Maternal Exploitation

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Maternal Exploitation

"Life isn't fair" is a phrase familiar to everyone. But to what extent do we really experience the bias that occurs in the natural world? Parental exploitation is a phenomenon occurring across the natural kingdom, but mostly absent in humans.

There are different theories regarding how parents invest in their offspring. The Smith-Fretwell model states that parents invest equally in their offspring, with all offspring being of equal quality.

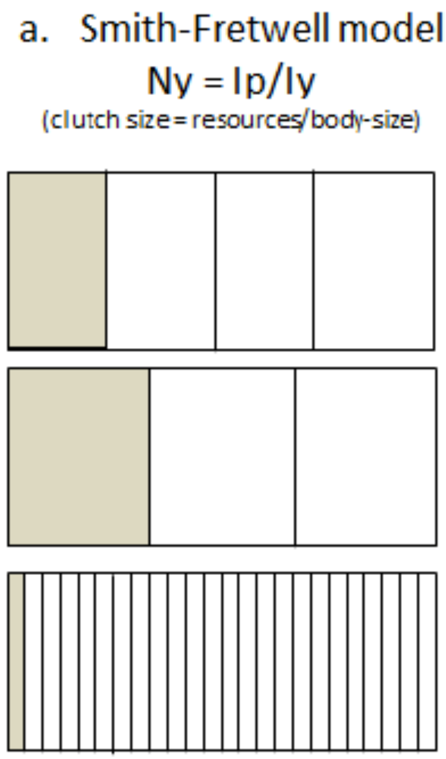

Figure 1

In this model the largest of the offspring, the shaded box in Figure 1 (Cassill, D., unpublished manuscript) is the same size as all the other offspring in the clutch. This model has three main assumptions. The first is that offspring number has an inverse relationship to the amount of energy devoted to individual offspring.

Second, the number of offspring does not have a direct effect on parental fitness. Thirdly the model assumes that offspring fitness increases with size, then decreases at a certain point (Carriere, 1994). According to this model, having larger offspring would enhance survival, they would have smaller clutch sizes. This model also maintains that the more energy invested in an offspring, the better that offspring's chance of survival (Smith et al., 1974).

A model in competition with this theory is that of Ghiselin, who proposes that parents do not invest equally in their offspring, with some given advantages not bestowed upon other offspring (Cassill D., unpublished manuscript).

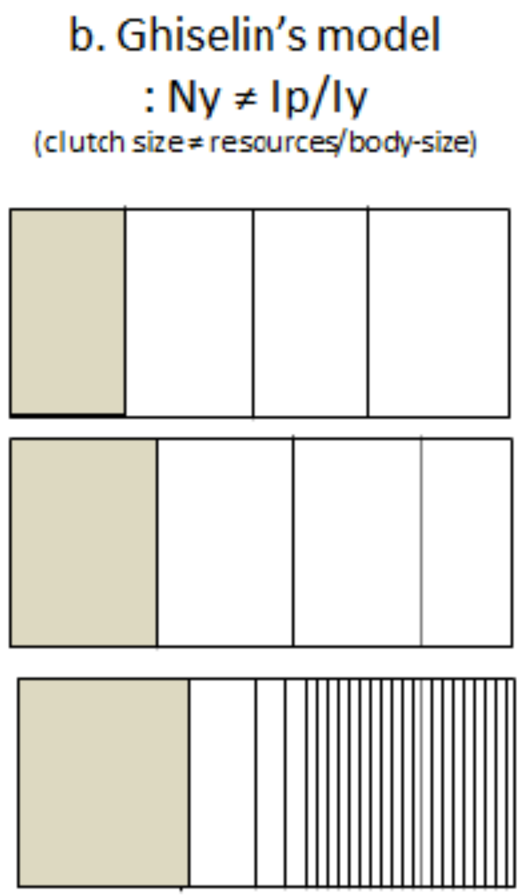

Figure 2

According to this model there will be one larger sibling, the shaded box in Figure 2 (Cassill, D., unpublished manuscript), and smaller offspring. The same amount of offspring can be produced as in the Smith- Fretwell model, however one offspring will be allocated more resources (greater investment) than the others and be more likely to survive than its siblings. The smaller siblings will often die (Cassill, unpublished manuscript).

Combining these two models arrives at an integrated model with similar assumptions. First, "at the time of reproduction, a mother's resources are finite." Second, "large-bodied offspring are more likely to survive than small-bodied offspring." Third, "maternal investments in offspring number per clutch-litter, offspring body-size and offspring diversity are linked, not to each other, but to environmental risks, primarily predation and scarcity." And finally, "the lifetime fitness goal of each mother and her mate is replacement." (Cassill, D., unpublished manuscript)

The models that support unequal parental investment distinguish between the core offspring, and marginal offspring. The core offspring would be those that receive superior maternal investment, and are most likely to survive to reproduce themselves, increasing their parent's fitness. The marginal offspring are those that receive little parental investment and are less likely to reach maturity. In the presence of abundance resources, all members of the clutch may survive. However, if there are limited or scarce resources, the marginal offspring will be the ones to die, not the offspring in which the parents have invested more. Parents will have clutches larger than they can support except in very favorable conditions because until the eggs hatch they do not have enough information regarding what resources will be available to them to support their offspring (Forbes, 2005). Efficient brood reduction is a benefit to unequal maternal investment, saves parents energy of maintaining a clutch larger than necessary, and increases parental fitness.

This paper will explore several ways that mothers skew the quality of their offspring. Four ways that parents do not invest equally in their offspring is through asynchronous hatching, setting up and permitting easy siblicide, feeding diversity, and fertility skew.

Hatching Asynchrony

Hatching asynchrony refers to the practice by some birds in which parents begin to incubate each egg as it is laid rather than incubating only after the entire clutch is laid. The first eggs will hatch before the last eggs, and thus have a head start on developing motor skills. The first hatchlings will be larger and stronger than the last hatchlings (Ballinger et al., 1990). This facilitates efficient brood reduction. The offspring that start developing first have advantages over their lesser-developed siblings. The last laid eggs have a phenotypic handicap, in that they are smaller, with less of a competitive edge against their older siblings. The first laid eggs will hatch before the last laid eggs and thus will be stronger and more able to out-compete the last hatched chicks for food. Hatching asynchrony generally overpowers other differences between the eggs, such as egg size or hormone differences. These secondary differences become more important when eggs hatch synchronously. Having a system where the strongest offspring are the most likely to survive increases the parents fitness by increasing the chances that they will have at least one offspring that survives, while keeping their cost of rearing extra offspring relatively small (Forbes, 2005).

The common grackle, *Quiscalus quiscula,* found throughout most of North America, is an example of a bird that practices hatch asynchrony. The mother bird incubates her first eggs before the clutch is complete, assuring that the first laid eggs will hatch before the last laid eggs. The common grackle typically lays a clutch of about five. Howe (1976) observed that the last hatched young from the clutch would frequently die of starvation very soon after they hatched. Howe also showed that the later laid eggs tended to be larger than the first laid eggs. This gives the last laid eggs the advantage of having more nutrients while they are developing in the egg, ensuring that they have a better chance of survival, should resources be abundant when they hatch. Producing a clutch that would ordinarily be too large for the parent grackles to support would maximize the parent's fitness if food resources are be particularly abundant. Unfortunately this small advantage is not great enough to off-set the disadvantage of hatching last, and the chicks from last laid eggs still frequently die. This unequal investment from the mother ensures that she can have the greatest number of offspring possible survive, while most efficiently using her food and energy resources.

The greater ani (*Crotophaga major*) is a large sized bird in the cuckoo family. It is found in Panama and Trinidad and throughout South America and northern Argentina. Several females lay their eggs in the same nest and will take turns incubating the eggs, and feeding the chicks. The greater ani has a unique practice in which females frequently eject the first laid eggs of other females in order to provide more room for their own eggs. This would mean, in terms of hatching asynchrony, that the middle laid eggs are incubated the longest. According to Riehl (2010), in this case, more resources were allocated to the middle laid eggs because they are the most likely to survive. The researchers showed that the mass of the first and last laid eggs were significantly smaller than the mass of the middle laid eggs, as shown in Figure 3 (Riehl, 2010). Large egg size has been correlated with increased hatching success, larger size at hatching as well as increased growth rate, and overall survival. Creating eggs is an energetically draining activity for a mother, and creating larger eggs takes more energy than

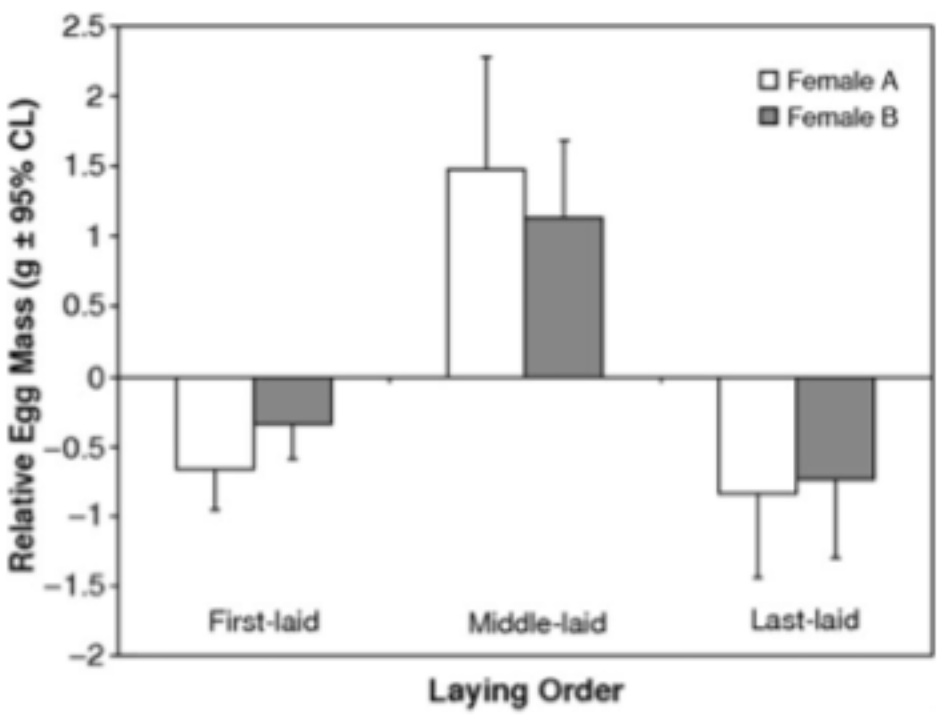

Figure 3

smaller ones. Thus, a mother would want to invest the most energy in the eggs that are most likely to survive. Riehl also showed that the mass of the last laid eggs would further decrease as the degree of hatching asynchrony increased. The last laid eggs were still the most likely to starve and never fledge, and the middle laid eggs are most likely to survive.

The common tern (*Sterna hirundo*), is a seabird found in Europe, North America, as well as Asia. They are among the species that bestow phenotypic handicaps to their offspring, as well as demonstrating staggered development. The last laid egg tends to be small, in addition to hatching last. The last laid egg hatches later than the first laid eggs because the mother begins incubating before she is finished laying her clutch of eggs.

Hatching asynchrony tracks food resources from year to year. If food is plentiful, all hatchlings could survive, however, if it is scarce "resources are not wasted on the chick least likely to survive, and starvation of the entire brood is prevented." (Bollinger, et al. 1990) By bestowing phenotypic handicaps and practicing hatching asynchrony with its young, the parents ensure that at least the largest of their brood will survive. Ballinger et al., (1990) showed that in common tern clutches of three eggs, the last laid egg was always the least likely to survive. Survival rates tend to be greatest when spring and early summer are warm, and become lower when they are cool. Therefore, the head start, or handicap, provided by hatching asynchrony can be negligible provided resources are readily available, but serves to maximize fitness when they are scarce.

Many species of birds will give great advantages to their first laid eggs by practicing hatching asynchrony, and bestowing fatal handicaps upon the chicks that are hatched last. These phenotypic handicaps result in unequal offspring. For birds, phenotypic handicaps can involve differences in the size of the chicks, and the amount and quality of the yolk of their eggs, which serve as their food source. Hatching asynchrony serves as a handicap for the later born birds because the first-born birds will be larger, and stronger. The mother bird can attempt to even the playing field by making last-laid eggs larger, however normally the power of hatching asynchrony is so large that even egg size will not overcome it. Birds can also distribute hormones unequally among her eggs, which could put the later laid eggs at a disadvantage or an advantage. However, even when the hormones work as an advantage towards the later laid eggs, it is hardly ever enough to overcome the effects of hatching asynchrony (Forbes, 2005). "Extensive work on brood-reducing species shows that hatching asynchrony is the cardinal handicap in sibling competitions." (Forbes, Wiebe 2009)

Siblicide

Siblings are not always kind to each other. This can extend far beyond not sharing or calling each other names as observed among human siblings. In some species, not being the first born sibling can mean certain death at the hands of the older sibling. Siblicide is most commonly seen in birds, and is somewhat mediated by hatching asynchrony, with the first born from the clutch being the largest and most prepared to win a fight against its smaller siblings.

Two distinct types of siblicide are recognized, obligate and facultative siblicide. In obligate siblicide, the younger sibling is frequently killed by the older sibling. Obligately siblicidal birds have hatching intervals that are longer than usual, ensuring that the first hatched chick will have a greater size advantage over the later hatched chicks. In facultative siblicide, the younger might be killed by the older, depending on the environmental conditions. If resources are abundant the older sibling will not necessarily kill the younger sibling, however if they are scarce they will be more likely to. Hatching asynchrony determines facultative siblicide, ensuring that one offspring has an advantage. Thus, the larger sibling can easily kill the smaller, younger siblings and not deal with unnecessary injury or expend vast amounts of energy.

This form of brood reduction is efficient, and ensures that at least one chick survives. Taking care of more chicks has a toll on the parents. The extra work can deplete parent's fat stores, expose them to more predators, or effect their pattern of feather replacement (Forbes, 2005). Thus, rearing more chicks may not always result in increased fitness for parents. Spare eggs or embryos are produced in the event that something happens to the first laid egg, and it does not survive. This way, the parents have a form of insurance that their genes will be passed on, increasing the parent's fitness. Smaller families of higher quality are the ultimate end result of siblicide (Rodríguez-Gironés, 1996).

The brown booby (*Sula leucogaster*) is located on islands and coasts of the Atlantic and Pacific islands. Brown boobies are one of the species that commit obligate siblicide. Older chicks always kill younger chicks, without influence from the parents. The only chance the younger sibling has to survive is if the older chick happens to die, which does not occur frequently. It is estimated that about 22% of the time the older chick will fail to hatch or will die (Tershy, 2000). Parents do not interfere with the siblicide ritual. The second born chick is at a natural disadvantage to the first born because it will be smaller and weaker, unless the first-born is weakened through a defect or disease. The two are not evenly matched, and the younger sibling is quickly killed.

Researchers are not sure of the evolutionary pathway that resulted in obligate siblicide. One school of thought proposes that obligate siblicide may stem from a lack of available resources, although there is not much evidence available to support this claim. There is data showing that even though the younger brown booby has little chance of survival it will still show increased aggression, as compared to other birds, from birth (Anderson, 1990). Hugh Drummond (2000) performed an experiment where he placed second born brown boobies in the nests of the blue-footed booby. Blue-footed boobies are closely related to the brown boobies, but do not demonstrate obligate siblicide. Drummond (2000) observed that the second born brown boobies were much more aggressive than the blue-footed boobies in the same role. They were so aggressive that they would at times even threaten the oldest blue-footed booby of the group. By having this aggressive nature hard-wired, the younger brown booby has a slightly higher chance of surviving against their older sibling.

The cattle egret (*Bubulcus ibis*) is a stocky, white heron that gets its name from its special relationship with cattle; the egret forages for flies and ticks from the cattle. In addition to exhibiting low levels of brood parasitism. Brood parasitism is when a bird lays its eggs in the nests of other birds. The cattle egret is an example of a species that practices facultative siblicide. Facultative siblicide involves frequent fighting in the nest, but not always death. The younger sibling will frequently be attacked, but only necessarily killed if food resources become scarce (Fujioka, 1985).

Asynchronous hatching occurs with cattle egret's typical brood of three eggs. The older sibling automatically has a size and strength advantage over the last born of the brood. Because of this disparity between the chicks, the older sibling almost always wins a fight over food. The older sibling's advantage is magnified by the feeding behaviors of the parents; Fujioka (1985) showed that 65% of the time when the parent egret came back to the nest with food for the chicks, the food would go to the older sibling. This study observed interactions between siblings in nine cattle egret nests. In two of the nine broods observed, the youngest sibling was killed when fighting with the older sibling.

Another study by Mock and Ploger (1987) created broods with synchronously hatching chicks, to compare to those with asynchronous hatching. They found that there was a higher rate of brood reduction via siblicide in the asynchronously hatching broods, even though there was less fighting among the chicks. The synchronously hatching chicks would compete more for food with their nest-mates because they had a greater chance of winning when there was no natural advantage among the siblings. Fujioka (1985) also found that synchronously hatched chicks fought more than those in asynchronous broods. Synchronously hatching broods, however, did not result in more surviving offspring than the asynchronously hatching broods. Asynchronous hatching and facultative siblicide ensures that energy is not wasted from unnecessary fighting, and ensures that efficient brood reduction occurs with the strongest chicks surviving.

The sand tiger shark, *Carcharias taurus*, is a fearsome looking, slow moving shark and can be found in the oceanic shorelines around North America, Japan, Australia, and South America. Sand tiger sharks engage in an extreme, and early form of siblicide termed intrauterine cannibalism. The largest, most developed of the embryos in the uterus kills and eats the other embryos. Sand tiger shark females have two uteri, so they give birth to two offspring, one from each uterus. Springer (1948) was the first to discover that the sand tiger shark exhibits intrauterine cannibalism when he found a 40 mm embryo inside the stomach of a 170 mm embryo. Gilmore et al., (1983) found evidence that the most developed embryo will target the other embryos that could prove to be competition, not just go after what would be the easiest target. For example when examining the uterus of a pregnant sand tiger shark, Gilmore et al. (1983) found that a 100 mm embryo had attacked a 51 mm embryo, even though there were other egg capsules in the uterus, which would have made a decidedly easier target. The 51 mm embryo had already developed teeth, thus it was a potential threat to the larger embryo. The researchers found more evidence that larger embryos selectively targeting more developed embryos and not unhatched egg capsules. Once developing embryos with teeth have been killed, the surviving embryo eats unfertilized ova for nutrition.

The reasons for siblicide are similar to the reasons behind why parents skew the quality of their offspring. With a limited number of resources, not every offspring can be of high quality, and one high quality offspring is better than two or several offspring of low quality. Mothers ensure that they have at least one surviving offspring while also maintaining their own health and survival.

Feeding Diversity

Mothers can skew the likelihood of their offspring's survival by providing unequal access to food. The parent can be directly responsible for how the food is allocated, such as the case where some eggs are larger than others, thus providing more nourishment for the growing embryos. In other cases, the offspring are responsible for how food is distributed. In mammals, this can be seen as competition for teats, where the stronger of the offspring will have a better chance of getting access to the best teat (Hartsock et al., 1977) Unequal access to food allows brood reduction to be delayed, so in the case that environmental conditions are favorable the parents may be able to support a large litter or clutch, but in the case that resources are scarce and environmental conditions are not favorable, the weakest of the clutch or litter will be the most likely to die.

Pigs (*Sus domesticus*) are a mammal that establish a rather stable nursing order after birth, with piglets only suckling from one or two teats. Teat specificity encourages survival because the piglets are able to feed frequently and without competition. Piglets will fight for teats shortly after birth, with the anterior teats being the most desirable (Hartsock et al., 1977). Piglets that weigh more at birth are more successful at obtaining and defending the most desirable places in the nursing order. Hartsock (1977) reported that anterior

Figure 4

teats produce more milk than the posterior teats, and that the piglets that suckled from these teats gained weight faster than those at the posterior teats, as shown in Figure 5 (Hartsock, 1977). Small piglets born into large litters are the most likely to die of starvation (Fraser et al., 1991).

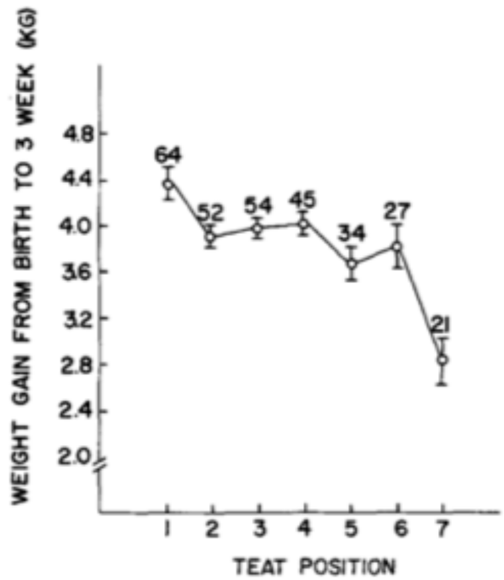

Figure 5

The presence of more productive teats, instead of all being equal, indicates unequal maternal investment and a favoritism towards piglets of higher birth weight, since they are the most likely to gain access to the more productive anterior teats.

The domestic European rabbit, *Oryctolagus cuniculus*, supplies only very limited maternal care for her offspring. Out of a twenty-four hour period she will return to her nest with her pups and nurse them for only three to four minutes, and not return until the next day. Rabbits have on average seven to nine young per litter, although there have been accounts of up to eighteen being born at once. The young engage in nipple switching, so more young than number of nipples can be reared. Mortality is greater in larger litters, and those with a lighter birth weight are more likely to lose competitions for access to nipples with their heavier siblings (Bautista et al., 2005). Pups that were born at a higher weight have better access to milk and grow faster than those born at lower weights, indicating that they had some advantages during gestation (Drummond et al., 2000). These heavier young not only have an advantage of increased competitive access to milk, they also are more efficient at converting milk to body mass (Rödel, 2008). Those born at lower weights are more likely to starve to death. Once the smaller young die, the larger, surviving pups can enjoy increased access to milk, and thus a higher quantity of milk per feeding session. Giving birth to pups of unequal size, and giving birth to more pups than the number of nipples available, favors efficient brood reduction, with those rabbits with low birth weight being more likely to starve to death. Giving birth to more young than the mother can feed ensures that she will have as large a surviving litter as possible, and unequal birth sizes ensure that the largest, strongest of the litter will be most likely to survive.

Birds are oviparous animals that lay eggs. Little to no development of the embryo occurs within the mother. The egg is the site where the embryo first begins to grow, and the bird will hatch when it has been sufficiently developed. The yolk within the egg is the developing bird's sole source of nutrition while it is in the egg. The red-winged blackbird (*Agelaius phoeniceus*) is a small bird that lays macrolecithal eggs (eggs with a large amount of yolk), and, like many songbirds confers maternal handicaps to their nestlings. When mother birds lay their clutch of eggs, they are not all the same size, and this size difference is a factor that contributes to the baby bird's likelihood of survival. Eggs of below average mass showed a high correlation with early mortality in red-winged blackbirds (Forbes and Wiebe 2010). Egg mass was also positively correlated with hatching mass, giving those in the larger eggs an immediate advantage. This finding is consistent with the fact that the yolk of the egg is the developing embryo's only source of food, thus hatchlings with more food would be born larger. Thus, larger eggs provide a genetic potential for a larger hatching mass, as shown in Figure 6 (Forbes and Wiebe, 2010).

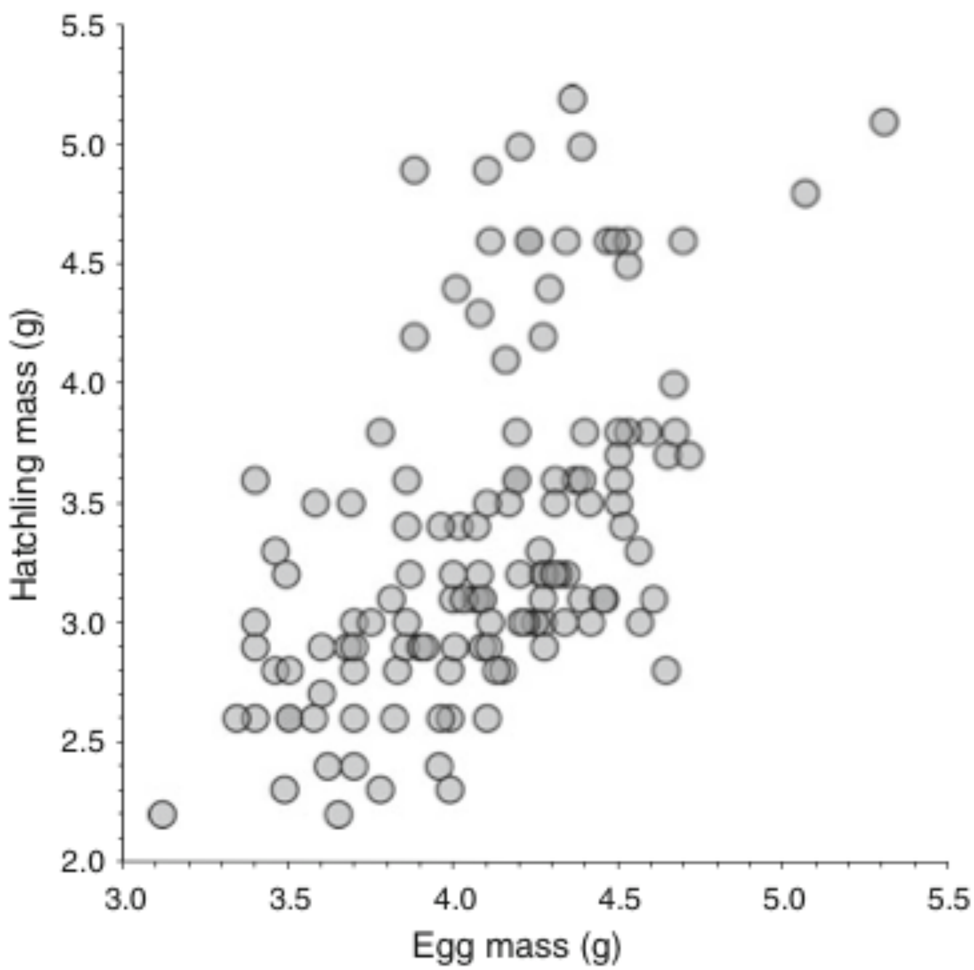

Figure 6

In terms of nestling survival, "there was a strong and negative relationship between egg mass and the probability of surviving to 9 days of age for marginal progeny."(Forbes and Wiebe 2010) This can be explained through sibling competition, as well as the fact that these hatchlings did not "carry sufficient nutrient reserves to survive early food deprivation." (Forbes and Wiebe 2010). Marginal offspring were characterized as those progeny that were given disadvantages, and core offspring were those that were bestowed advantages, as far as hatching asynchrony, immune system complements, hormonal titre, and egg size. In contrast to the differences observed in marginal offspring, core offspring were not affected by mean mass of eggs, the number of offspring at the time of hatching, or hatch date. This difference can be explained by the fact that "core offspring hatching from eggs with below average mass….enjoy first access to parentally provided food and hence were less reliant on nutrient reserves for early survival." (Forbes and Wiebe 2010). In the cases where marginal offspring subsisted long enough to fledge, there are little observable differences between them and the core offspring.

Fertility Skewing

Another way that females invest unequally in their offspring is through fertility skew. Not all offspring produced will be capable of reproduction. This is most evident in social Hymenoptera (an order of insects including bees, ants, and wasps). Fertile males will be produced, and their only purpose is fertilization. Females who are not capable of reproduction care for their mother, the queen, and her young . Alexander (1974) found that the inequality of the sex ratio found in these types of species evolved because it would increase the fitness of the queen, even though it does not necessarily increase the sterile individual's inclusive fitness.

Eusocial social organization is considered one of the most complex and elaborate in the natural world. Rather than focusing on one's own reproduction, the members of these societies promote their own fitness through closely related relatives. A female ant will have about 75% of their chromosomes in common with the other females of their colony (Forbes, 2005). By promoting the health of the queen and the rest of the colony they are in essence promoting their own fitness, even though they will never reproduce. Eusociality is mostly seen in social insects, however there are examples of it occurring in select mammals.

The fire ant, *Solenopsis invicta*, is an aggressive species of fire ant that is native to South America and has become invasive in many other parts of the world. They display eusocial behavior, which is typical among all ant species. Not all members of the colony are capable of reproduction. There is a queen, the reproductive males, and the worker and soldier female ants. The worker and soldier ants are effectively sterile. Studies have been conducted that demonstrate that the queen controls the sex ratio within the colony. The queen tends to lay more male than female eggs (Passera et al., 2001). In experimental conditions, colonies without a queen produced more individuals capable of reproduction than did colonies that had a queen. The researchers found that the production of sexual individuals was mediated by pheromones transmitted by the queen. When a dead queen was introduced to a colony that previously had no queen, the production of sexual individuals was reduced, although was not as low as when a live queen was present. Also, when a live queen was introduced to a previously queenless colony that had developed a large number of sexual individuals the sterile worker ants would kill sexual individuals, indicating the great control the queen has over the sexuality of the rest of the colony (Vargo et al., 1986). Production of sterile workers and sexual individuals can also vary by season. More workers are produced in the summer to help the colony survive the fall and winter, when more individuals will die. More reproductive individuals need to be born early in the season so they can mate before winter (Cassill, 2002). The queen manipulates when sterile and reproductive offspring are produced according to when it will increase her fitness.

The European honeybee, *Apis mellifera*, is native to Europe, Asia, and Africa, and is one of forty-four species of honeybee. The European honeybee is an eusocial insect. Most hives contain one queen, although it is possible for two queens to coexist in one hive. Drones are the reproductive males of the hive. They do not collect pollen or nectar, their life purpose is to fertilize a virgin queen. Drones are haploid from unfertilized eggs, they only have one set of chromosomes, which they inherit from their mother. Females are diploid from fertilized eggs. The queen lays eggs and the worker bees maintain the hive and care for the young (Forbes, 2005). In the case where fertile female worker bees are produced and lay eggs the queen and other workers will actively reject these eggs, because they favor the worker's fitness rather than the queen's. Other workers will assist the queen in getting rid of these eggs because they are more related to the queen's offspring than those from another worker (Ratnieks et al., 1989). Occasionally diploid males will be born, although they serve no purpose for the overall success of the hive. Since diploid males are useless to the hive they produce a chemical that stimulates the other members of the hive to eat him, and thus providing a purpose for the hive, instead of just being a drain on its resources (Forbes, 2005).

Most eusocial species are insects, however there are two mammals that exhibit this behavior as well (O'Riain, 2008). One of which is the naked mole rat, a fairly small, unique mammal. Naked mole rats are also unique in that they are the only mammalian thermoconformer (their body temperature changes according to the outside temperature), and they lack pain sensation in their skin. Jarvis (1981) conducted a study of a colony of forty naked mole rats, and found that only a single female and two or three males will breed. The remaining naked mole rats were divided into castes and performed various tasks, such as gathering food or maintaining their underground tunnels. "Nonworkers" are also present in this society, and will be the larger of the naked mole rats. The "worker" naked mole rats are diploid, unlike some eusocial insects, such as ants, which are haploid. The breeding female is determined partly by growth rate from birth. Even within a single litter, some mole rats will grow faster than others. The breeding female will be one of the larger females.

Unequal maternal investment is ultimately beneficial to the parent's fitness by either facilitating efficient brood reduction or creating altruistic sterile offspring. The trade off between clutch size and quality can be mediated by unequal maternal investment, with a few high quality offspring and several lower quality offspring as insurance in case of the failure of the higher quality offspring, or in the chance that resources are plentiful and predation is low.

More work needs to be done in this field to fully understand all of the ways that unequal maternal investment affects offspring outcomes. To conduct studies that will benefit this field one needs information both on the number and quality of the offspring produced per clutch. An interesting example of where there is more potential for research in this area is with the data regarding the eggs of loggerhead turtles. There are vast amounts of data regarding the number of eggs, but not any comparing the eggs, birth order, or weight of young at birth. Some of the data collected is as follows:

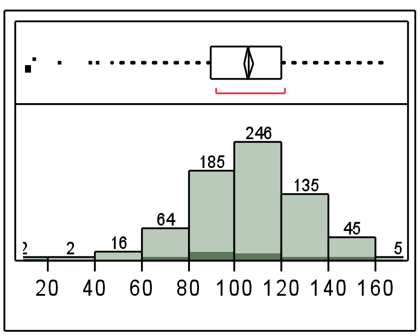

Figure 7: Clutch size (number of eggs laid per clutch) by the loggerhead sea turtle (*Caretta caretta*). The mean clutch size was 105 (n = 700). Data were provided by David Addison, Director of the Conservancy of Southwest Florida, Naples, Florida. Data were analyzed using JMP Statistical Software.

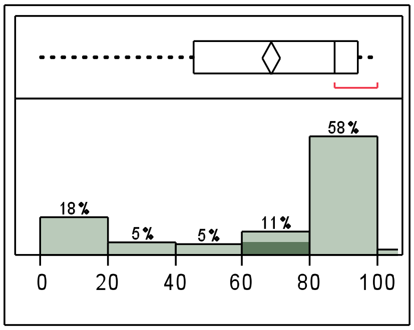

Figure 8: Percent of each clutch of eggs that hatched. Out of a mean of 105 eggs, 87% successfully hatched (median, n = 748).

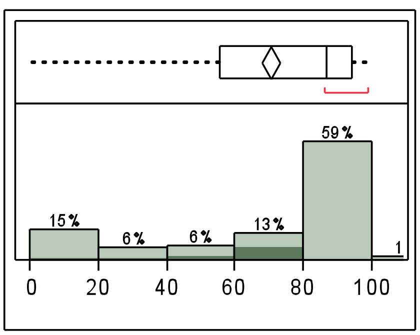

Figure 9: Percent of each clutch in which hatchlings successfully dug themselves out of the nest and made it to the Gulf of Mexico. Of the original 105 eggs per clutch, 87% of hatchlings made it to the Gulf of Mexico (n = 695).

To determine maternal investments according to Dr. Cassill's model, data on the size of individual sea turtle offspring is needed. Are offspring of equal size per the assumption of the Smith-Fretwell model or are they diversified per the assumption of Ghiselin's model? To support the idea of maternal investment one would expect to see that those eggs that successfully dug themselves out of the nest would weigh more than those who were not able to, and perhaps were one of the first laid eggs.

Evidence of unequal maternal investment across the natural world would do much to strengthen the argument. It is hard to obtain this evidence is some types of species because one cannot always fully observe different types of animals. For example, it is easy to observe birds because many times their nests are out in the open and it is easy to observe them from the time they hatch to the time the fledge, and even beyond that. It is much harder to observe mammals where the young gestate inside the womb and afterwards raise their young in spaces that are more inaccessible to humans. Advances in these areas will further advance our knowledge of parental investment.

In conclusion, unequal parental investment can be seen in many different species and through different mechanisms, all of which contribute to maximizing parental fitness. Although it may not seem particularly fair to doom some offspring and give advantages to others, asynchronous hatching, siblicide, feeding diversity, and fertility skewing ultimately benefit the species as a whole.

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