

Kin influences on fertility: A theoretical framework tested with a review of the literature

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Abstract

Far from being an asocial process, reproductive decision-making in humans is affected by family and other social networks. However, the direction and strength of kin effects is inconsistent across studies. Explaining this variation requires a better understanding of what various fertility outcomes mean functionally and of each individual's strategic interests. A previous review demonstrated that kin have a beneficial impact on one aspect of childbearing: the survival of a woman's children. The influence of family on fertility is a little more complicated to study, however, since decisions regarding age at first birth, the pace of reproduction, and total number of births can be made independently of one another. Further complicating matters, woman and her kin do not always have the same strategic considerations, so that kin may hinder, rather than help, fertility. In this paper we develop a framework for comparing various accounts of why kin affect fertility. We test these possibilities by compiling and analyzing a database of kin effects on fertility from the literature. Focusing on how parents and in-laws might affect different fertility outcomes, we find that parents are more likely than in-laws to have anti-natal effects on a woman's total fertility, and age at first birth, but not on inter-birth intervals.

1. Introduction

Kin are known to affect reproductive outcomes in humans, and in nearly all species that behavioural ecologists have studied. From an evolutionary perspective this is not surprising given the inclusive fitness benefits they stand to gain from doing so in well-mixed populations. However, there are various mechanisms by which kin may exert their influence, and socio-ecological factors that moderate these effects. Behavioural ecologists are usually proudly agnostic about mechanisms, arguing that their predictions are only about ultimate outcomes such as fitness. However, given that researchers often can only collect data that are proxies for fitness, and given the prevalence of societies in evolutionary disequilibria where individuals are not fitness-maximizing, being explicit about the mechanisms involved can lead to dramatically different middle range predictions. Failure to acknowledge the variety of potential mechanisms involved, and the contributions of socio-ecological variation may explain why debate about kin effects on reproductive outcome persists.

We divide the evolutionary proposals into two kinds of mechanisms; ones whereby kin *were selected* to promote each others' fitness, and mechanisms for which aligned interests are irrelevant, and situations where kin's interests are less aligned. In the first group we include; 1) kin providing direct help, 2) kin buffering a woman from extrinsic mortality risks, and 3) kin providing cultural information. In the second we include 4) kin as a cue to environmental context. We discuss these mechanisms in section 2. In section 3 we consider the interaction of these proposals with the fertility metric being studied.

In section 4 we consider contexts that may moderate kin effects. We included situations where their interests are less aligned; when 5) kin compete for resources, and 6) kin are affinal rather than consanguineal, in addition to situations where it is clearer that psychological mechanisms regarding reproductive decision-making are misfiring as is the case in 7) post-demographic transition settings. We stress that these perspectives are not mutually exclusive, as the effect of kin on fertility is likely to be context dependent, and natural selection is a cumulative process that may have built on successive adaptations guiding kin-interactions.

We then test these accounts in sections 5 and 6 by considering the empirical literature across the social sciences regarding kin effects on reproduction. There have been few attempts to systematically review this literature, at least with this broad scope. In part this is because synthesizing such a varied literature is conceptually difficult (see Sear & Coall, 2011 for a notable example), and in part because no simple theoretical account is likely to explain all the variation that we see in kin effects across studies. To make matters more difficult, most studies were not designed to test between the theoretical accounts.

We focus on several possible sources of variation in the literature that may help us disambiguate between theoretical accounts and integrate seemingly contradictory findings: 1) the fertility metric used 2) the relationship of the kin member to the woman and 3) how kin presence is operationalised.

2. Comparing mechanisms

2.1. Kin as direct help

Most of the evolutionary literature on how kin affect fitness focuses on the extent to which related individuals provide direct help – usually in the form of alloparenting or food provisioning. The fact that humans tend to raise multiple dependent young at a time has led some to argue that humans have undergone particularly strong natural selection for kin and non-kin cooperation in reproduction (Hill & Hurtado, 2009; Hrdy, 2009; Sear & Coall, 2011), or for biparental care (Geary, 2000; Hewlett, 1992).

There is debate about the extent to which this makes humans cooperative breeders given that the term is usually reserved for species where individuals forgo reproduction for the benefit of the cooperative unit (Clutton-Brock, 2002; Hrdy, 2009; Kim, Coxworth, & Hawkes, 2012; Strassmann, 2011). By this account, cooperative kin units would out-compete non-cooperative kin units. This implies that, on average, individuals with more kin, and thus presumably more kin help, would have higher reproductive success than those with fewer kin, even though some individuals would pay temporary costs for the sake of the cooperative kin unit.

However, testing this at the individual level can run into difficulties if some individuals are more likely to pay fitness costs in the cooperative venture. For example, in some cooperatively breeding primate species older children stay around to help alloparent their younger siblings (Kleiman, 1979), such that parental presence may actually reduce an individual's fitness, even though the cooperative system is being selected for. Similar intergenerational conflicts of interest have been proposed in humans (Cant & Johnstone, 2008; Hill & Hurtado, 2009; Lahdenperä, Gillespie, Lummaa, Russell, & Sorci, 2012; Mace & Alvergne, 2012) and children have been suggested as helpers at the nest in various contexts where they provide alloparental care for their siblings (Crognier, Villena, & Vargas, 2002; Kramer, 2005; Turke, 1988). For this reason, we separate out the predictions for this account in Table 1 into the effects of providing versus receiving aid. This is important to take into account lest particular samples over-represent helpers rather than receivers, for example.

Bearing this caveat in mind, this theoretical framework suggests the importance of kin provisioning of direct help as a mechanism by which kin improve each other's fitness. If the gains of kin cooperation include more direct help – including, but not limited to alloparental aid – kin presence should allow an individual to attain higher fitness on average. The predictions would be broadly similar whether kin invest in a reproductive individual's embodied capital or in their children directly.

2.2 Kin as extrinsic mortality buffers

It is worth considering kin help that buffers an individual from extrinsic mortality risks separately as it can have different consequences for life history strategies (Chisholm, 1993; Quinlan, 2007) even though this account also predicts positive effects of kin on reproductive success. For example, if family members reduce a woman's chances of dying from causes over which she has no control, she can afford to delay reproduction and invest in her embodied capital, assuming this would payout in terms of her long-term fitness. Note, these predictions are only straightforward if the woman in this scenario cannot

directly affect her own mortality risk through investments in her own embodied capital. In other words the mortality risks should be extrinsic for the recipient, even though others in her kin network may be able to affect them.

In practice, it is hard to imagine such mortality sources that are completely random with respect to one's own decisions. For example, while pathogens are often considered one such source of extrinsic mortality (Cervellati, Sunde, & Valmori, 2012; Quinlan, 2007), an individual might experience long-term fitness benefits in such a context from energetic investments in their own immune system even if it means delaying reproduction (Christe, Glaizot, Strepparava, Devevey, & Fumagalli, 2012; Norris, 2000). Consistent with risks having both extrinsic and intrinsic components, Quinlan has also shown peak investment in children at intermediate levels of pathogen loads (2007). Of course, the degree to which mortality risks are extrinsic versus within the control of a developing individual or her kin can be modelled as a continuous function. However, the problem for the empirical enterprise when risks are not purely extrinsic is that predictions will depend on the shape of the functions relating fitness to investments in reducing partially intrinsic risks. These curves are also likely to be age-specific. Unfortunately, evolutionary anthropologists seldom have data that speak to the exact nature of the relationship or fail to incorporate the relevant epidemiological data into our theorizing (e.g. Li, Daling, & Emanuel, 2003; Pelletier, 1993).

Table 1 considers predictions for the simplest scenarios where kin can affect a reproductive age individual's or their children's mortality risks in ways that the individual themselves cannot. This might be the case if donors are at different life stages than recipients, or if there are efficiencies of scale to cooperation. An example of the latter might be the ease with which several individuals may ward off predators, while an individual, or one with an infant, could not. We consider kin as buffers to adults' and infants' mortality separately as they make different predictions for different life history events (Charnov & Schaffer, 1973). Additionally, people are subject to different mortality risks through the life course.

2.3 Kin as sources of cultural information

Humans acquire much of their behavioural repertoire by learning and adopting cultural norms. Kin may exert influence on a woman's reproductive behaviour via this pathway, by transmitting information about reproductive norms. While social learning mechanisms often leave individuals vulnerable to acquiring maladaptive behaviours, gene-culture co-evolutionary accounts focus on the adaptive benefits of biases for attending to local statistical and moral norms (Boyd & Richerson, 1985; Chudek & Henrich, 2011; Feldman & Laland, 1996; Whiten, Hinde, Laland, & Stringer, 2011).

Cultural evolutionary models have demonstrated that individuals can gain fitness benefits by copying more common behaviours, and the behaviour of prestigious others (Enquist, Eriksson, & Ghirlanda, 2007; Henrich & McElreath, 2003; Perreault, Moya, & Boyd, 2012; Richerson & Boyd, 2005). Given that optimal reproductive decisions for a local socio-ecology are seldom apparent or amenable to much individual learning, they are exactly the kind of traits about which it is useful to rely on social learning (Boyd & Richerson, 1995; Laland, 2004) – e.g. when to start reproducing, how long to breastfeed, whether to adopt post-partum sex restrictions, whether to commit infanticide. The cross-cultural variation in various reproductive outcomes attests to the likely different optimal strategies in different socio-ecological settings (Hewlett, 1991).

This means that reproductive aged individuals and their kin should have psychological biases to conform to prevalent reproductive behaviours, and the reproductive behaviour of high status individuals. This mechanism suggests that kin would be *norm promoters*. As such, kin may help a woman acquire information about cultural norms, especially if they have more or better access to information. In case of conformist biases kin would help a woman acquire statistically prevalent reproductive decisions, while their influence in the case of prestige biases would promote whatever reproductive behaviour is high status. This dynamic could produce context-specific effects of kin depending on locally appropriate norms, even though these may be maladaptive at times (Dawkins, 1976; Richerson & Boyd, 2005).

Variations of this account can also predict that kin, or specifically parents, would systematically promote *pro-natal norms*. First, in societies experiencing fast intergenerational changes in reproductive

norms – as is the case in transitioning contexts – parents and in-laws are likely to have more pro-natal norms, than their offspring. As such, they may exert a pro-natal influence. Second, insofar as there is within-population variation in fertility preferences, parents will be a self-selected group of people with more pro-natal preferences than the population average. Therefore, their social messages to their children are likely to be pro-natal. Third, Newson et. al. propose that pro-natal messages from kin result from the inclusive fitness benefits that kin gain from encouraging a woman’s reproductive success (2007; 2005). They argue that women would have evolved to pay attention to norms in social groups where a greater proportion of individuals were kin who promoted fitness-enhancing norms. A mismatch between such past environments and current social networks full of non-kin results in the adoption of non fitness-maximizing norms (Newson & Richerson, 2009). Various cultural evolutionary models have shown that increased reliance on horizontal or oblique transmission – that is learning from non-parental sources – can lead to reproductive behaviours that would not have been favoured by natural selection, such as those associated with the demographic transition (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981).

A slightly different mechanism whereby kin may promote *pro kin-group norms* need not result in pro-natal effects at the individual level. By this account, groups (potentially of kin) with coordinated norms regarding resource allocation for reproduction would have been selected for, along with institutions that penalized people who violated these norms (Newson et al., 2007). We term these moral norms since they rely on 3rd party intervention (e.g. ostracism or punishment) to stabilize them. This account suggests another reason why individuals might be designed to care about local norms, although its predictions are not confined to selection at the level of the kin group (Chudek & Henrich, 2011; Henrich, 2004). While coordinated equilibria with higher reproductive success would be selected for, the need for inducements such as punishment or ostracism in such cases would imply that at least some individuals are being coerced into inclusive fitness losses for the benefit of the kin (or larger) group. Like cooperative breeding, this is another theory that is better suited to predictions at the group level than at the individual level, but generally kin groups with cultural norms that improved reproductive efficiency would be selected for.

Generally the kin as *norm promoters* hypothesis suggests that kin should have context-specific effects depending on what is locally appropriate. These may even be anti-natal in contexts where maladaptive norms are acquired via social learning. However, the *pro-natal norms* perspectives expect kin effects to be more fitness-enhancing in general, than the *norm promoters* perspective does. Finally, if kin promote *pro-kin group norms* via ostracism and punishment this implies that individuals would be engaging in more individually fitness enhancing behaviour otherwise in the absence of kin.

2.4 Kin presence as a cue about one’s environment

A somewhat different way that kin can affect life-history strategy is by being cues to the type of environment in which one lives. In this case, the fact that kin have aligned genetic interests is incidental. For example, kin presence might be a cue to low mortality risks in one’s environment, rather than actually changing these mortality risks (Chisholm, 1993). Alternately, some authors have suggested that parental absence may be a cue to the instability of relationships, and the likelihood and importance of finding a long-term investing mate in a given environment (Belsky, Steinberg, & Draper, 1991; Thornton & Camburn, 1987). In both of these cases it is unclear why the sample of one’s nuclear family is a good cue to adult socio-ecology given what a limited sample it represents, and the availability of other demographic cues beyond the family. The empirical findings associated with these frameworks do seem robust, at least in the industrialized settings where most have been conducted, and demand cogent causal theories.

Several researchers have suggested that people develop their life history strategies in childhood (Belsky et al., 1991; Ellis, Shirtcliff, Boyce, Dearing, & Essex, 2011; Frankenhuis & Panchanathan, 2011) as they receive input about the kinds of environments in which they live. If this is true, and kin are acting as a cue to environmental condition, we might expect particularly large effects of parental absence in childhood. According to these accounts kin presence should not have an effect on reproductive success since the psychological mechanisms were designed to help individuals develop optimal reproductive

behaviour for their given circumstances or socio-ecological context. If there are systematic reasons why the kin cues during childhood do not match the individual's actual adult environment, then the mechanism might misfire resulting in decreased reproductive success. For example, if a short-term war kills off lots of parents, a child in that context may develop a fast life history strategy even if their later environment is stable and has low mortality risks. While such cases would be maladaptive, the theoretical framework relies on the assumption that on average the pace of socio-ecological or cultural change was relatively slow, such that childhood environments were somewhat predictive of adult ones.

3. Not all proxies for fitness are created equal

So far we have mostly considered what the various evolutionary accounts predict with respect to kin effects on reproductive success. However, researchers seldom have data on lifetime reproductive success and rely on other fertility measures as proxies for fitness. While most evolutionary accounts predict that humans have fitness maximizing adaptations, the relationship of a woman's age at first birth (AFB), inter-birth intervals length (IBI), total live births (TLB), to fitness are unclear. Not surprisingly, many evolutionary social scientists have focused on kin effects on child mortality rates (Sear & Mace, 2008), which have clearer consequences for an individual's fitness. All else equal, earlier ages at first birth, shorter inter-birth intervals and a higher number of total live births should also be selected for in any organism. However, such a Darwinian demon that maximizes all aspects of fitness simultaneously is a fiction as there are known tradeoffs and limits to such strategies in all organisms. The tradeoffs are especially marked in a species such as humans who have altricial offspring requiring much investment, and who have a slow life history, taking a long time to reach reproductive maturity.

The different accounts described above make different predictions about kin effects on different fertility metrics. Furthermore, various fertility metrics may be of theoretical interest in their own right. In this section we elaborate on each account's predictions with respect to 1) reproductive onset, 2) reproductive pace, and 3) reproductive output.

3.1 Reproductive onset: Age at first birth

Because humans need to acquire many skills and resources to be successful reproductive adults, investments in an individual's own growth and learning at the expense of an earlier start to reproduction may pay out in the long run (H Kaplan, Hill, Lancaster, & Hurtado, 2000). However, such a gamble would only pay off if an individual could be fairly certain that they would not die before reaching reproductive maturity (Charnov & Schaffer, 1973; Stearns, 1976). Furthermore, earlier reproduction is particularly advantageous in expanding populations (Lewontin, 1965), a feature that likely characterized much of human evolutionary history (Wells & Stock, 2007). This means that the optimal age at first birth will be some function of the likelihood of surviving to reproductive age, the advantages of being able to have a longer reproductive career, the long term reproductive benefits to extending development and the population growth rate. All of these parameters are likely to be ecologically and culturally variable.

According to the first account, if kin help each other by providing direct provisioning they should expedite an individual's reproductive onset on average. Note however, that in the case that the younger generation is helping the parental generation reproduce as helpers-at-the-nest (Kramer, 2005; Turke, 1988), parental presence may in fact increase their age at first birth, especially if they have a reproductive-aged mother and father producing full siblings (Cant & Johnstone, 2008).

Alternately, if kin are buffering a reproductive aged individual from mortality risks in a way that the individual could not do so themselves, as the second account proposes, kin presence may delay a person's age at first birth, particularly in contexts where investing in embodied capital earlier on is advantageous but trades off with reproduction. If kin's help instead buffers ego's infants from mortality risks, it is less clear why or how that should affect ego's reproductive onset without making additional assumptions. The fourth account similarly predicts that if kin presence is a cue to low extrinsic mortality risks it may indicate to a developing child and teenager that delaying age at first birth in pursuit of embodied capital is a sensible strategy. It is less clear why early kin (particularly parental) presence, as a cue to the availability of high investing partners should delay age at first birth without additional

assumptions about search time that are likely sex-specific. We do not consider this variant of the fourth account further.

The different versions of cultural transmission accounts make different predictions regarding AFB. The kin as norm promoters account suggests that kin should influence individuals to start reproducing at a normative age, or at the age that high status models do. Such kin effects would be especially likely to show up when there is a discrepancy between kin's and ego's knowledge about optimal or socially appropriate timing. Additionally, inter-generational discrepancies in reproductive norms should result in older kin having more pro-natal effects on age at first birth, as might be the case in transitional contexts. According to the more pro-natal kin cultural transmission accounts, kin presence should reduce age at first birth. Finally, if kin promote pro-kin group norms, this may either increase or decrease ages at first birth depending on how resources are best distributed among reproductive individuals in the group.

Table 1. Summary of predicted kin influences on reproductive outcomes by theoretical account.						
<i>If a hypothesis predicts that kin have a pro-natal, pro-child survival or pro- faster life history effect, it is coded as "+". If the account would predict kin are anti-natal or promote a slower life history it is coded as "-". A "." means the account does not make a clear directional prediction, while "0" denotes that it predicts no effect. Some predictions require additional assumptions referred to in the text.</i>						
	Account	Specific variant	Outcomes			
			Inclusive Fitness	Age First Birth	Inter Birth Interval	Total Live Births
Mechanism	1.Direct help	Provide help	+	-	-	-
		Receive help	+	+	+	+
	2.Extrinsic mortality buffers	Reduce teen or adult mortality	+	-	-	.
		Reduce infant mortality	+	.	.	-
	3.Cultural information	Norm promoters
		Pro-natal norms	+	+	+	+
		Pro-kin group norms	-	.	.	.
	4.Environmental Cue	Regarding mortality	0	-	-	.

3.2 Reproductive pace: Inter-birth Intervals

All else equal, a faster reproductive rate – i.e. shorter IBIs – should increase one's fitness. However, there are known costs to both the mother (King, 2003) and child (Blurton-Jones, 1987) of insufficient birth spacing. Short birth intervals can take their toll on mother and child both because of physiological and economic resource constraints. Cross-site variation in nutritional stress, benefits of prolonged breast feeding, and the burden of having multiple young infants (e.g. they inhibit mobility in more nomadic contexts) would result in different optimal birth spacing (Anderies, 1996).

According to the first account, kin provisioning should allow a woman to recover both physiologically and economically faster after a child is born. Kin can also alleviate the burden of having multiple heavily dependent offspring. In this case, kin presence should reduce IBIs. It is worth noting that

this assumes that kin are providing substitutable help for which there are diminishing returns to investment (H Kaplan, 1996; Kushnick, 2012), otherwise a woman might stand to benefit from investing more per child if there are increasing returns the more investment in the child she gets, thus lengthening her birth interval.

The second account's predictions are less clear. If kin buffer an adult woman from otherwise extrinsic mortality risks it may behave her to extend birth spacing – assuming some benefits to longer IBIs – since she is not as pressed to reproduce as soon as possible. However, if kin reduce infants' extrinsic mortality rates it is unclear that this should have any effect on a mother's IBI or breast feeding duration. For a given socio-ecology there is likely some optimal length of breast-feeding duration and the fact that some number of infants or children will die from random causes later on should not change this optimal value. Assuming that all of an individual's children will experience the same extrinsic mortality risks, the mother does not have the luxury of waiting to determine whether an infant will survive these risks in order to decide whether to invest in it or not via breastfeeding.

If kin presence is a cue to environmental extrinsic mortality rates it is more likely to be a cue to adult than infant mortality rates since adult mortality risks are seldom the same as those for infants. While there are reasons to doubt that kin presence is a particularly good indicator of mortality rates compared to other demographic cues, were this account accurate it would make similar predictions as the second account, namely prolonged IBIs in the presence of kin. Similarly, if parental absence is a cue to the low availability of long-term investing mates, it is unclear why it should affect IBI decisions any more than the actual amount of investment a woman is getting or has gotten from her partner(s).

Each of the cultural transmission accounts makes similar predictions for IBI as they do for AFB.

3.3 Reproductive output: Total fertility

Finally, more live births would seem directly beneficial to a woman's fitness, but because of tradeoffs between the number and quality of children, this metric does not necessarily translate to a greater number of reproductive offspring (Lawson & Mace, 2011; Smith & Fretwell, 1974). The greater the costs to raising a child to be a successful adult, the lower the expected optimal number of live births for a given budget. Additionally, perceptions of how much investment each child needs to become a competent adult may matter even more than actual investment needs in parents' decision-making. For example, perceptions that each child requires tertiary education, may reduce the *perceived* optimal number of children, even if these investments in quality are maladaptive and do not translate to higher fitness (H Kaplan, 1996). High extrinsic mortality rates are also likely to encourage higher fertility rates, since death that is random with respect to investments in each child mean each live birth is expected not to require a full childhood of investment. This means that there is likely to be large inter-site variation in actual or perceived optimal total fertility.

Each account's predictions for total fertility are largely the same as they are for IBI. If family provides direct aid, they should allow a person to produce more children without sacrificing child quality, resulting in a positive association between kin presence and TLB. Cultural transmission mechanisms affecting total fertility are likely to produce similar effects as those affecting AFB and IBIs, although the advent of modern contraception facilitates changing total fertility without affecting mean IBIs, for example by timing reproductive onset and cessation more precisely.

If kin buffer adult mortality risks this might prolong an individual's reproductive career without necessarily changing their optimal trade off between number and quality of children. The primary reason we might see a positive association between such kin buffering and higher total fertility is if constraints on speed of reproduction were not allowing individuals to produce their optimal number of children before dying. In essence this type of kin help would increase an individual's reproductive budget much as is the case according to the first account.

If kin cooperation has increasing returns to scale they might buffer *children* from extrinsic mortality risks in a way that a parent could not accomplish on their own. Again this should not necessarily affect the optimal trade off between quantity and quality of offspring. Some authors have argued that extrinsic risks result in diminishing returns to investments in children (Coall, Dickens, & Nettle, 2013; Quinlan, 2007), but this assumes that all investments are designed to reduce mortality

risks. However, if there are returns to embodied capital independent of these mortality risks – e.g. being a skilled forager will be valuable given that you survive predation risks in childhood – reducing these risks does not change the optimal investments in these sorts of capital. This means that for a given reproductive budget and optimal allocation of resources between quality and quantity of surviving offspring, kin presence might reduce total fertility. In other words, if a woman is more assured of her childrens' survival in the presence of kin, then she might reduce fertility, expecting that more of her children will survive. These predictions mirror those formalized in some models (Mace, 1998).

4. Socio-ecological contexts moderating kin effects

4.1 When kin compete over resources

So far we have mostly considered situations where kin have aligned reproductive interests. However, there may be socio-ecological contexts where kin are more likely to compete over resources than non-kin. We consider two scales at which this may happen; the local group scale and among siblings competing over parental resources. The latter dynamic is nested within the former population structure.

If selection happens at a local group scale (e.g., because dispersal is limited), kin are more likely to be one's direct competitors. This has been shown to limit the evolution of kin altruism (Boyd, 1982; Gardner & West, 2004). Several anthropologists have shown that kin benefits are muted in contexts with more local resource competition or among kin who are more likely to compete (i.e. patri-kin in a patrilocal context) (Borgerhoff Mulder, 2007; Strassmann & Garrard, 2011). Note, for this scale of competition the prediction is that kin altruism will be reduced in particular contexts, *not* that having kin around as competitors will be worse than having non-kin around as competitors.

Within such groups of individuals with varying relatedness there are other scales at which kin compete, for example among siblings competing over parental resources – often operationalised as the household in anthropological research. In models of such sibling competition, members of the unit are often assumed to be of equal relatedness (e.g. all full siblings) so that increasing number of kin effectively increases the amount of competition over a limited resource (Borgerhoff Mulder, 1998; Volland & Dunbar, 1995). This is in contrast to usual group level resource competition, where increasing the number of kin only marginally increases the competition over the resource, and does so to the same extent as increasing the number of non-kin in the group. Therefore at the lower level of competition over parental resources increasing the presence of kin – i.e. having more siblings – may in fact decrease an individual's reproductive success.

Even though mathematically competition at the parental level can be described as a form of local resource competition where members of the group are equally related, keeping the distinction between levels of organization helps clarify predictions about the directionality of kin effects at each level, and allows consideration of interactions between the two levels. It also resolves some seemingly contradictory results in the literature. The group-level local resource competition literature suggests that as patches become poorer per capita, altruism between philopatric kin should be reduced (Johnson et al., 2001; Silk & Brown, 2008). However, in human societies we often see that sibling competition is more detrimental among richer households as these are often the only families who have heritable wealth, such as land, that can affect inheritors' reproductive success (Borgerhoff Mulder, 2007; Gibson & Gurmu, 2011; Sear, 2008; Volland & Dunbar, 1995). In essence, limited heritable wealth can create a context of sibling competition where none existed before.

In contexts where kin are more likely to be in conflict over group level resources, they should be less altruistic towards each other. This may result in weaker pro-natal effects on age at first birth, *ibi* and total fertility, (or reduced delays to AFB in contexts where children would otherwise be helpers at the nest). However, if kin are in competition over parental resources such as dowry or bridewealth inheritance, increased kin presence (in this case number of siblings) *can* have anti-natal effects.

4.2 Contexts of sexual antagonism

Additionally, affinal kin's interests might not be completely aligned because they are not genetically related to each other, even though they are partly motivated to coordinate their reproductive efforts. For example, a woman's parents-in-law are expected to encourage their son's fitness interests more than hers. However, in contexts with lifelong monogamy, those interests should be the same since each member of the pair bond's fitness is dependent on the other's. Even in less monogamous contexts some couples' reproductive interests will conflict more than others'.

In certain socio-ecological contexts or individual partnerships with more sexual antagonism affines may behave in such a way that benefits their sons' reproductive interests at the expense of a woman's fitness. In the evolutionary literature researchers often assume that males should be more willing to reproduce in suboptimal conditions than a woman would because of asymmetric costs of reproduction (Penn & Smith, 2007). Kokko & Jennions point out the logical fallacy of such arguments that are based on sunk costs and ignore Fisherian sex ratio theory (2008). Only males that have a good chance of replacing their partner, for example because they are high status, have high genetic quality or because they live in contexts with female skewed sex ratios, should be willing to behave in such a way that is detrimental to her reproductive success. In-laws with genetic interests more in line with their son than with their daughter-in-law should have similar effects, again only when intersexual conflicts of interests would be expected.

It might be surprising then that the empirical literature often shows that in-laws have pro-natal or fitness-enhancing effects on women's reproduction, even relative to her own parents (Leonetti, Nath, Hemam, & Neill, 2005; Snopkowski & Sear, 2012). There are several possible reasons for this. First, in post-demographic transition contexts people's utility may not be tied to reproductive success. Conflicts of interests with in-laws may result in their preventing a woman from pursuing utility via educational or career opportunities that would otherwise inhibit her reproduction. Second, empirically finding that in-laws in sexually antagonistic contexts reduce fitness might be difficult if they do so by increasing the risk of maternal mortality. In such cases the sample will over-represent luckier women who have survived such risks, and incorrectly appear to show fitness-enhancing effects of affines.

In contexts of sexual antagonism, it is easier to make predictions about affines' effects on age at first birth than about other fertility metrics. A woman's in-laws should encourage a woman to reproduce as soon as possible after marriage if they are more certain that her current offspring will be related to them than her future offspring. These expectations of lower relatedness to a woman's future offspring and thus greater conflict may arise in situations with particularly high male mortality, or where divorce and remarriage rates are high. However, predictions for the effect of affines on IBIs are less clear. Uncertainty about their relatedness to a woman's offspring in the distant future might motivate affines to encourage a shorter IBI so that they get more grandchildren while their son has access to the woman. Alternately, a woman's in-laws may prefer the woman to invest more in her current child (e.g. breastfeed longer) if that child is more likely to be related to its paternal grandparents than future offspring are. The logic here parallels that of the genomic imprinting literature showing that genes inherited from the father encourage a fetus to be larger and more demanding of the mother, than the same genes inherited via the mother (Haig, 1996). It is also unclear what this account would predict in terms of affines' effects on total fertility.

4.3 Pre- versus Post- Demographic transition contexts

It is also likely that kin effects will vary as a function of timing and location of the transition. Here we highlight a couple of processes whereby the demographic transition may moderate the effects of kin on reproductive outcomes corresponding to the various mechanisms set out in section 2.

Children seem to be perceived as requiring more investment in post-demographic transition contexts (H Kaplan, 1996), thus shifting the allocation of resources towards quality rather than quantity. It is worth making clear that the fact that perceptions of need deviate so greatly from what would be necessary for fitness maximization in post-demographic transition settings suggest the importance of maladaptive culturally evolved norms. However, it is unclear that this changes the potential

reproductive benefits of direct aid from kin. On the other hand, post-demographic transition societies also tend to be ones where kin networks are more diffuse and alternate sources of direct aid are available (i.e. governmental welfare programs and a higher reliance on spouses within the nuclear family). This might simply reduce the baseline rates of kin help or actually reduce the effect of extended kin. Ultimately, making predictions about the effect of governmental and spousal aid on the effect of kin depends on how perceived payoffs relate to investments. For example, if as has been argued (H Kaplan & Gurven, 2005; H Kaplan, 1996), people expect increasing returns to investments in children in post-DT societies, kin should be motivated to invest more in children as the government or spouses invests more. Alternately, if there are diminishing returns to investments, kin effects might be muted as governments increasingly provide for children's education.

Reductions in mortality rates have often been implicated as a causal mechanism of the demographic transition (Caldwell, 1976). This suggests that in post-demographic transition societies kin have less of a role to play in buffering otherwise extrinsic mortality risks. This suggests that kin effects – whatever their directionality – should be weaker via this mechanism. However, if kin availability is being perceived as a cue to adult mortality rates there may be a mismatch between what these indicators mean in post-demographic transition environments (e.g. that kin live farther apart) and what they meant for most of human evolutionary history.

The various cultural transmission accounts make different predictions about the effects of kin in post-demographic transition settings. If kin are norm promoters we might expect them to help in a way that increases an individual's utility or status in whatever way is locally appropriate. In pre-demographic transition contexts wealth and fitness are often correlated, while they are often divorced in post-demographic transition societies where individuals are not fitness-maximizing, instead pursuing other status goals (Goodman, Koupil, & Lawson, 2012; HS Kaplan, Lancaster, Johnson, & Bock, 1995; Low, Simon, & Anderson, 2002). This suggests that kin might be more anti-natal in post-demographic transition contexts, especially when reproductive goals interfere with other status seeking behaviour. If instead kin have more pro-natal norms by virtue of intergenerational changes in reproductive norms we might expect kin to have stronger pro-natal effects in transitioning contexts. Alternately, kin may express pro-natal norms by virtue of the inclusive fitness benefits they gain from doing so (Newson et al., 2007). In this case, they should be expected to have equally strong effects in post- and pre- transition contexts. The fact that kin networks are more diffuse in post-transition contexts suggests that the base rate availability of kin might be lower leading to population-level associations between low kin availability and lower fertility (Newson & Richerson, 2009; Turke, 1989), but this does not necessarily mean that the individual-level kin effects within society should be any weaker.

5. Methods

5.1 Review inclusion criteria

In order to weight the relative likelihood of the various theoretical accounts, and the influence of the various parameters discussed above we conducted a review of the literature. In our review we included all English-language studies which have looked at the impact of kin presence on women's fertility. Articles incorporating teenaged and older females were included in the review, and we coded whether the effects were reported for a sample of women separately or jointly for a mixed sample of men and women. Most of the literature published before 2008 was recovered via a systematic review which resulted in 81 articles containing 284 effects. This was supplemented with a literature review of articles published by the middle of 2012, and additional targeted searches for the pre-2008 literature which uncovered 59 articles with 269 effects. Because of the English language restriction we have probably oversampled from Anglophone first world contexts as these account for 38.6% of the 140 articles in the review.

We attempted to maintain generous inclusion criteria with respect to how kin presence was measured. We searched both for effects of named relatives, and for articles which used more indirect means to analyse the relationship of kin presence and fertility. The former refer to studies which

correlated the presence of particular family members with fertility outcomes. These family members include parents, parents-in-law, children, and siblings. These we have termed ‘specific’ kin. The latter studies have investigated non-specific indicators of kin presence such as living with the extended family as opposed to in a nuclear family, and being raised by biological parents rather than coming from a non-intact family. When possible we extracted information about specific kin relations from these articles as well. For example, in a patrilocal setting living with an extended family largely reflects the presence of a woman’s parents-in-law in the household. We have also noted the sex of the kin when possible.

We also make the distinction between papers that operationalize kin as available versus kin as helpful or influential. We exclude the latter because finding that helpful kin or kin with pro-natal attitudes affect a target woman’s reproductive behaviour tells us nothing about whether kin more generally *are* helpful or *do* have pro-natal attitudes. For example, some papers have shown that a mother’s preference for grandchildren is positively associated with her daughter’s fertility desires (Axinn, Clarkberg, & Thornton, 1994; Bailey, Bruno, Bezerra, Queirós, & Oliveira, 2003). However, some of these same papers show that mothers overall have lower fertility preferences for their daughters than the daughters themselves have. This suggests that mothers in these scenarios might actually have anti-natal effects, although the data in such studies is insufficient to make a conclusion either way.

There are many bodies of literature which relate to the broad topic of kin and fertility which we have not included in this review. Firstly, we restrict our analysis to fertility outcomes and preferences – i.e., age at first birth (AFB), interbirth interval or rates of progression to high order births (IBI), total live births (TLB) or total live children if the former was unavailable, teen pregnancy (TP), fertility preferences and desires, and a handful of miscellaneous fertility outcomes such as probability of having given birth recently. This means that we have not included any data on the influence of kin on other reproductive behaviours, such as contraceptive use, union formation, marital births or non-marital births (a composite of union formation and fertility behaviour). We also exclude studies on the effects of a woman’s partner. Obviously, a woman needs to have a partner at some stage during the process of producing a child, but there is a substantial body of literature on reproductive decision-making within couples, and how much influence men have over their partner’s fertility decisions. This literature is also large and complex, and a separate review is needed to deal with it appropriately. Similarly, we exclude data on polygyny and fertility, though again a large literature exists on this topic – co-wives are not strictly kin to the woman, and are the result of her partner’s reproductive decisions. We also exclude the literature on the intergenerational transmission of fertility *unless* the 2nd generation woman’s number of siblings was used as a proxy for her mother’s fertility. We are interested in whether women have kin around them at the time they are deciding to start, or already, reproducing, rather than in childhood. However, much of the literature, particularly concerning teen pregnancy or age at first reproduction, seldom differentiates between the presence of kin during childhood and the teen years – when reproductive decision making is on the horizon. Therefore we include all articles using family of origin indicators. There is a small literature on changes in fertility of immigrants and their children which we exclude because of the complexity of the social contexts involved, but it is important to note that these often reveal the importance of family of origin as well as non-kin social influences in the receiving country (Booth & Kee, 2009; Massey, 1981). Finally, we exclude the handful of studies which have investigated the impact of kin on male fertility behaviour only.

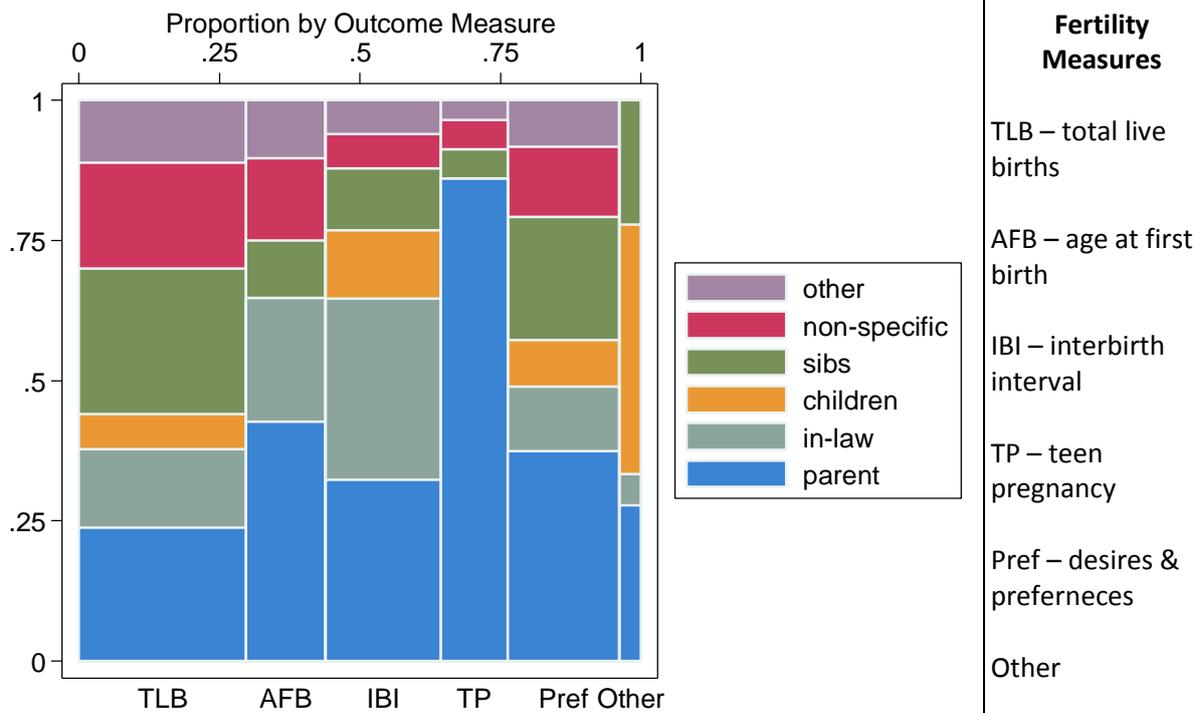
We also restrict our analysis to those studies which collected quantitative data and performed statistical analysis to demonstrate correlations between a kin measure(s) and fertility outcome(s). Qualitative studies and those which presented only descriptive data are therefore excluded. Furthermore, only published material, excluding abstracts and conference proceedings, were included.

5.2 Coding Scheme

As a result we have compiled a database of 553 kin effects from 140 articles. Of these, we could assess the direction of the effect for 520 and determine whether they are statistically significant at a two-tailed p-level of 0.05 for 517. In addition to coding effects by kin type and fertility metric (see Figure 1 for distribution of these), we coded several other features of the studies and populations to test our hypotheses. Kin presence or involvement was operationalised in a variety of ways. We coded these as;

vital status, co-residence, emotional closeness, material investment, quantity, and other miscellaneous. Co-residence was further coded as either at the household or regional (i.e., village/town/city) level. Finally, fertility context was coded as high (≥ 4 live births per woman) or low (< 4 live births per woman). For nationally representative datasets we coded the study according to the most common subsistence practice or national fertility average. See Table 2 for description of outcome and predictor variables.

Figure 1. Proportion of effects in the dataset that represent each outcome measure and each kin category. $N= 481$.



5.3 Data extraction

From each article we extracted as many kin effects as were published, even if they were not the primary target of the authors' research question. If the authors divided their sample by characteristics that were not of theoretical interest to our review we collapsed these into a single combined effect using random effects meta-analytic models when possible, or weighted averages when standard errors were not given. Several articles also offered various analyses to estimate the effect of interest. In these cases we extracted the effects from models with the most covariates, under the assumption that these resulted in the best estimates of the effect of kin presence per se.

When kin presence was operationalised as a series of dummy codes we often had to make judgements about the relevant categories for comparison. For the literature on kin presence at and before adolescence we took "both parents present" to be the relevant reference category since it was the normative and more common arrangement – compared to "both parents absent," for example, which we ignored. On the other hand, for the literature looking at kin presence in adulthood we took "no kin present" as the reference category when possible, since this was the most common comparison available. When co-residence and vital status categories were conflated in dummy codes, we compared "kin alive but not co-residing" categories to "kin dead" to gauge the effect of vital status, and to "kin co-residing" to extract the effect of "co-residence"

5.4 Analysis

In this paper we use vote counting methods to describe the effects in the dataset. Because the full dataset consists of a diverse array of fertility outcomes, study structures, and kin predictors, this allows us to consider patterns most broadly. This method involves tallying the direction of the kin effects, i.e. either as pro-or anti-natal. We have done this in two ways; first by counting the direction of the effect regardless of statistical significance (i.e. $p=1$), and by only tallying the direction of effects reported as significant at the $p=0.05$ level while coding the other effects as not significant. One concern with the latter method is that real effects from small samples – which in our case are more likely to come from pre-demographic transition contexts – might not be reported as significant, while very small effects from large national surveys – usually from post-demographic transition contexts – will be counted as significant. The directionality of the effects overall, however, should not be thus biased. We can also compare the results of vote-counting using these two counting procedures to test for possible biases in the literature. For example, if researchers are motivated to publish only pro-natal kin effects, we might expect to see a greater proportion of such effects using significance coding. This excess would represent spurious, but easier to publish, associations that might result from statistical fishing expeditions. However, given the systematic differences between studies of different sample sizes we must be careful in our interpretation were we to find such discrepancies. While there are several reasons to be wary of vote-counting, and it is statistically less powerful than other meta-analytic techniques (Gurevitch & Hedges 1999), we believe it is a useful first step in assessing the state of this diverse literature. Furthermore several studies have shown the relative similarity of results using vote-counting and more complex meta-analytic techniques (Cwikel, Behar, & Rabson-Hare, 2000; Strassmann & Garrard, 2011).

Similarly, while we collected data on kin effects on fertility desires and miscellaneous other fertility metrics these are excluded from the detailed analysis because of their heterogeneity. When testing for differential effects of in-laws we also exclude the literature on teen pregnancies as affines can seldom affect teen pregnancies. This means that we cannot compare their effects on this outcome to those of parents. The bulk of our analyses will focus on vital status and co-residence indicators as they were most common accounting for 61% of effects in the database, and most consistently operationalized.

a) Kin effects			b) Predictors		
	<i>Freq.</i>	<i>%</i>		<i>Freq.</i>	<i>%</i>
<i>Effect Direction</i>			<i>Outcome Measure</i>		
No effect	4	0.84	<i>Age first birth</i>	69	14.35
Anti-natal	199	41.54	<i>Inter birth interval</i>	100	20.79
Pro-natal	259	54.07	<i>Total births</i>	141	29.31
Don't know	17	3.55	<i>Teen pregnancy</i>	57	11.85
	479		<i>Decision/ preference</i>	96	19.96
<i>Effect Direction (if significant)</i>			<i>Other</i>	18	3.74
Anti-natal	83	17.33		481	
Pro-natal	131	27.35	<i>Kin Type</i>		
Not significant (ns)	246	51.36	<i>Non-specific</i>	60	12.47
Don't know (dk)	19	3.97	<i>Parent</i>	184	38.25
	479		<i>in-law</i>	79	16.42
<i>Effect Direction (ns & dk subset)</i>			<i>Kids</i>	36	7.48
0	4	1.51	<i>siblings</i>	83	17.26
anti	116	43.77	<i>other</i>	39	8.11
pro	128	48.30		481	
Don't know	17	6.42	<i>Kin Operationalisation</i>		
	265		<i>vital</i>	105	21.83
			<i>presence - house</i>	187	38.96
			<i>presence - village</i>	27	5.63
			<i>emotional</i>	26	5.41
			<i>number</i>	124	25.78
			<i>other</i>	12	2.49
				481	
			<i>Fertility context</i>		
			<i>high 4+</i>	252	52.50
			<i>low 0-3</i>	228	47.50
				480	

6. Results

6.1 Description of full database

Table 3 shows that the articles in our dataset come from across the social sciences, although the plurality are from demography. Evolutionary approaches the question of kin presence are arguably over-represented in this literature. However, both of these effects might reflect the author's biases and their relative familiarity with the literature from these domains. The large samples used for estimating the effects in our database (median 1000, IQR=[360-3453]) likely reflect the demographic bias of the literature.

Table 3. Primary author's discipline.		
	Freq.	Percent
Subject		
Anthropology	20	16.00
Demography	35	28.00
Economics	14	11.20
Health	11	8.80
Natural science	8	6.40
Other social science	16	12.80
Psychology	3	2.40
sociology	18	14.40
	125	
Evolutionary		
no	91	72.22
yes	35	27.78
	126	

A preliminary look at the outcome and independent variables of interest shows that the majority of effects in our dataset are not significant. This makes it particularly important to compare the results of both the $p < 0.5$ and the $p < .05$ coding schemes to determine if certain kinds of results are more likely to be published when significant, or if they show a particular direction. Thus we also show the $p < 0.5$ direction code of the subset of effects that are either not significant or for which significance could not be determined.

Regarding predictors, the plurality of the effects we extracted measured total fertility, followed in frequency by metrics of reproductive onset (combining teen pregnancies and age at first birth papers). The inter-birth interval effects are third most common and include event history studies of progression to subsequent births as well as continuous outcomes such as mean birth intervals. The most common kind of specific kin investigated are parents, and while effects of siblings appear rather numerous in our dataset these include several studies that used number of siblings as controls in their models and a substantial part of the intergenerational transmission of fertility literature. The most common operationalization of kin presence involved measuring co-residence in a household, which admittedly varies in its social significance by site and participant's life stage. Number of kin is quite common, particularly as a way of operationalizing sibling presence. The societies in the sample are about equally distributed between high and low fertility settings. For the vast majority of effects ($n=384$) we were able to code them with respect to effects on women's fertility .

Figure 1 shows that the types of reproductive outcomes measured are not the same for all kin types. Relatively more studies are conducted on reproductive onset when the kin are parents, than when any other kin are investigated. Table 4 similarly shows that different kin are operationalised in different ways. This suggests caution when interpreting specific kin effects without considering the articles other methodological choices.

<i>Kin Type</i>	<i>Kin operationalization</i>					<i>Total</i>
	<i>vital</i>	<i>co-resident</i>	<i>emotional</i>	<i>number</i>	<i>other</i>	
<i>Non-specific</i>	0	37	14	6	1	58
	0.00	63.79	24.14	10.34	1.72	100.00
<i>parent</i>	67	98	10	8	1	184
	36.41	53.26	5.43	4.35	0.54	100.00
<i>in-law</i>	17	59	1	2	0	79
	21.52	74.68	1.27	2.53	0.00	100.00
<i>kids</i>	6	4	0	16	10	36
	16.67	11.11	0.00	44.44	27.78	100.00
<i>siblings</i>	9	2	1	71	0	83
	10.84	2.41	1.20	85.54	0.00	100.00
<i>other</i>	6	12	0	21	0	39
	15.38	30.77	0.00	53.85	0.00	100.00
<i>Total</i>	105	212	26	124	12	479
	21.92	44.26	5.43	25.89	2.51	100.00

6.2 Direction of effect by kin type

Figure 2 shows the proportion of effects that are pro-natal as opposed to anti-natal, both considering all effects, and only significant effects. Figure 2a shows these patterns for all fertility outcomes (AFB, IBI, TLB, teen pregnancy, preferences and miscellaneous others). The similar patterns across these two samples suggest that there is little difference regarding the coding schemes. More interestingly, we note that parents have anti-natal effects more often than in-laws do. Figure 2 b-d shows that this is driven by their effects on total live births and, as predicted, on age at first birth. In fact, there is no difference between parents and affines on IBIs; both parents and in-laws are overwhelmingly likely to increase the rate of reproduction by shortening the inter-birth interval. Figure 3 shows that when kin presence means that family members co-reside, their effects are less pro-natal than when kin are operationalised as alive or dead.

Figure 2. Proportion of effects that are pro natal as a function of kin category and fertility metric. With 95% CIs. The number of effects represented by each bar is shown in parentheses. The left column shows the direction of all effects while the right column shows the direction of significant ($p < .05$) effects only.

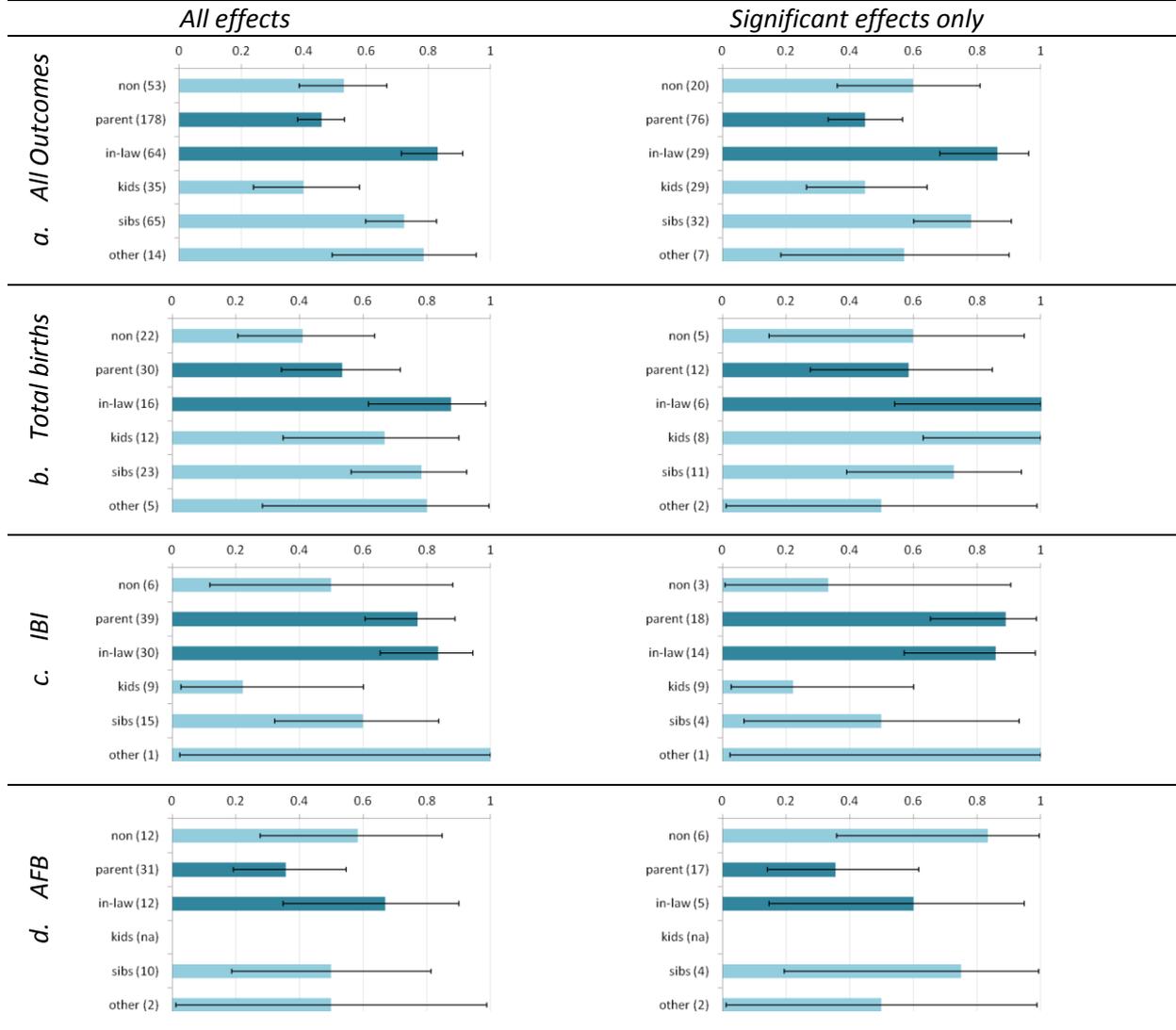
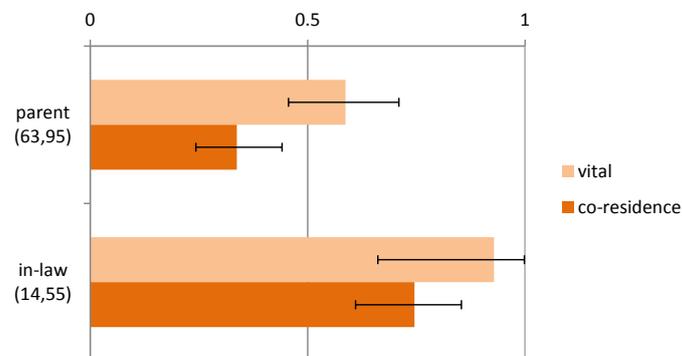


Figure 3. Proportion of effects that are pro-natal as a function of kin category and kin operationalization. With 95% CIs. The number of effects represented by each bar is shown in parentheses. All effects regardless of significance are included.



7. Discussion

The literature on the impact of kin on fertility outcomes needs careful interpretation. While the improvement of child survival is an unambiguous sign of a beneficial effect on a woman's fitness, influences on fertility outcomes may not have the overall effect of increasing her reproductive success. Increasing a woman's reproductive rate, for example, is not necessarily in her genetic interests. Furthermore, there are multiple mechanisms by which family members might exert an influence on a woman's reproductive outcomes. These may have different effects depending on the fertility metric and socio-ecological context under study.

The review of the literature tentatively supports the importance of considering which fertility metric is being investigated, the relationship of the kin member to the woman, and how that kin member's presence is operationalised when predicting the likelihood that family will have pro-natal effects. Both in-laws and parents are similarly likely to expedite progressions to next births (or shorten inter-birth intervals). However, parents are more likely to delay their children's first births than in-laws are, and to reduce their overall fertility. This might reflect genetic pleiotropic effects, children losing intergenerational conflicts regarding reproductive timing, or parents encouraging investments in embodied capital at the expense of earlier reproduction. Furthermore, both parent and in-law effects on reproduction are less likely to be pro-natal if their presence means co-residence rather than vital status. We believe this is most likely because co-residence with family members of an older generation denotes some dependence and perceived inability to provide for children by whichever local standards are relevant. Furthermore, co-residence might imply having a smaller per person resource base that can be used for future children.

These descriptive summaries do not adequately control for the various confounds in the designs of these studies. Larger studies are more likely to be conducted in low fertility societies. Most first birth analyses investigate the effect of parents. In-laws are more likely to be operationalised as co-resident than other kin members are. This means that stronger conclusions about how the strength of kin influences on female reproduction varies as a function of their relatedness, how they are operationalised and the fertility metric under consideration await proper meta-regressions that allow us to consider such confounds.

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