



Developmental Plasticity in Fat-Patterning of Ache Children in Response to Variation in Inter-Birth Intervals: A Preliminary Test of the Roles of External Environment and Maternal Reproductive Strategies

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Original Research. Developmental Plasticity in Fat-Patterning of Ache Children in Response to Variation in Inter-Birth Intervals: A Preliminary Test of the Roles of External Environment and Maternal Reproductive Strategies

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Abstract: A firm link between small size at birth and later more centralized fat-patterning has been established in previous research. Relationships between shortened inter-birth intervals and small size at birth suggest that maternal energetic prioritization may be an important but unexplored determinant of offspring fat patterning. Potential adaptive advantages to centralized fat storage (Baker et. al., 2008) suggest that relationships with inter-birth intervals may reflect adaptive responses to variation in patterns of maternal reproductive effort. Kuzawa (2005, 2008) has argued that maternal mediation of the energetic quality of the environment is a necessary component of developmental plasticity models invoking *predictive adaptive responses*. This study tested the general hypothesis that shortened inter-birth intervals would predict more centralized fat patterning in offspring. If long-term maternally-mediated signals are important determinants of offspring responses, then we expected to observe a relationship between the average inter-birth interval of mothers and offspring adiposity, with no relationship with the preceding interval. Such a finding would suggest that maternal, endogenous resource allocation decisions are related to offspring physiology in a manner consistent with Kuzawa's description. We observed exactly such a relationship among the Ache of Paraguay, suggesting that maternally-mediated signals of environmental quality in utero may be important determinants of later physiology. The implications of these findings are reviewed in light of life history and developmental plasticity theories and our ability to generalize the results to other populations. Recommendations for further empirical research are briefly summarized.

I. Introduction

A number of previous studies link in utero experience of energetic scarcity—typically measured as small size at birth—to later body composition outcomes including more centralized adiposity (Baker et al 2008 for review). In general, human biologists have been interested in these relationships in light of their potential linkage to the phenomenon of developmental plasticity (Kuzawa, 2005; Gluckman and Hanson, 2004), in which environmental factors experienced during development lead to life-long physiological alterations (Schlichting and Pigliucci, 1999). The presence of developmental plasticity is ubiquitous throughout nature, and it is often cited as an adaptive mechanism for dealing with environmental heterogeneity (Levins 1968, Schlichting and Pigliucci 1999, West-Eberhard 2003). Centralization of adiposity is a particularly noteworthy phenomenon in this respect because it represents a potential adaptation (Williams, 1966; Curio 1973) to energetically marginal environments. Abdominal fat cells are at least four times more sensitive to lipolytic endocrine signals than their counterparts in peripheral depots such as the arms and legs (Bjorntorp and Eden, 1996). In an ancestral environment characterized by day to day fluctuation in energetic intakes that are generally short-term in nature and potentially modifiable by additional foraging effort, enhanced centralization of fat storage could improve energy availability for moderate-intensity activity in a fasting state, providing advantages in energy collection (Baker, 2007; Baker et. al. 2008). If this were the case, mechanisms whereby developing fetuses detect signals of scarcity and respond in this manner could evolve as examples of the phenomenon of *adaptive developmental plasticity* (Levins 1968; Schlichting and Pigliucci 1999, Baker, 2007, Baker et al 2008). Development of such a mechanism might provide additional benefits to standard selection of fixed genetic responses in that during times of plenty a greater amount of resources could be invested in muscle tissue and associated physical performance, maximizing energetic collection through enhancing performance. The necessary signal might be provided by experiences of in utero scarcity (Kuzawa 2005, Baker et. al., 2008; Baker, 2007) which would be reflected in small size at birth; however, Kuzawa has rightly argued against the theoretical plausibility of a direct link between in utero experiences and later physiology based on the idea that this direct experience is an unreliable indicator of future environments within a single lifetime. Instead, Kuzawa (2005, 2008) has argued for the presence of “intergenerational inertia”, in which mothers provide mediated signals of environmental quality to their offspring based on their own experiences. He provides a number of empirical results supporting the plausibility of this suggestion, some of the most compelling of which are observations that among rhesus macaques the mother’s own birth weight predicts that of her offspring (Price and Coe, 2000) and that direct nutritional supplementation has been found to perform poorly in reducing low birth weight incidence in human populations (Ceesay et. al., 1997).

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3 Shortened inter-birth intervals have been repeatedly linked to small size at birth (Conde-
4 Aguelo, et. al., 2006; Zhu et. al., 1999; Khan and Khan, 1998), suggesting that maternal
5 reproductive decisions are related to offspring in utero experiences directly. If so, then
6 measuring relationships between variation in inter-birth intervals and offspring fat patterning
7 may provide a way to initially clarify if and how mothers might mediate the environment of
8 their developing offspring in a way that provides reliable signals and allows the possible
9 evolution of developmentally plastic responses that are adaptive in nature. A potentially
10 useful, but ultimately incomplete, starting point for this assessment is the Smith-Fretwell
11 (1974) model of a trade-off between quantity and “quality” of offspring. The model provides a
12 key, germane point: an inherent trade-off between increased reproduction and the fitness of
13 offspring exists since increasing reproduction decreases the per-capita energetic availability to
14 offspring. The model was originally developed for understanding litter and clutch size in which
15 the per-capita decrease in energy in relation to litter or clutch size is immediate and well-linked
16 to the literature on trade-offs in life-history theory (Walker et. al., 2008; Charnov and Ernst,
17 2006). A simple prediction made in the spirit of this model, when extended to iteroparous,
18 long-lived species such as humans, would be that shortened inter-birth intervals are directly
19 related to energetic shortfalls in utero experienced by offspring and reflected in small size at
20 birth. The Smith-Fretwell model makes the assumption that the mother’s relative strategy of
21 allocation to offspring is time/situation invariant—she allocates resources evenly across all
22 offspring. A simple extension that relaxes this assumption and allows mothers to weigh current
23 and future reproduction against self-maintenance and adjust endogenous resource allocation
24 to these competing demands *at each specific point in time* (Ellison 2003; Stearns, 1992) makes a
25 plausible link with what is known about developmental plasticity. The overall framework of
26 such a decision model is captured in Figure 1, which allows a disaggregation of the probability
27 of conception and the amount of resources allocated to each offspring at each bout of
28 reproduction. Such a disaggregation appears justified given that mothers clearly modulate the
29 probability of conception based on energetic status, balance, and flux (Ellison, 2003) and it
30 allows for mothers to adjust this from pregnancy to pregnancy based on long-term exposures
31 as well as short-term environmental inputs.

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46 If we assume, then, that offspring will always respond to scarcity in utero by increasing
47 centralization of fat-patterning, then we may relate this outcome to different measurements of
48 inter-birth intervals aimed at distinguishing whether maternal reproductive strategy and
49 associated endogenous resource allocation is an important determinant of offspring physiology.
50 In doing so, we can make a preliminary test of the idea that mothers may mediate energetic
51 signals to their offspring. This will perhaps clarify whether offspring developmental responses
52 are linked to short-term exogenously-determined variation in resource availability or to
53 maternally-mediated signals of scarcity reflecting her own priority rules for resource allocation
54 (Kuzawa 2005, 2008; Baker et al 2008). In an attempt to discriminate between exogenous
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environmental effects and endogenous maternal resource allocation decisions, this study tests for relationships between two different measures of inter-birth intervals and offspring fat-patterning among Ache children two to fifteen years of age. Inter-birth intervals are operationalized as: (1) the inter-birth interval immediately preceding the birth of each study participant, or (2) the long-term “average” inter-birth interval of the mother. Obviously, the two measures will be related; however, if a relationship between increasingly centralized fat-patterning and the preceding interval is observed in the absence of a relationship with the long-term average interval of the mother, it may suggest that short-term exogenously-determined resource fluctuations are the signal driving the developmentally plastic response. If a relationship with the long-term average interval is observed in the absence of a relationship with the preceding interval, then it suggests that maternally-mediated effects, perhaps similar to those envisioned in Kuzawa’s intergenerational inertia model are at work. The results of the study indicate initial support for the idea that maternal resource allocation preferences are important in determining offspring fat patterning; however, they suggest a different relationship between these two variables than was initially expected in the study. The findings suggest specific strategies should be employed in further research, which are reviewed. Implications of the study for Kuzawa’s model, as well as for applications of the Smith-Fretwell model to humans, are briefly reviewed.

II. Materials and Methods

Hypotheses and Variables

We tested two hypotheses in this study. First, we tested the prediction that shortened preceding inter-birth intervals would result in more centralized fat-patterning in offspring. Second, we tested the prediction that shortened “average” inter-birth intervals of mothers would predict increased centralization of fat patterning in offspring. We operationalized centralization of fat-patterning using the ratio of the subscapular skinfold measure to that of the triceps (Malina 1996). As centralization of fat-storage increases, so does the subscapular/triceps skinfold ratio. This is reflected in Figure 2, where three “categories” of centralization of fat-patterning are presented, with a case of equivalent measurements yielding a ratio of 1, a case with a ratio greater than 1 reflecting more centralized adiposity, and a third case with a ratio less than 1 reflecting more peripheral fat-patterning. In our sample, the average subscapular/triceps skinfold ratio was greater than 1 (1.298). This ratio (and each individual component—the subscapular and triceps skinfold measures) was related to these two measures of inter-birth intervals, with the expectation that the ratio would shift in the direction of a larger value in response to shortened inter-birth intervals.

To adequately assess the predictions, we attempted to control for a number of potential confounding effects. Mother’s weight (both the long-term average and their weight

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3 immediately preceding the year of pregnancy resulting in the birth of the child) was included in
4 an attempt to control for maternal nutritional status. Age at first birth was included as well to
5 reflect quality of early-life development of the mother, assuming that earlier reproduction
6 would be linked to earlier menarche reflecting nutritional status during development. To
7 control for the possibility reduced energy availability to later-born offspring of mothers—due to
8 either maternal depletion (Tracer, 2003) or decreased per-capita energetic availability with
9 increasing family size—we included both parity (completed fertility of the mothers at the time
10 of the study) and birth order as a potential control variables as well.
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16 In spite of these efforts, limitations in the data precluded adequate control for a number
17 of other potentially important confounding effects. First, genetic effects were unmeasured
18 because neither subscapular nor triceps skinfold measures were available for either mothers or
19 fathers. Genetic contributions to fat-patterning are known to exist (Bouchard, 1996) and are
20 unmeasured in the current study. A lingering problem related to maternal physiology, first
21 pointed out by Hill and Hurtado (1996) was an inability to control for variation in the intrinsic
22 ability of mothers to produce offspring—given an equal amount of resources, some residual
23 variation in this ability between mothers could be present and remains unmeasured in this
24 study. Additionally, a number of post-natal environmental factors related to energetic balance,
25 including dietary saturated fat (Laitinen et. al., 1992; Law et. al., 1992) and activity levels were
26 not measured in this study. Ideally, all of these variables would have been measured while
27 attempting to establish relationships between inter-birth intervals and offspring fat patterning.
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34 ***Study Population***

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36 The Ache, a group of recently-settled hunter-gatherers residing in rural Eastern
37 Paraguay are ideal for studying the effects of maternally-mediated signals of scarcity upon
38 offspring fat patterning. Previous research suggests that the Ache suffer universal chronic
39 energetic stressors across development and throughout their lives (Hill and Hurtado, 1996).
40 While it does not appear that Ache children are born small (Hill, unpublished data), an
41 unpublished analysis on the growth and nutrition of Ache children suggested that as much as
42 2/3 of the population between two and fifteen years of age are stunted in stature growth
43 (Baker, unpublished data). Unfortunately, low resource availability and heavy work-loads
44 characterize their lifestyle (Hill and Hurtado, 1996), suggesting that research that might
45 potentially be confounded by a greater access to resources will be successfully conducted
46 there. An additional benefit for an evolutionary and ecological study such as this is the fact that
47 the Ache are historically hunter-gathers who only settled into sedentary life within the past
48 thirty-five years, and who still depend upon foraging for a significant portion of their livelihood.
49 This will allow us to assess these relationships within a context more similar to the environment
50 in which humans evolved, perhaps allowing us to gain greater insight into the nature of
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3 physiological adaptation in settings not as affected by modern technology and healthcare as
4 our own.
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7 ***Data Collection and Analysis***

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9 We collected anthropometric measurements for forty-four children in three Ache
10 communities in Eastern Paraguay during July and August, 2003. All measurements were
11 collected by a single data collector (Baker) with significant experience in anthropometry. Due
12 to time constraints introduced by our need to provide medical care to a number of seriously
13 sick members of each community, measurements were taken on the right side only and
14 repeated measures and precision assessments were not performed. Data was collected on pre-
15 formed data collection sheets by an assistant data collector to avoid recollection bias in the
16 short period of time between measurement and recording of the data. In each community, we
17 attempted to gather a universal sample of children ages five to fifteen years. These data were
18 then combined with reproductive data from the Ache Demographic Database, and with
19 maternal anthropometric data from the Ache Anthropometric Database, both provided by Hill
20 and Hurtado. The inter-birth intervals (both short and long-term) of the sample mothers
21 appeared very similar to those of Ache mothers in general, averaging 31 months for the
22 “average” inter-birth interval and 34 months for the preceding interval.
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31 These data were analyzed using standard regression methodologies. This involved
32 regressing the subscapular/triceps skinfold ratio, as well as the individual triceps and
33 subscapular skinfold measurements, against the immediately preceding inter-birth interval and
34 the mother’s average life-long inter-birth interval at the time of observation. Controls for
35 maternal condition (birth order, parity, mother’s body weight) and other potential confounders
36 (age, sex) were included in the analysis. Backward selection was implemented in which an
37 original model was fit including all predictor variables, non-informative predictors were
38 eliminated, one at a time, and the model re-fit (Neter et. al., 2001). While many
39 epidemiologists recommend inclusion of all relevant “known” effects on the outcome to be
40 measured in a study (Aschengrau and Seage, 2003), there are potential drawbacks to such a
41 strategy. The principal drawback to this approach is that many of these variables may be non-
42 informative (in the statistical sense—they do not improve model fit, diagnostic measures, or
43 the “r-squared” value) in the particular study setting utilized in this study. If so, these non-
44 informative predictors can bias the regression parameters (Greene, 2003), indicating a sacrifice
45 would be made in the study’s ability to accurately assess the relationship to be measured.
46 Since a power calculation suggested only limited power to detect real effects of the
47 independent variable ($\beta = 0.21937$), we decided to eliminate these non-informative
48 variables in this preliminary study in favor of maximizing our ability to accurately estimate the
49 parameters in the regression model. Thus, final models reported here included only those
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3 variables shown to have an informative value. The final models were assessed graphically for
4 multicollinearity in the predictors (using correlation plots between the predictors) as well as
5 formally using Variance Inflation Factors (Neter et. al., 2001). Overall model bias introduced by
6 left-out variable error (Mauro, 1990) was assessed using the Mallow's C-p statistic. Overall
7 diagnostics of model fit include residual by fit plots and normal plots of the residuals (Neter et.
8 al., 2001). All diagnostics suggested appropriate fit of the final models, with little indication of
9 left-out variable error.
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14 III. Results

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17 The analyses suggested no relationship between the subscapular/triceps skinfold ratio
18 with the interval preceding the birth of the study subject ($F = 0.32$, p -value = 0.82935). The
19 analysis suggested significant relationships between the mother's average inter-birth interval
20 and both the subscapular/triceps skinfold ratio ($\beta = 0.14047$, $t = 2.68727$, p -value = 0.0109)
21 and the triceps skinfold itself ($\beta = -2.34349$, $t = -2.18567$, p -value = 0.0356); however, the
22 direction of the observed effect was in the opposite direction from that originally predicted to
23 characterize a relationship between the inter-birth interval and a signal of scarcity to the
24 offspring. No effect of inter-birth intervals (either preceding or average) was observed in
25 conjunction with the subscapular skinfold ($F = 0.62$, p -value = 0.6095). As the average inter-
26 birth intervals of Ache mothers increased, so did the subscapular/triceps skinfold ratio (Table 1,
27 Figure 3). This was due to a reduction in the triceps skinfold as the mother's average inter-birth
28 interval increased (Table 2, Figure 4). The final model relating the average inter-birth interval to
29 the subscapular/triceps skinfold ratio accounted for 39.78% of the variance in the ratio ($F =$
30 9.37 , p -value = 0.0001). The final model relating average inter-birth intervals to the triceps
31 skinfold accounted for 31.26% ($F = 6.76$, p -value = 0.001) of the variation in the triceps skinfold.
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39 The model predicting the subscapular/triceps skinfold ratio also included mother's
40 weight and the offspring's birth order. As birth-order increased, so did the ratio ($\beta =$
41 0.132971 , $t = 4.41$, p -value = 0.001), perhaps suggesting a relationship between offspring
42 centralized adiposity and potential maternal depletion. As mother's average weight increased,
43 the subscapular/triceps skinfold ratio actually decreased ($\beta = -0.017424$, $t = -3.05$, p -value =
44 0.0043), suggesting that increased mother's average weight—perhaps reflecting either
45 increased nutritional status, baseline physiological capacities, early-life environment, or all
46 three—could be important in understanding mother/offspring relationships as well. No
47 interaction effect was observed, however, suggesting a separate role for this from that
48 suggested for the inter-birth interval itself. The model predicting reduced triceps skinfold as
49 the driving force in the increase of the ratio included the same two variables, birth order ($\beta =$
50 -2.17703 , $t = -3.51897$, p -value = 0.0012), and mother's average weight ($\beta = 0.34208$, $t =$
51 2.91923 , p -value = 0.0061). Figures 2 and 3 graphically represent the two results: increasing
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3 subscapular/triceps skinfold and a decreasing triceps skinfold as average inter-birth intervals
4 increase.
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9 10 **IV. Discussion**

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12 At first blush, the results of the study seem to indicate that neither the preceding or
13 average inter-birth intervals are related to offspring adiposity in the way envisioned by this
14 study. We think, however, that when properly evaluated the results suggest another
15 conclusion. If we assume that offspring consistently respond to in utero energetic scarcity by
16 becoming more centrally adipose, then the observed results suggest that maternal endogenous
17 rules for prioritizing the allocation of resources—presumably reflected in the average inter-
18 birth interval—are directly related to offspring developmental plasticity in the form of
19 increasingly centralized adiposity. The reflection of this in the subscapular/triceps skinfold ratio
20 is due to decreases in the triceps skinfold, suggesting greater emphasis upon storage in the
21 abdomen. While we anticipated that shortened inter-birth intervals would be related to
22 increasing adiposity in the offspring, the observation that extended inter-birth intervals are
23 related to centralized fatness leads directly to the conclusion that maternal endogenous
24 prioritization is potentially responsible for signaling offspring of environmental scarcity. This
25 may be true because of the nature of a very general decision model underlying maternal
26 reproductive decisions (Figure 1). At each step beyond the birth of a child, the mother decides
27 whether to reproduce or not and this clearly reflects her physiological preferences for
28 current/future reproduction (step 1 of the model in Figure 1). Once the decision to reproduce
29 has been made, however, she will also decide to what degree she allocates resources either to
30 self-maintenance or to the developing fetus. (Step 2 in the model). Given this set of
31 relationships, mothers with more conservative preferences (those who tend to prefer self-
32 maintenance in general) may be likely to reproduce less frequently as well as to allocate fewer
33 relative resources to gestating offspring. If so, then less frequent reproduction could clearly be
34 linked to signals of scarcity to offspring, resulting in developmental plasticity and observed
35 increases in centralization of adiposity. It is also true, however, that mothers may choose to
36 reproduce less frequently but to allocate an equal amount of resources to each child. If so,
37 then we might expect to see either no evidence of birth order effects or a dampened effect. In
38 this study, we observed increasing centralized adiposity with birth order, driven by decreases in
39 the triceps skinfold, that was both statistically significant and physiologically important. This
40 observation suggests that maternal resource constraints do exist, but only further tests will
41 decide whether this relationship is due to maternal depletion, or relative de-valuing of
42 reproductive effort later during reproductive life.
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While intriguing, these results are preliminary in nature. The inability within this study to control for a number of confounding effects limits the inferences that may be drawn from it. Further cross-sectional studies of this kind will only go so far in discerning the relative effects of exogenous environment and endogenous/maternal factors on shaping offspring body composition. Only further studies that are longitudinal in nature and possess the ability to control for maternal nutrition during pregnancy, variation in maternal physiological capacities and her own associated development, and a variety of post-natal environmental influences on adiposity will clearly determine whether models invoking maternal mediation of environmental cues (such as Kuzawa's intergenerational inertia model) are adequate explanations for links between in utero experiences and later offspring adiposity. Ideally, such a study would be designed with evolutionary logic in mind (Baker et al 2008), yielding specific, testable predictions that advance evolutionary theorizing about life-history and physiological variation in humans. The results of this research also suggest that the Smith-Fretwell model may be a useful framework for understanding maternal/child health and the determinants of developmental plasticity in offspring physiology, but not without modification. Relaxing assumptions about the temporally static nature of maternal decisions to reproduce or not, or how much of her available energetic resources to invest in either reproduction or self-maintenance proved to be useful in the current study. Humans are a long-lived, iteroparous species whose decisions should be expected to be dynamic, varying over time based upon current as well as anticipated conditions (Charlesworth, 1980; Levins, 1968). At the same time, they are also likely to be subject to constraints imposed by the process of canalization, in which phenotypes become progressively less flexible up to adulthood (Schmalhausen, 1949; Shlichting and Pigliucci, 1999). Ideally, a clearer understanding of how the exogenous environment, maternal reproductive decisions and resource prioritization, and offspring fat patterning relate will require extensions of both the Smith-Fretwell model and developmental plasticity theory to elucidate the role of how mother's resource allocation preferences are shaped by her own developmental experiences.

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Table 1. Results of Multiple Regression:**Subscapular/Triceps Skinfold Ratio by Mother's Average Inter-birth Interval (Years)****F = 9.37 (p = 0.0001)****R-squared = 39.78 %**

Parameter	Estimate	Standard Error	T-statistic	P-Value
Constant	1.48826	0.379484	3.92181	0.0004
Average IBI	0.140407	0.0522487	2.68727	0.0109
Birth Order	0.132971	0.0301471	4.41073	0.0001
Mother Kg	-0.017424	0.00571027	-3.05134	0.0043

Table 2. Results of Multiple Regression:**Triceps Skinfold (Millimeters) by Mother's Average Inter-birth Interval (Years)****F = 6.76 (p = 0.001)****R-squared = 31.26 %**

Parameter	Estimate	Standard Error	T-Statistic	P-Value
Constant	4.43327	7.78746	0.569283	0.5728
Average IBI	-2.34349	1.07221	-2.18567	0.0356
Birth Order	-2.17703	0.618655	-3.51897	0.0012
Mother Kg	0.34208	0.117182	2.91923	0.0061

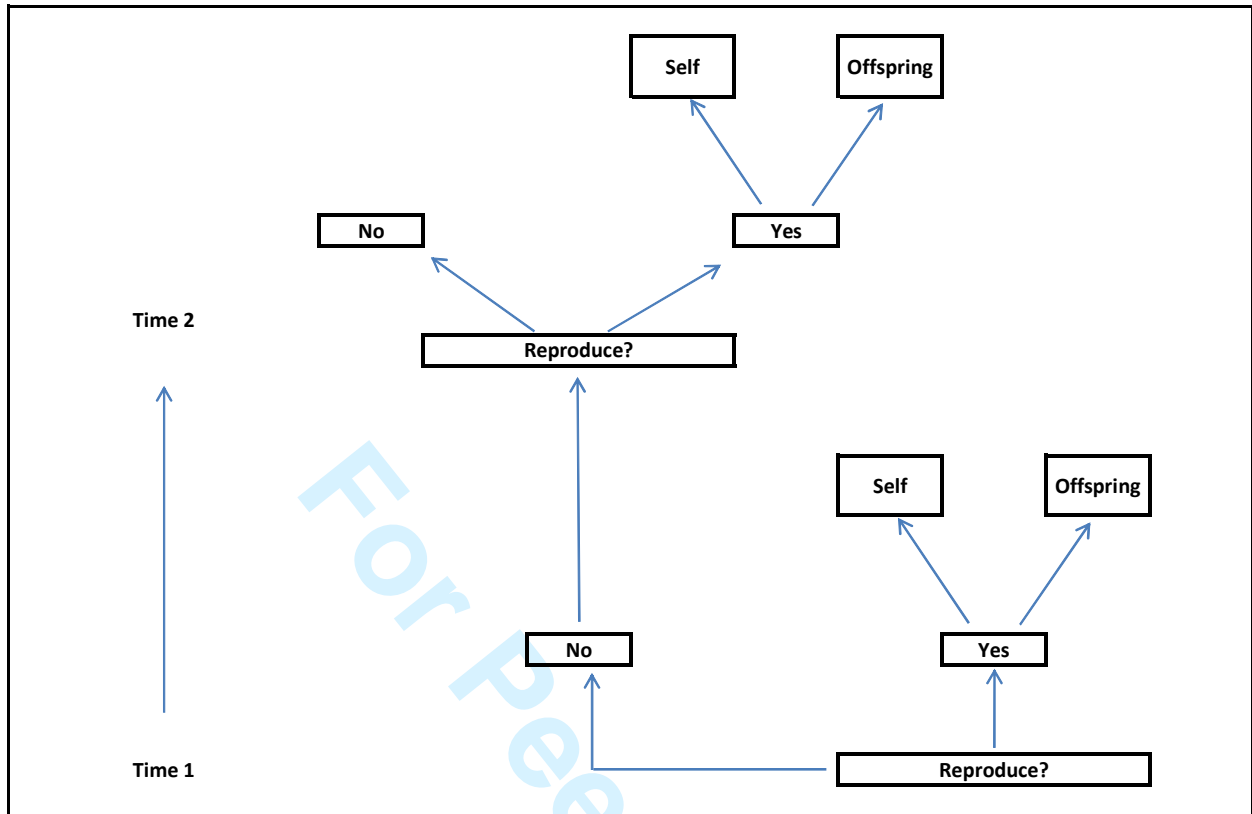


Figure 1. Maternal Reproductive Investment Decisions. At each time step, mothers must decide whether or not to reproduce, as well as how much to invest in self-maintenance versus reproduction.

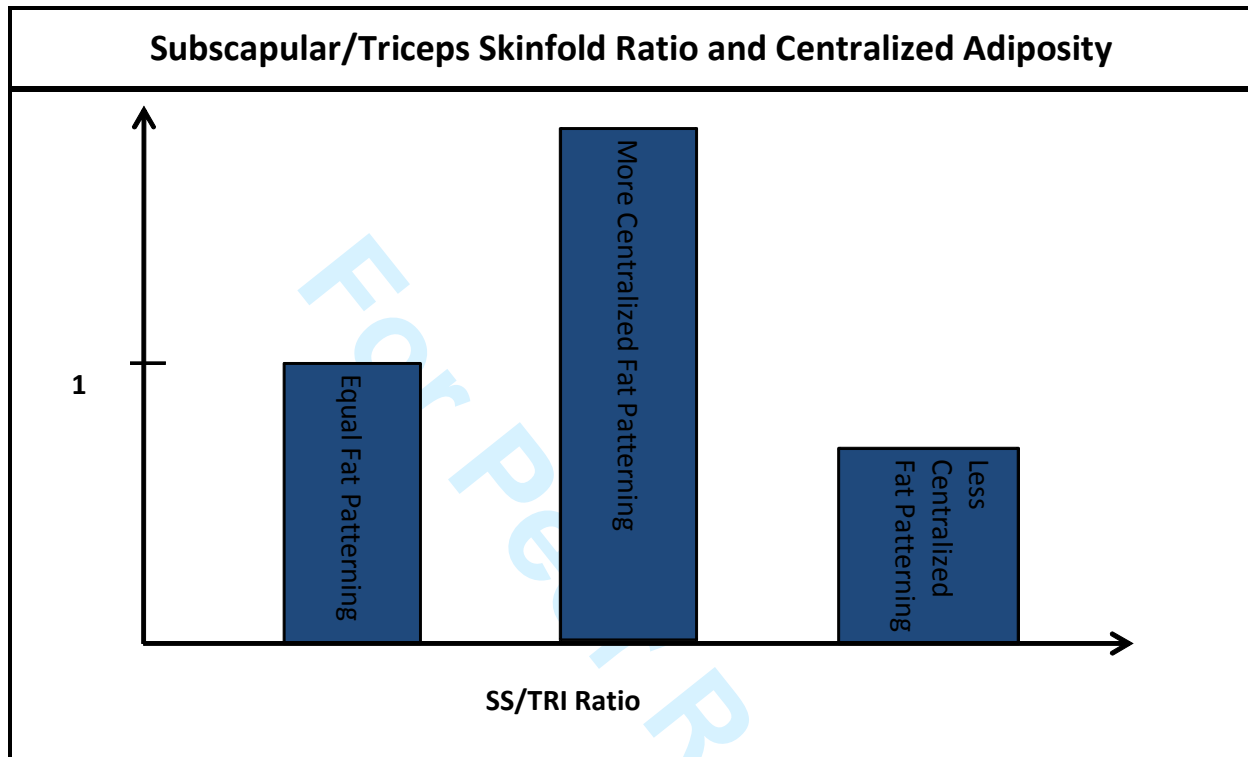


Figure 2. The ratio of the subscapular to the triceps skinfold will increase as more fat is stored in the abdomen. This may occur because the triceps skinfold is smaller, because the subscapular skinfold is larger, or—more likely—both.

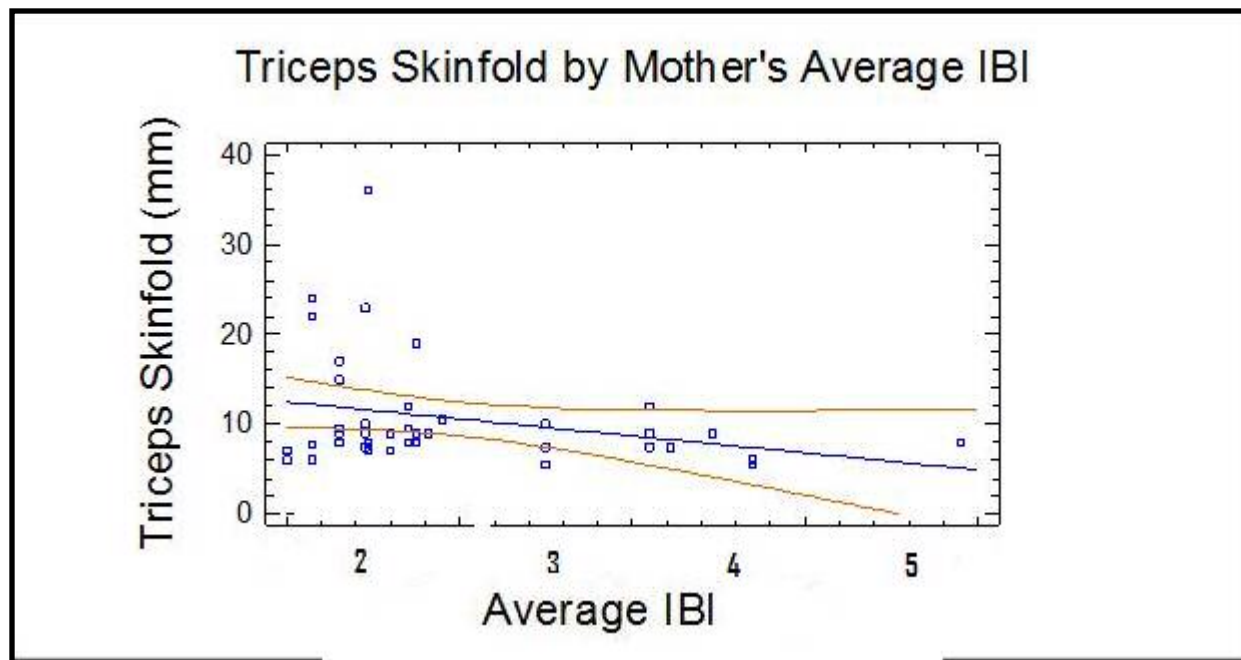


Figure 4. As the mother's average inter-birth interval increases, the triceps skinfold decreases.

References

- Aschengrau A, Seage G (2003) Essentials of Epidemiology in Public Health. 2nd Edition. New York: Barlett and Jones.
- Baker J, Hurtado AM, Pearson OM, Jones T (2008). Evolutionary Medicine and Obesity: Developmental Adaptive Responses in Human Body Composition. In: Evolutionary Medicine and Health: New Perspectives. Wenda Trevathan, James McKenna, E.O. Smith, Edrs. New York: Oxford. Pp.
- Baker J (2007) *The Evolutionary Ecology of Thrifty Metabolism: Early-Life Signals of Environmental Instability and Later Body Composition in Humans*. Dissertation Manuscript. University of New Mexico.
- Bjorntorp, P., & Eden, S. 1996. Hormonal Influences on Body Composition. In: Human Body Composition. Roche AF & Lohman SB, Edrs. Champaign: Human Kinetics. 424 p.
- Ceesay, S.M., Prentice, A.M., Cole, T.J., Foord, F., Weaver, L.T., Poskitt, E.M., et al. (1997). Effects on Birth Weight and Perinatal Mortality of Maternal Dietary Supplements in Rural Gambia: 5 Year Randomised Control Trial. *British Medical Journal*, 315:786-790.
- Charlesworth B (1980) Evolution in Age-Structured Populations. Oxford: Oxford UP.
- Conde-Agudelo A, Rosas-Bermudez A, Kafury-Goeta AC (2006) Birth Spacing and the Risk of Adverse Perinatal Outcomes: A Meta-Analysis. *JAMA*. 295(15):1809-1823.
- Curio, E. (1973). Towards a Methodology of Teleonomy. *Experientia*, 29, 1045-1059.
- Ellison, P (2003) Energetics and Reproductive Effort. *Am J of Hum Biol*. 15(3):342-351.
- Gluckman, P.D. & Hanson, M.A. 2004. The Developmental Origins of the Metabolic Syndrome. *Trends in Endocrinology and Metabolism*. 15(4): 183-187.

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3 Khan KS, Chien PF, Khan NB (1998) Nutritional Stress and Reproduction: A Cohort Study Over Two
4 Consecutive Pregnancies. *Acta Obstet Gynecol Scand.* 77(4):395-401.
5
6

7
8
9 Kuzawa, CW. 2005. Fetal Origins of Developmental Plasticity: Are Fetal Cues Reliable Predictors of
10 Future Nutritional Environments? *Am J of Hum Biol.* 17:5-21.
11
12

13
14 Kuzawa, CW (2008) The Developmental Origins of Adult Health: Intergenerational Inertia in Adaptation
15 and Disease. In: *Evolutionary Medicine and Health: New Perspectives.* Wenda Trevathan, James
16 McKenna, and E.O. Smith, Edrs. Oxford University Press.
17
18

19
20
21 Laitinen, J., Pietilainen, K., Wadsworth, M., Sovio, U., & Jarvelin, M.R. (2004) Predictors of Abdominal
22 Obesity Among 31-year-old Men and Women Born in Northern Finland in 1966. *European Journal of*
23 *Clinical Nutrition.* 58:180-190.
24
25
26
27

28
29
30 Law, C.M., Barker, D.J., Osmond, C., Fall, C.H., & Simmonds, S.J. (1992). Early Growth and Abdominal
31 Fatness in Adult Life. *Journal of Epidemiology and Community Health,* 46(3), 184-186.
32
33

34
35
36 Levins, R. 1968. *Evolution in Changing Environments: Some Theoretical Explorations.* Princeton:
37 Princeton University Press.
38
39

40
41 Neter J, Kutner MH, Nachtsheim CJ, Wasserman W. 2001. McGraw-Hill. Boston.
42

43
44 Williams, G.C. (1966). *Adaptation and Natural Selection.* New York: Sinauer.
45

46
47 Price, KC and Coe, CL (2000) Maternal Constraint on Fetal Growth Patterns in the Rhesus Monkey
48 (*Macaca mulatta*): the intergenerational link between mothers and daughters. *Human Reproduction.*
49 15(2):452-457.
50
51

52
53
54 Schlichting, C.D., & Pigliucci, M. (1998). *Phenotypic Evolution: A Reaction Norm Perspective.* New York:
55 Sinauer.
56
57
58
59
60

1
2
3 Schmalhausen, I.I. (1949) Factors of Evolution. Philadelphia: Blackstone.
4
5

6 Smith, CC and Fretwell, SD (1974) The Optimal Balance Between Size and Number of Offspring. The
7
8 American Naturalist. 108:499-506.
9
10

11 West-Eberhard, MJ (2003) Developmental Plasticity and Evolution. New York: Oxford University Press.
12
13

14 Zhu BP, Rolfs RT, Nangle BE, Horan JM (1999) Effect of the Interval Between Pregnancies on Perinatal
15
16 Outcomes. N Engl J Med. 340(8):589-94.
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
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