Resource exploitation and relatedness: implications for offspring size variation within broods

Stephanie J. Kamel and Paul D. Williams

S. J. Kamel (http://orcid.org//0000-0002-9965-6522)(kamels@uncw.edu) and P. D. Williams, Dept of Biology and Marine Biology, Center for Marine Science, Univ. of North Carolina Wilmington, 601 S. College Rd., Wilmington, NC 28403, USA.

Much of the theory on offspring size variation within a brood relies on unequal maternal allocation of resources to each embryo. However, maternal allocation strategies are subject to an inherent conflict between mothers and offspring: individual offspring, being more closely related to themselves than to their siblings, should always prefer a larger share of the available resources than that which is optimal from their mother's perspective. Thus, in species where mothers cannot unilaterally impose a resource allocation strategy, offspring can respond to this conflict by competing for more resources than is maternally optimal. Here we show that variation in offspring size within a brood can arise as a by-product of competition between siblings over a common resource, even when 1) there are no competitive inequalities within families, and 2) maternal investment per brood is fixed. Moreover, we show that size variance among offspring increases with increasing levels of competition, brought about by decreasing relatedness among siblings. Conflict thus offers a simple, testable and, potentially general, explanation for the wide variability in offspring size seen in nature. This extends explanatory hypotheses for offspring size variation beyond those of maternal effects, under which most explanations have been subsumed to date.

The number of surviving offspring is the fundamental currency of evolutionary ecology, and offspring size is often the fundamental determinant of offspring fitness (Stanton 1984, Bernardo 1996, Fox and Czesak 2000). Conventional models for the evolution of offspring size assume that parents have a finite amount of resources to allocate to offspring and that larger offspring are fitter. Parents therefore face a tradeoff between the number of offspring they can produce and the size of those offspring (Lack 1947, Smith and Fretwell 1974, Roff 1992). Consequently, if there is an optimum offspring size in a given environment, then variation in the resources available to a parent should lead to variation in clutch, not offspring, size (reviewed by Guinnee et al. 2007).

Over the last decade it has become increasingly clear that there is substantial intraspecific variation for offspring size not only within and among populations, but within and among broods, clutches, and fruits of the same parent (Shaanker et al. 1988, Marshall and Keough 2008, Guinnee et al. 2007, Sadras and Denison 2009). Explanations for variation within and among conspecific populations usually focus on the environmental factors influencing parental investment (Bernardo 1996, Marshall and Keough 2008). For example, variation among females or among different broods of the same female can be explained by changes in optimal levels of offspring provisioning, brought about by changes in environmental quality or maternal condition (reviewed by Rollinson and Rowe 2016). In contrast, the causes of intra-brood variation are largely unexplored. The most common explanations ascribe such variation to either non-adaptive, stochastic variation in provisioning (Rivest 1983, Moran and Emlet 2001), or as an adaptive maternal bet-hedging strategy in varying environments (Geritz 1995, Leishman et al. 2000, Marshall et al. 2008).

However, maternal allocation strategies are subject to an inherent conflict between mothers and offspring: since mothers typically divide their resources among many offspring at the expense of each individual's fitness, each individual offspring would prefer a greater share of parental resources than parents have been selected to give (Trivers 1974, Parker et al. 2002). That is, from the offspring's perspective, its optimal size is greater than that of the maternally determined optimum, and the conflict between parents and offspring over parental investment will occur to the extent that the genetic interests of the parents and offspring diverge (Hamilton 1964, Trivers 1974). These conflicts arise from the relatedness asymmetries that are a simple consequence of sexual reproduction. Mates, for instance, are often unrelated and often have differing optimal levels of parental care and offspring provisioning (Arnqvist and Rowe 2005). Mothers are equally related to all of their offspring, but each offspring is more closely related to itself than to either its siblings or parents (Trivers 1974). Finally, offspring can compete directly with siblings who may or may not share the same father (Mock and Parker 1997).

Importantly, the mating system – through its effects on the relatedness of interacting individuals – can be a critical determinant of the intensity of family conflict (Mock and Parker 1997, Haig 1999, 2000, Hardling et al. 2003, Schrader and Travis 2008). All else being equal, multiple mating by females (polyandry) increases the likelihood that broodmates will be half-, rather than full, -sibs, so that the taking of parental resources at the expense of a sibling therefore entails diminishing inclusive fitness costs as the degree of polyandry rises (Elgar and Crespi 1992, Kamel et al. 2010a). These calculations can often be complicated by other factors that are likely to affect the magnitude and resolution of conflicts among family members (Mock and Forbes 1992, Rollinson and Hutchings 2013), but the least ambiguous cases are likely to involve taxa where offspring can exert some degree of control over resource acquisition.

Much of the work on parental investment has been undertaken in species where parents control the resources available to offspring (Ahnesjö 1996, reviewed by Mock and Parker 1997). In some species, females tend to enforce an egalitarian distribution of food items to offspring; in others, parents skew their investment in favor of particular offspring (Smiseth et al. 2007). However, it is critical to acknowledge that there are many instances where mothers are not able to unilaterally impose an allocation strategy on their offspring, thus making it possible for offspring to influence the distribution of resources. In species that internally brood developing offspring, or package embryos in nurseries such as brood chambers, egg masses, or capsules, offspring can influence parental investment after fertilization via sibling competition over resources. Offspring packaging is widespread across taxa (amphibians: Brown et al. 2008, fish: Wourms 1977, molluscs: Shaw and Sauer 2004, and plants: Shaanker et al. 1988); for example, many gastropod molluscs package their eggs in capsules and developing embryos compete with one another for extraembryonic yolk in the form of nurse eggs (Thorson 1950, Lloyd and Gosselin 2007). Moreover, levels of parental investment to a brood, once encapsulated, are fixed, epitomizing a system with pure intrabrood conflict (sensu MacNair and Parker 1979), unaffected by offspring begging and other complex forms of parental manipulation and counter-response (Lessells and Parker 1999, Parker et al. 2002). When conflict among offspring is asymmetric, such as when a subset of the strongest and/or largest offspring receive greater than average amounts of resources due to being physically superior to their siblings, unequal resource distributions and size differences among offspring will occur (Aikio and Pakkasmaa 2003, Forbes and Wiebe 2010). However, the question of what to expect in terms of the variance in resource distributions, when all offspring are more or less competitively equal, remains unanswered.

Here we present a numerical model that explores how the distribution of resources among offspring within a brood changes as a function of the degree of competitiveness exhibited by all offspring in that brood. Specifically, we consider the question of how variance in offspring resource acquisition changes as a function of a given fixed exploitation strategy, and thus acts to generate offspring size variation. We also demonstrate how decreases in the average relatedness among broodmates influence the evolution of selfish resource exploitation strategies. Our results indicate that size variance within-broods should covary negatively with average relatedness among offspring, and hence, covary positively with the degree of polyandry in a population. We suggest that conflict offers a simple, testable and, potentially general, explanation for the wide variability in within-brood offspring size seen in nature.

Model description

We present a numerical model in which offspring can directly compete with each other for a maternally provisioned resource, where all offspring possess a fixed, nonplastic resource exploitation strategy, y, that is shaped evolutionarily by the expected degree of within-brood relatedness (Frank 1995, Taylor and Frank 1996). That is, as a given individual's relatedness to a randomly chosen brood mate decreases, the optimal strategy of offspring is to utilize the maternally-provided resource more selfishly. Therefore, the expression of competition does not depend on a perception of an individual's relatedness to one's brood mates.

To concretely examine the evolutionary effect of competition on the distribution of discrete resources amongst offspring, we model the level of competition as a satiation level; that is, the point at which a given offspring, having acquired a certain number of resources, will stop competing with its siblings over the remaining resources. Mothers are assumed to allocate T total resources to n offspring in a fixed environment, so that the optimal maternal allocation strategy is T/n number of resources per offspring. When offspring and maternal strategies coincide (i.e. offspring are clones), each offspring will satiate after consuming $y^* = T/n$ resources. In this case, satiation at the mean number of resources per offspring results in no variance ($\sigma^2 = 0$) in offspring resource acquisition.

At the other extreme, offspring will continue to compete for resources regardless of the amount they have already acquired. Under this scenario, and with the additional assumption that handling times are small (i.e. the consumption time of a resource unit is negligible), each individual will compete equally for every resource unit, so that $y^* = T$. In this case, the distribution of resources amongst offspring will therefore be approximately binomial, with the probability of a given individual obtaining k resources being given by $\binom{T}{k}\left(\frac{1}{n}\right)^k\left(1-\frac{1}{n}\right)^{T-k}$, where $1/n$ is the probability of successfully obtaining a resource unit at any given time. In this case, the variance among offspring in resource acquisition is given by $\sigma^2 = T(1/n)(1-1/n)$.

Analytical variance expressions for the cases lying between these two extremes, in which the competition level varies from high to low, are difficult to obtain, and so we examine this distributional change numerically. In all simulations, total resources are chosen to be $T = 100$, and total offspring numbers, $n = 20$, so that the mean number of resources per offspring is $T/n = 5$. Exploitation levels progressively greater than this imply ever greater among-sibling competition for resources, reflecting reduced within-brood relatedness. For each simulation, following resource competition,

offspring were ordered from lowest (1) to highest (20) resources acquired, and the variance in resource acquisition was calculated. This process was then repeated 10 000 times, with the means of the resources acquired for the offspring, again arranged from lowest to highest, being taken as the expected distribution of resources. Results are presented as means ± SD.

That the level of selfish resource use within a group is expected to evolve as a function of within-group relatedness can be demonstrated via an analytic model. We assume that the fitness, W, of an individual, with exploitation y, in a population with exploitation level given by z (the mean exploitation within a brood), can be written as

$$W(y,z) = \frac{y}{z} G(z) \qquad (1)$$

Where $G(z)$ is the average fitness in a brood with z as the exploitation level (alternatively, $G(z)$ measures the resources available to brood mates), and so decreases with z (i.e. higher resource exploitation reduces resources and hence brood fitness; Taylor and Frank 1996). Note that at $y = z$, $W = G(z)$ and individual fitness is equal to brood mean fitness.

Letting x be the genic value of the trait y implies that $dy/dx = 1$ (since x fully governs the expression of y) and $dz/dx = R$, where R is the relatedness of the individual bearing the y trait to a randomly chosen member of the z group, so that R = 1 corresponds to a relatedness of 1 and identity of the traits y and z (see Taylor and Frank 1996 for model details). Therefore, differentiating (1) via the product rule with respect to the genic value of y gives

$$\frac{dW}{dx} = \frac{G(z)}{z} + \frac{y}{z^2}\left[z\frac{dG(z)}{dz} - G(z) \right]R \qquad (2)$$

Equating this expression to zero and evaluating at $y = z = y*$ gives an implicit definition of the level of exploitation that is expected to evolve (the evolutionary stable strategy, or ESS), $y*$, as a function of relatedness, R. Implicitly differentiating this expression with respect to relatedness R then determines how this ESS exploitation level is expected to evolve given a change in relatedness:

$$\frac{dy*}{dR} \propto G(y)\frac{dG(y)}{dy} - y\left(\frac{dG(y)}{dy}\right)^2 + yG(y)\frac{d^2G(y)}{dy^2} . \Big|_{y = y*} \qquad (3)$$

Equation 3 states that, given an increase in relatedness, the direction of change in the ESS level of exploitation is given by the sign of its right hand side. Since G is a decreasing function of its argument, the first two terms on the right hand side of Eq. 3 are negative. Further, when G is a linear function, the third term on the right hand side of Eq. 3 is zero (as the second derivative of a linear function is always zero) and the ESS level of exploitation, $y*$, increases as relatedness, R, decreases. The same qualitative conclusion can be drawn for any decreasing function, G, which is concave down (giving a negative second derivative). Thus, ESS exploitation typically decreases with increasing relatedness.

Results

Simulation results indicate that, when offspring are provisioned from a common pool of limited resources, increases in the levels of competition result in greater variance in resource acquisition among offspring within a brood. As within-brood relatedness decreases, and selection favors increasingly exploitative offspring, the variance within a brood in the number of resources increases rapidly from zero (i.e. where all offspring satiate at 5 resource units) and reaches a plateau at high levels of exploitation (i.e. all offspring attempt to acquire approximately 10 resource units; Fig. 1). This plateau occurs because even if offspring continue to compete for resources due to very high exploitation values, the probability of obtaining ever more resources becomes increasingly smaller. Importantly, exploitation levels shape not only the total within-brood variance in offspring resource acquisition, but also the qualitative pattern of resource distribution across offspring within each brood as well (Fig. 2). For low levels of exploitation (i.e. high relatedness), the distribution of resources is a rapidly saturating concave function (Fig. 2b). As exploitation increases to moderate levels, saturation becomes increasingly delayed, and the function describing the distribution of resources approaches a linear form (Fig. 2c). Finally, further increases in exploitation (i.e. low relatedness) produce a logistic-type distribution of resources across brood members (Fig. 2d). Further numerical simulations show that these qualitative patterns are robust across parameter space (Fig. 3).

Discussion

This work demonstrates that evolved differences in resource exploitation are brought about by decreases in the average relatedness among brood mates. As a consequence, these evolved differences in exploitation result in variation in offspring size within a brood. Moreover, we show that variance in the distribution of resources among offspring increases
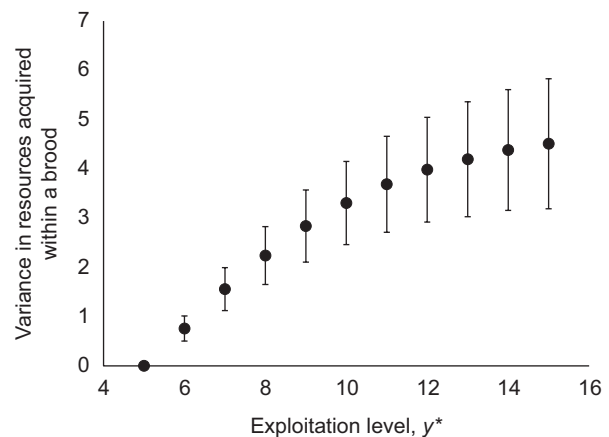

Figure 1. Mean ± SD of the within-brood variance in per offspring resource acquisition as a function of offspring exploitation level, $y*$. Total resources $T = 100$, and total number of offspring $n = 20$, so that 5 is the average number of resources per offspring. Each point represents the mean of the variance in offspring resource acquisition as a function of the given exploitation level (x-axis), averaged over 10 000 runs. When offspring satiate at the mean number of resources (5), variance is zero. This rises quickly as exploitation increases, then levels off as the number of resources become higher than an offspring can ever expect to acquire.
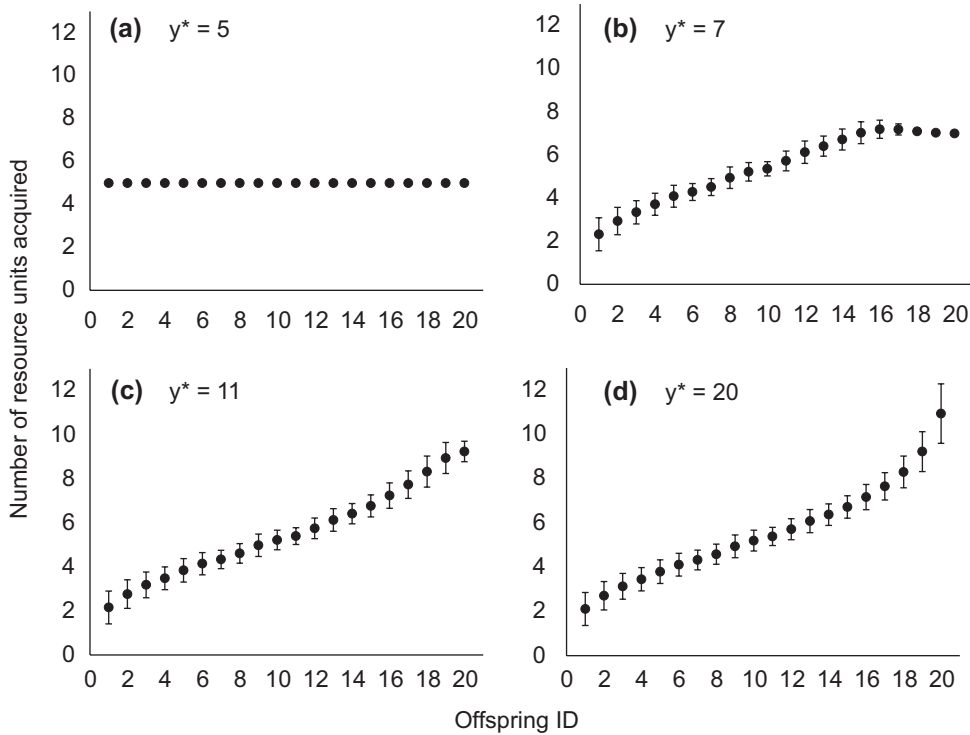
Figure 2. Mean ± SD of the number of resources per offspring as a function of exploitation level. Each figure represents a different qualitative regime of offspring size distributions. Total resources is again $T = 100$, and total number of offspring is $n = 20$. Figures are arranged so that offspring 1 has the fewest resource units (RU) and offspring 20, the most. After each realization, offspring are ranked from least to most resources acquired, then averaged over 10 000 runs. (a) In the absence of competition over resources, all offspring saturate at the mean number of resources (5 RU) and hence achieve the same size. (b) Resource distributions have saturating functional forms, with lower exploitation levels (7 RU) saturating more rapidly. (c) As exploitation levels increase further (11 RU), resource distributions across brood-members become more linear. (d) Still further increases in exploitation levels (20 RU) produce logistic-type resource distributions.
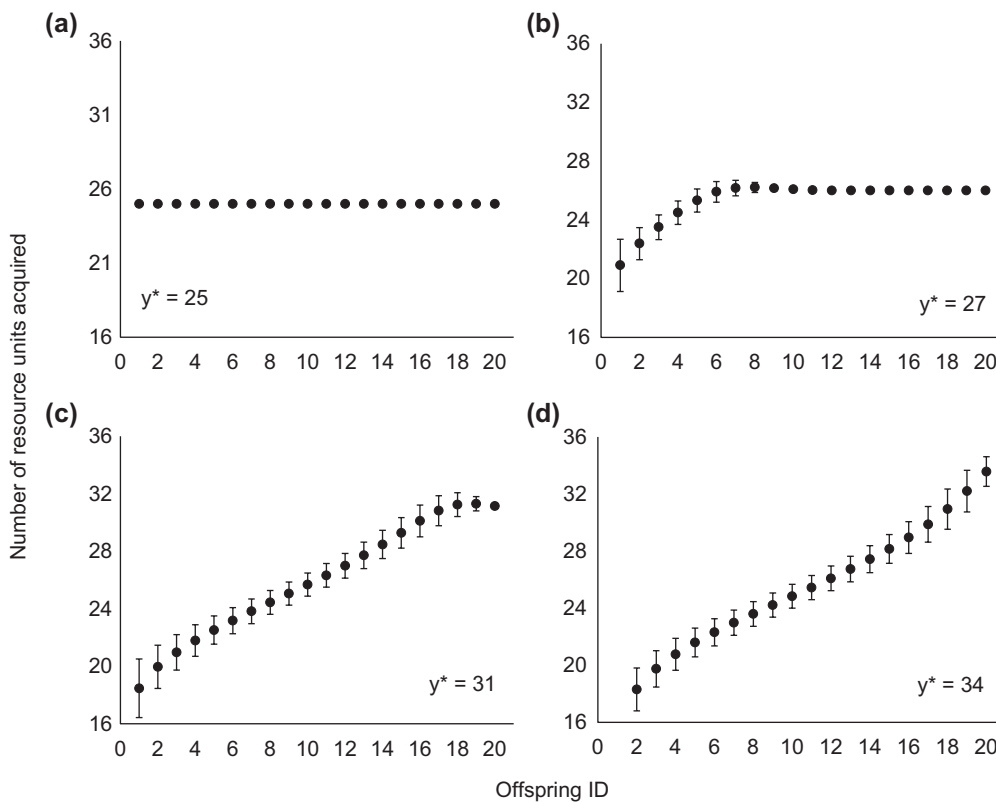

Figure 3. Mean ± SD of the number of resources per offspring as a function of exploitation level, and using $T = 500$ resources. Satiation levels: (a) 25 RU; (b) 27 RU; (c) 31 RU; (d) 34 RU.

with increasing levels of exploitation, such that more exploitative broods have more variable offspring sizes. These results provide a new mechanism to explain the vast amount of offspring size variation seen in nature (Marshall and Keough 2008, Forbes and Wiebe 2010, Kosman and Pernet 2011): that it is a consequence of the inevitable conflicts of interest that arise in families of sexually reproducing organisms over the optimal distribution of parental resources among siblings (Kamel et al. 2010b).

Setting the stage for sibling interactions

Evolved differences in sibling competition have been empirically demonstrated in several taxa (Stockley and Parker 2002, Long 2005, Schrader and Travis 2008). In many bird species, begging can be used as a mechanism for nestlings to obtain a greater share of parental resources at the expense of their siblings (Briskie et al. 1994, Caro et al. 2016). Comparative analyses in passerine birds have shown that the loudness of nestling begging varies significantly among species (Briskie et al. 1994) and that the intensity of sibling competition can skew the distribution of parental resources among nestlings (Royle et al. 1999). Both the loudness of begging and the intensity of sibling competition show a strong positive association with the level of multiple paternity within broods, which results in reduced intrabrood relatedness. Similarly, Lloyd and Martin (2003) found that, across 70 species of birds, higher levels of extra-pair paternity (again used as a proxy for average relatedness) are related to more rapid prenatal development, arguing that earlier hatching might provide a competitive advantage over siblings.

In mammals, the intensity of sibling competition within litters is related to the number of offspring competing for access to milk from each nipple (Stockley and Parker 2002). This can vary between a situation where offspring numbers exceed the number of nipples and competition for milk can sometimes be fatal (Cameron 1973), to a situation where the effects of sibling competition are seen even if the number of available nipples exceeds offspring numbers (e.g. access to only one side of the mother during suckling; Gilbert 1986). In a comparative analysis of carnivorous and insectivorous mammals, prenatal growth rates increase significantly with the intensity of postnatal sibling rivalry, reflecting a competitive advantage in scrambles for access to the milk supply (Stockley and Parker 2002).

While, in this case, sibling rivalry is measured as an increase in the number of offspring per nipple, Long (2005) shows that, in primates, the probability of decreased relatedness to future offspring leads to higher prenatal growth rates in offspring. Species with more potential female promiscuity are characterized by a higher rate of fetal growth than in more monogamous species, and this pattern is most pronounced in taxa where there is the opportunity for direct fetal access to the maternal bloodstream, reflecting greater offspring control over resource acquisition (Long 2005; but see Lessells and Parker (1999) for a discussion of inter- versus intra-brood conflict). These studies serve to broadly highlight that, across species, differing intensities of sibling competition have evolved and that mating system variation, through its influence on the average relatedness among siblings, can be a potent selection pressure shaping these outcomes. Moreover, while our model makes the assumption of complete offspring control over resource acquisition, these studies also suggest that opportunities for sibling conflict to influence offspring size variation may also occur when siblings and parents directly interact.

Implications for offspring size variation

That sibling relatedness can significantly influence within-brood variation in offspring size has important implications for our understanding of life history evolution (Roff 1992). Offspring size affects dispersal and establishment, vigor, and reproduction (Stanton 1984, Bernardo 1996, Fox and Czesak 2000) and, given that fitness and size are often so intimately linked, the long standing theoretical prediction has been that, for a given constant environment, maternal fitness is maximized by a uniform egg size. Despite this prediction, offspring size variation within broods is commonly observed in natural populations (Marshall and Keough 2008, Forbes and Wiebe 2010, Kosman and Pernet 2011). Explanations for this divergence between theory and practice have largely relied on mechanisms involving adaptive maternal responses. For example, mothers might differentially allocate resources to offspring in a brood based on paternal quality or some other measure of favoritism (Mock and Forbes 1992, Sheldon 2000, Hammerschmidt et al. 2011) or might produce a range of offspring sizes in the face of environmental uncertainty, to ensure that at least a few offspring approach the optimal size in some unpredictable future environment (Philippi and Seger 1989, Koops et al. 2003, Marshall et al. 2008). These types of mechanisms require a significant degree of parental control over resource allocation to offspring and the resulting range of offspring sizes will then be the phenotypic distribution that maximizes maternal fitness (Crean and Marshall 2009). However, the ability of parents and offspring to develop counter-responses to tactics exhibited by the other party need to be considered (Uller 2008). For example, in a number of plant systems, hormones involved in resource uptake are exclusively synthesized by offspring tissue, whereas hormones involved in restricting transport of nutrients into the seeds are exclusively produced by maternal structures (Ravishankar et al. 1995). Our model provides a mechanism by which the variance in resource acquisition (and hence offspring size) is not dependent upon such considerations, but instead is an emergent property of selection for increased resource exploitation, and extends hypotheses beyond those of adaptive maternal effects, under which most explanations have been subsumed to date. Given that multiple mating and parent–offspring and sibling interactions are exceptionally common, this work greatly broadens the conditions under which one might expect within-brood offspring size variation to arise.

Our model also contrasts with much of the work on offspring size variation which suggests that the outcome of sibling competition for parentally supplied resources will depend on the degree to which siblings differ from one another in their competitive abilities (Schrader and Travis 2012). For example, in many birds asynchronous hatching results in initial size disparities among nestlings. These disparities then determine the outcome of sibling competition, with earlier hatched nestlings outcompeting their later hatched siblings

(Mock and Forbes 1995). Size differences among offspring thus result from asymmetric competition due to initial differences in size or competitive ability. Our model invokes no such disparities; all offspring have the same initial size and all possess the same competitive ability within a given brood. This situation might best be realized in species that encapsulate their offspring and provision them with food in the form of trophic eggs (e.g. non-social and eusocial arthropods, gastropods, amphibians, fishes; reviewed by Perry and Roitberg 2006). Several studies have suggested that trophic egg-laying should evolve only when egg size is constrained (Polis 1984, Dixon and Guo 1993, Mock and Parker 1997). For example, morphological constraints on egg size, such as the size of the ovipositor or pelvic aperture, may prevent small females from producing large eggs (Congdon and Gibbons 1987). Through sibling competition, offspring gain the ability to respond to conflicts over optimal maternal resource allocation, which can then become an important influence on the distribution of resources and, as such, might play an important role in shaping the patterns of within-brood size variation. When the initial parental investment per offspring is equal, this should limit the possibility of asymmetric competitive interactions. Thus, the question of what to expect in terms of resource distributions when all offspring are more or less competitively equivalent arises.

The relationship between promiscuity and average sibling relatedness suggests a potential avenue for empirically investigating sibling conflict as the driving force behind offspring size variation. Specifically, our model proposes the testable prediction that within-brood variance in size should covary with historically different levels of polyandry across populations or species. A survey of the literature reveals broad trends in the direction predicted by the model. For example, across species of gibbons (*Hylobates*), the coefficient of variation in offspring size is greater in polyandrous than monogamous species (see Geissmann and Orgeldinger 1995 for data on neonatal weights), a pattern also found in plants (Waller 1982, Susko and Lovett-Doust 2000) and fish (Schrader and Travis 2005). It is possible that some variation in offspring size due to stochastic processes influencing resource acquisition could arise. Certain offspring might, simply by chance, happen to obtain slightly more resources early in development leading them to outcompete other siblings. In this case, the observed variance in offspring size would not be expected to correlate with mating system, average relatedness or other variables that would influence the intensity of conflict, and should thus be easily discounted by comparative analyses. Furthermore, it would be informative to address whether qualitative changes in the patterns of resource distribution across siblings are observed. Environmental quality has been shown to influence the relationship between investment per offspring and offspring fitness, such that optimal maternal investment per offspring increases as environmental quality decreases (Smith and Fretwell 1974). For example, optimal egg size in juvenile Atlantic salmon *Salmo salar* is larger when the quality of the stream in which they are developing is lower (Rollinson and Hutchings 2013). Our model predicts that variance is highest when promiscuity is high (and average sibling relatedness is incidentally low) but that this result is qualitatively similar when

the amount of maternal resources allocated to a brood varies. While the amount of maternal investment might vary across environments, however, the variance in size would be expected to change little.

Additionally, polyandry not only reduces offspring relatedness but also increases genetic variation (and thus, potentially, variation in offspring quality) within a brood. This could represent a confounding factor since the higher incidence of within-brood variation in offspring size in polyandrous species may not necessarily be due to selection on offspring selfishness but rather due to increased variation in the ability of offspring, who were sired by different fathers, to acquire resources (Aguirre and Marshall 2012). Assessing the importance of paternal effects on offspring size will be a necessary next step in our understanding of the influence of mating system on size variation. For example, using a series of crosses with single versus multiple pollen donors, Pélabon et al. (2015) found that paternal effects explained less than 4% of the overall variance in seed mass in the Euphorb species, *Dalechampia scandens*, a result observed in several other species of angiosperms (Marshall and Ellstrand 1986, Marshall 1988). Encapsulating gastropods would be a particularly useful group in this regard, as sires are distributed among several capsules within a clutch, with each capsule having varying numbers of sires and levels of sibling relatedness (Kamel unpubl.). In this instance, paternal quality and sibling relatedness are uncoupled across capsules and could be used, much like the fruits within an infructescence, to independently evaluate the effects of paternal genes versus intrabrood relatedness.

Despite the complexity inherent in understanding the relationships between mating systems, conflicts of interest and offspring size, by making a minimum of assumptions, we present a model of resource exploitation in which selection for increased selfishness generates variation in resource acquisition among brood mates. In doing so, we suggest that the wide variability of offspring size across taxa is not simply dependent on ecological and developmental factors but is also strongly influenced by levels of relatedness among kin.

References

Aguirre, J. D. and Marshall, D. J. 2012. Does genetic diversity reduce sibling competition? Evolution 66: 94–102.

Ahnesjö, I. 1996. Apparent resource competition among embryos in the brood pouch of a male pipefish. – Behav. Ecol. Sociobiol. 38: 167–172.

Aikio, S. and Pakkasmaa, S. 2003. Relatedness and competitive asymmetry – implications for growth and population dynamics. – Oikos 100: 283–290.

Arnqvist, G. and Rowe, L. 2005. Sexual conflict. – Princeton Univ. Press.

Bernardo, J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. – Am. Zool. 36: 216–236.

Briskie, J. V. et al. 1994. Begging intensity of nestling birds varies with sibling relatedness. – Proc. R. Soc. B 258: 73–78.

Brown, J. L. et al. 2008. Tactical reproductive parasitism via larval cannibalism in Peruvian poison frogs. – Biol. Lett. 5: 148–151.

Cameron, G. N. 1973. Effect of litter size on postnatal growth and survival in the desert woodrat. – J. Mammal. 54: 489–493

Caro, S. M. et al. 2016. Sibling conflict and dishonest signaling in birds. – Proc. Natl Acad. Sci. USA 113: 13803–13808

Congdon, J. D. and Gibbons, J. W. 1987. Morphological constraint on egg size – a challenge to optimal egg size theory. – Proc. Natl Acad. Sci. USA 84: 4145–4147.

Crean, A. J. and Marshall, D. J. 2009. Coping with environmental uncertainty: dynamic bet hedging as a maternal effect. – Phil. Trans. R. Soc. B 364: 1087–1096.

Dixon, A. F. G. and Guo, Y. Q. 1993. Egg and cluster size in ladybird beetles (Coleoptera, Coccinellidae) – the direct and indirect effects of aphid abundance. – Eur. J. Entomol. 90: 457–463.

Elgar, M. A. and Crespi, B. J. (eds.) 1992. Cannibalism. Ecology and evolution among diverse Taxa. – Oxford Science Publ.

Forbes, S. and Wiebe, M. 2010. Egg size and asymmetric sibling rivalry in red-winged blackbirds. – Oecologia 163: 361–372.

Fox, C. W. and Czesak, M. E. 2000. Evolutionary ecology of progeny size in arthropods. – Annu. Rev. Entomol. 45: 341–369.

Frank, S. A. 1995. Mutual policing and repression of competition in the evolution of cooperative groups. – Nature 377: 520–522.

Geissmann, T. and Orgeldinger, M. 1995. Neonatal weight in gibbons (*Hylobates* spp). – Am. J. Primatol. 37: 179–189.

Geritz, S. A. H. 1995. Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density. – Am. Nat. 146: 685–707.

Gilbert, A. N. 1986. Mammary number and litter size in Rodentia: the "one-half rule". – Proc. Natl Acad. Sci. USA 83: 4828–4830.

Guinnee, M. A. et al. 2007. The causes and consequences of variation in offspring size: a case study using *Daphnia*. – J. Evol. Biol. 20: 577–587.

Haig, D. 1999. Multiple paternity and genomic imprinting. – Genetics 151: 1229–1231.

Haig, D. 2000. The kinship theory of genomic imprinting. – Annu. Rev. Ecol. Syst. 31: 9–32.

Hamilton, W. D. 1964. Genetical evolution of social behaviour. – J. Theor. Biol. 7: 1–52.

Hammerschmidt, K. et al. 2011. Differential maternal allocation following mixed insemination contributes to variation in oocyte size in a sea squirt. – Mar. Ecol. Prog. Ser. 422: 123–128.

Hardling, R. et al. 2003. Dynamics of the caring family. – Am. Nat. 161: 395–412.

Kamel, S. J. et al. 2010a. Reproductive biology, family conflict, and offspring size in marine invertebrates. – Integr. Comp. Biol. 50: 619–629.

Kamel, S. J. et al. 2010b. Family conflicts in the sea. – Trends. Ecol. Evol. 25: 442–449.

Koops, M. A. et al. 2003. Environmental predictability and the cost of imperfect information: influences on offspring size variability. – Evol. Ecol. Res. 5: 29–42.

Kosman, E. T. and Pernet, B. 2011. Intraspecific variation in larval size and its effects on juvenile lophophore size in four bryozoans. – Mar. Ecol. Prog. Ser. 429: 67–73.

Lack, D. 1947. The significance of clutch size. – Ibis 89: 302–352.

Leishman, M. R. et al. 2000. The evolutionary ecology of seed size. – In: Fenner, M. (ed.), Seeds: the ecology of regeneration in plant communities, 2nd edn. CABI, pp. 31–57.

Lessells, C. M. and Parker, G. A. 1999. Parent–offspring conflict: the full-sib-half-sib fallacy. – Proc. R. Soc. B 266: 1637–1643.

Lloyd, J. D. and Martin, T. E. 2003. Sibling competition and the evolution of prenatal development rates. – Proc. R. Soc. B 270: 735–740.

Lloyd, M. J. and Gosselin, L. A. 2007. Role of maternal provisioning in controlling interpopulation variation in hatching size in the marine snail *Nucella ostrina*. – Biol. Bull. 213: 316–324.

Long, T. A. F. 2005. The influence of mating system on the intensity of parent–offspring conflict in primates. – J. Evol. Biol. 18: 509–515.

MacNair, M. R. and Parker, G. A. 1979. Models of parent–offspring conflict. III. Intra-brood conflict. – Anim. Behav. 27: 1202–1209.

Marshall, D. L. 1988. Postpollination effects on seed paternity – mechanisms in addition to microgametophyte competition operate in wild radish. – Evolution 42: 1256–1266.

Marshall, D. L. and Ellstrand, N. C. 1986. Sexual selection in *Raphanus sativus*: experimental data on nonrandom fertilization, maternal choice, and consequences of multiple paternity. – Am. Nat. 127: 446–461.

Marshall, D. J. and Keough, M. J. 2008. The evolutionary ecology of offspring size in marine invertebrates. – Adv. Mar. Biol. 53: 1–60.

Marshall, D. J. et al. 2008. Offspring size variation within broods as a bet-hedging strategy in unpredictable environments. – Ecology 89: 2506–2517.

Mock, D. W. and Forbes, L. S. 1992. Parent offspring conflict: a case of arrested development. – Trends Ecol. Evol. 7: 409–413.

Mock, D. W. and Forbes, L. S. 1995. The evolution of parental optimism. – Trends Ecol. Evol. 10: 130–134.

Mock, D. W. and Parker, G. A. 1997. The evolution of sibling rivalry. – Oxford Univ. Press.

Moran, A. L. and Emlet, R. B. 2001. Offspring size and performance in variable environments: field studies on a marine snail. – Ecology 82: 1597–1612.

Parker, G. A. et al. 2002. Intrafamilial conflict and parental investment: a synthesis. – Phil. Trans. R. Soc. B 357: 295–307.

Pélabon, C. et al. 2015. Does multiple paternity affect seed mass in angiosperms? An experimental test in *Dalechampia scandens*. – J. Evol. Biol. 28: 1719–1733.

Perry, J. C. and Roitberg, B. D. 2006. Trophic egg laying: hypotheses and tests. – Oikos 112: 706–714.

Philippi, T. and Seger, J. 1989. Hedging one's evolutionary bets, revisited. – Trends Ecol. Evol. 4: 41–44.

Polis, G. A. 1984. Intraspecific predation and "infant killing" among invertebrates. – In: Hausfater, G. and Hrdy, S. B. (eds), Infanticide: comparative and evolutionary perspectives. Aldine De Gruyter, Berlin, pp. 87–104.

Ravishankar, K. V. et al. 1995. War of hormones over resource allocation to seeds: strategies and counter-strategies of offspring and maternal parent. – J. Biosci. 20: 89–103.

Rivest, B. R. 1983. Development and the influence of nurse egg allotment on hatching size in *Searlesia dira* (Reeve, 1846) (Prosobranchia, Buccinidae). – J. Exp. Mar. Biol. Ecol. 69: 217–241.

Roff, D. A. 1992. Life history evolution. – Sinauer.

Rollinson, N. and Hutchings, J. 2013. Environmental quality predicts optimal egg size in the wild. – Am. Nat. 182: 76–90.

Rollinson, N. and Rowe, L. 2016. The positive correlation between maternal size and offspring size: fitting pieces of a life-history puzzle. – Biol. Rev. 91: 1134–1148.

Royle, N. J. et al. 1999. Sibling competition and the evolution of growth rates in birds. – Proc R. Soc. B 266: 923–932.

Sadras, V. O. and Denison, R. F. 2009. Do plant parts compete for resources? An evolutionary viewpoint. – New Phytol. 183: 565–574.

Schrader, M. and Travis, J. 2005. Population differences in pre- and post-fertilization offspring provisioning in the least killifish, *Heterandria formosa*. – Copeia 2205: 649–656.

Schrader, M. and Travis, J. 2008. Testing the viviparity-driven-conflict hypothesis: parent–offspring conflict and the evolution of reproductive isolation in a Poeciliid fish. – Am. Nat. 172: 806–817.

Schrader, M. and Travis, J. 2012. Variation in offspring size with birth order in placental fish: a role for asymmetric sibling competition? – Evolution 66: 272–279.

Shaanker, R. U. et al. 1988. Parent–offspring conflict, sibling rivalry, and brood size patterns in plants. – Annu. Rev. Ecol. System. 19: 177–205.

Shaw, P. W. and Sauer, W. H. H. 2004. Multiple paternity and complex fertilisation dynamics in the squid *Loligo vulgaris reynaudii*. – Mar. Ecol. Prog. Ser. 270: 173–179.

Sheldon, B. C. 2000. Differential allocation: tests, mechanisms and implications. – Trends. Ecol. Evol. 15: 397–402.

Smiseth, P. T. et al. 2007. Parents influence asymmetric sibling competition: experimental evidence with partially dependent young. – Ecology 88: 3174–3182.

Smith, C. C. and Fretwell, S. D. 1974. Optimal balance between size and number of offspring. – Am. Nat. 108: 499–506.

Stanton, M. L. 1984. Seed variation in wild radish – effect of seed size on components of seedling and adult fitness. – Ecology 65: 1105–1112.

Stockley, P. and Parker, G. A. 2002. Life history consequences of mammal sibling rivalry. – Proc. Natl Acad. Sci. USA 99: 12932–12937.

Susko, D. J. and Lovett-Doust, L. 2000. Patterns of seed mass variation and their effects on seedling traits in *Alliaria petiolata* (Brassicaceae). – Am. J. Bot. 87: 56–66.

Taylor, P. D. and Frank, S. A. 1996. How to make a kin selection model. – J. Theor. Biol. 180: 27–37.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. – Biol. Rev. Camb. Phil. Soc. 25: 1–45.

Trivers, R. L. 1974. Parent–offspring conflict. – Am. Zool. 14: 249–264.

Uller, T. 2008. Developmental plasticity and the evolution of parental effects. – Trends Ecol. Evol. 23: 432–438.

Waller, D. M. 1982. Factors influencing seed weight in Impatiens capensis (Balsaminaceae). – Am. J. Bot. 69: 1470–1475.

Wourms, J. P. 1977. Reproduction and development in chondrichthyan fishes. – Am. Zool. 17: 379–410.