's spouse (e.g. if B is C's nephew, B is the nephew of A's spouse); additionally, record the full coefficient of relatedness between B and C.
 - If B is married to some individual D:
 - Find the entry in the individual dyads table corresponding to the dyad A and D.
 - If A and D are blood relatives (as determined in part I above), store the fact that B is the spouse of A's [blood relationship of D to A] (e.g. if D is A's uncle, B is the spouse of A's uncle); additionally, record the full coefficient of relatedness between A and D.

Appendices

- Open the entry in the individual dyads table corresponding to the dyad A and B, and record the data for any affinal relationship found in the previous two steps. (If relationships were found between both A and B's spouse, and B and A's spouse, record the data for the relationship with the higher coefficient of relatedness.) The coefficient of relatedness between A and B's spouse (or B and A's spouse) calculated here may serve as an index of affinal relatedness (as in Hill and Dunbar 2003).

APPENDIX C

Composition of return rate samples

Table C.1. Composition of return rate samples.

| | <i>Ages</i> | <i>N individuals</i> | <i>% sample hunt hours = 0</i> | <i>% sample fish hours = 0</i> | <i>% sample non-rice harvest hours = 0</i> | <i>% sample rice harvest hours = 0</i> |
|---------|-------------|--------------------------|--|--|--|--|
| Males | 0-9 | 241 | 94% | 76% | 88% | 88% |
| | 10-19 | 173 | 42% | 6% | 52% | 32% |
| | 20-29 | 78 | 12% | 8% | 53% | 37% |
| | 30-39 | 56 | 5% | 0% | 29% | 20% |
| | 40-49 | 47 | 2% | 0% | 32% | 19% |
| | 50-59 | 18 | 17% | 0% | 39% | 28% |
| | 60-69 | 18 | 17% | 6% | 39% | 28% |
| | 70-79 | 14 | 64% | 29% | 29% | 43% |
| | 80+ | 1 | 100% | 0% | 0% | 0% |
| Females | 0-9 | 240 | 97% | 83% | 87% | 87% |
| | 10-19 | 163 | 77% | 10% | 23% | 29% |
| | 20-29 | 62 | 66% | 13% | 21% | 27% |
| | 30-39 | 53 | 72% | 8% | 23% | 11% |
| | 40-49 | 39 | 51% | 15% | 5% | 23% |
| | 50-59 | 18 | 72% | 17% | 6% | 11% |
| | 60-69 | 15 | 87% | 40% | 20% | 27% |
| | 70-79 | 5 | 80% | 80% | 20% | 0% |
| | 80+ | 4 | 100% | 25% | 0% | 25% |

Note: Zero time allocation values reflect both participation rates and sample error.

APPENDIX D

Additional figures from the analysis of caloric transfers between families

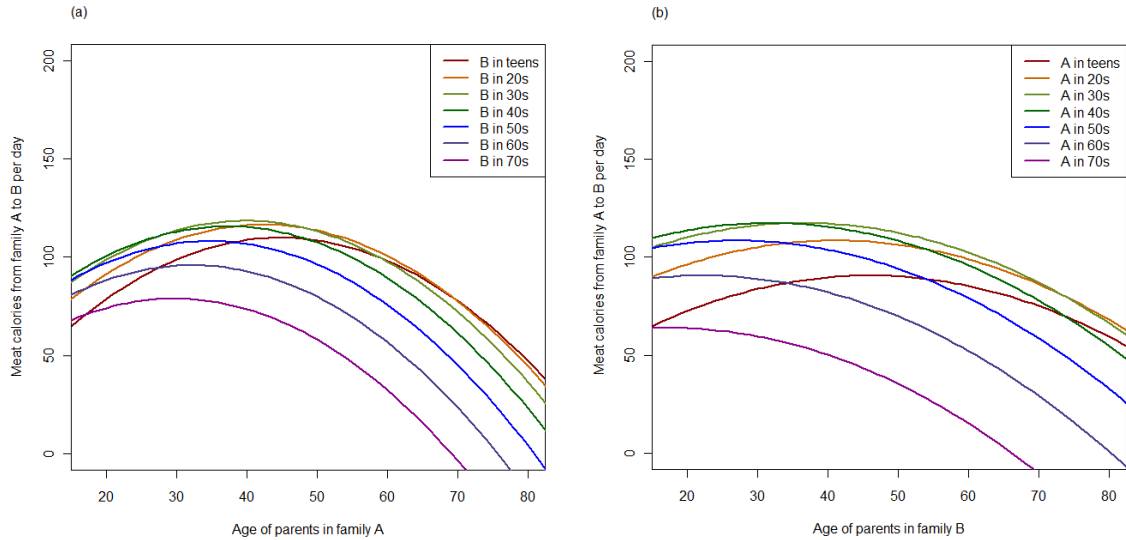


Fig. D.1. Predicted independent effects of the ages of donor family A and recipient family B on gross meat calories (game and fish) transferred between closely related ($r = 0.25$) nuclear families (based on model estimates in table 5.1).

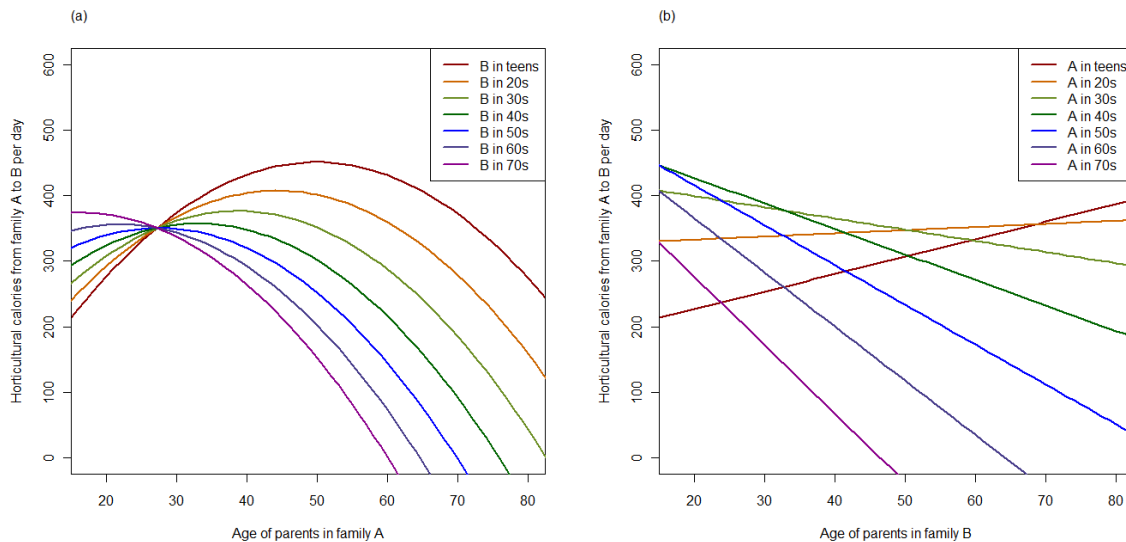


Fig. D.1. Predicted independent effects of the ages of donor family A and recipient family B on gross horticultural calories transferred between closely related ($r = 0.25$) nuclear families (based on model estimates in table 5.2).

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