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**EVOLUTION OF MATERNAL INVESTMENT STRATEGIES
FOR THE ORDER CROCODYLIA**

By

Ileisy Lobaina

A thesis submitted in partial fulfillment
of the requirements of the
University Honors Program
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CERTIFICATE OF APPROVAL

Honors Thesis

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ABSTRACT

The order Crocodylia includes two alligators, six caimans, thirteen crocodiles and two gharials species. In this study, the maternal investments by species in the order Crocodylia in offspring number, offspring size at hatch, and female body size were determined and compared to the predictions of the Smith-Fretwell maternal investments model and an alternative maternal investment model. The findings of this study contradict the Smith-Fretwell model and support the alternative model. The Smith-Fretwell model predicts that mothers who produce a larger number of offspring must sacrifice the quality of their offspring. Results showed that hatchlings were about the same size regardless of the number of eggs produced. On the other hand, according to the alternative maternal investment model, the predation rate on crocodilian offspring is far less than that of fish offspring but far greater than that of bird or mammal offspring. In addition, offspring mortality by starvation is less of an issue for crocodilians than it is for mammals and birds but it is a greater threat for crocodilians than it is for most species of fish.

INTRODUCTION

Crocodylia is an order of large reptiles that includes the true crocodiles, alligators, caimans, and gharials. Crocodylians appeared 83.5 million years ago in the Late Cretaceous period. Currently, two alligator species and six species of caimans form the Family Alligatoridae. Thirteen species of crocodiles compose the Family Crocodylidae. Lastly, two species of gharial belong to the Family Gavialidae. In general, offspring mortality for species in the order Crocodylia occurs in the nest at the egg stage, caused by desiccation or suffocation when a hatchling is unable to hatch out of the shell or, after hatching, to crawl out of the nest soil. Other sources of offspring mortality are predators, starvation, diseases, accidents or catastrophes.

In this study, the maternal investments by species in the order Crocodylia were investigated. Offspring number and offspring size at hatch for each Crocodylian species were determined. My results were compared to the predictions of the Smith-Fretwell model and the alternative model.

Christopher Smith and Steven Fretwell (1974) published a paper describing maternal investment by mothers. In their model, mothers could increase offspring size to enhance offspring survival, but they had to sacrifice offspring number per clutch. In other words, a mother that produced more offspring would produce smaller offspring. According to an alternative maternal investment model (Cassill, unpublished data), the goal for each sexually mature female is the survival of two sexually mature offspring to replace her and her mate. To meet this goal, females must overproduce offspring because, unfortunately, most offspring die before maturity. According to the alternative maternal investment model (Cassill, unpublished data), the quality and quantity of offspring per clutch is a result of environmental risk factors. For example, females tend

to produce a few, low quality (small sized offspring) offspring when neither predation nor starvation are risk factors. Some shark fit this maternal investment strategy. Females produce many low quality offspring when predation is the dominant risk factor. Females produce a few high quality offspring when scarcity is the dominant risk factor and when both predation and scarcity are risks. Elephants are an example of a maternal investment of few, high quality offspring. In ants, honeybees and termites, reproductive queens produce a few large, fertile offspring and many, low quality, infertile offspring. In addition, the alternative maternal investment model predicts that offspring quality (size) is independent of offspring number per clutch.

Below, the natural history of each crocodylian species is outlined.

I. Family Alligatoridae

The **Chinese alligator** (*Alligator sinensis*) is native to China, especially to the Yangtze River (Gallagher 2011). They live in places of low-elevation and freshwater sources, including marshes, lakes, streams, and ponds (Thorbjarnarson 2002). Males are about 1.5 m long but some have been recorded up to 2.2 m (Thorbjarnarson & Wang 2001). Females average 1.4 m but some are 1.7 m long (Mertz 2003). The minimum size of reproduction in females is 110 cm (Thorbjarnarson & Wang 2001). Females weigh about 36 kg. The lifespan of the Chinese alligator in captivity is 70 years (Mertz 2003).

Chinese female alligators build nests on land near lakes or rivers in late June to early July (Thorbjarnarson & Wang 2001). These consist of vegetation and mud. They lay an average of 10 to 40 eggs and cover them with vegetation. Females guard the nest by visiting it frequently. Males have no parental involvement. The incubation

period for this species is about 70 days. Like all crocodylians, the sex of the offspring is determined by the temperature of the egg while in the incubation period. Females are produced at temperatures below 28°C and males are produced at temperatures above 33°C. An even number of male and female Chinese alligators is produced at a temperature of 31°C. Eggs hatch in September. Females will help the hatchlings exit the eggs by slowly rolling them around in her mouth and lightly cracking the shell by pressing it between the roof of the mouth and the tongue. She also removes debris covering the nest. The hatchlings weigh about 30 g and are about 21 cm long right after hatching. She will then bring them to the water in her mouth. The mother will remain near the young alligators through the first winter but little is known about the actual interactions between adult Chinese alligators and their young (Mertz 2003). Hatchlings grow rapidly for the first five years of life and maturity is reached after five or seven years of age. While adult Chinese alligators prey mostly on fish, snails, clams, small mammals, waterfowl and even turtles, hatchlings and juveniles eat insects and other small invertebrates. Because of their size and despite their mothers' protection, juvenile alligators and eggs are at risk of predation by other larger animals such as birds, fishes and even other adult alligators (Therbjarnarson & Wang 2001).

The **American alligator** (*Alligator mississippiensis*), the larger of the two species of alligators existing today, is found in North and South Carolina, Georgia, Florida, Louisiana, Alabama, Mississippi, Arkansas, Texas and Oklahoma (Lance 1989). Males measure from 3.4 m to 4.6 m in length, and can weigh 453 kg. Females, on the other hand, are smaller measuring around 3 m and weighing about 295 kg. Females reach

sexual maturity at 1.8 m long when they are about 10 years old, but meet breeding conditions when they are 20 years old. American alligators eat a variety of animals, including fish, turtles, snakes, and mammals such as muskrats and raccoons. Any animal in or near the water is basically a potential prey for these alligators.

American alligators start to breed in the spring (Lance 1989). The female will build a nest out of vegetation, leaves, sticks and mud near the water. She will then lay 20 to 50 eggs, which she will then cover with even more vegetation. First-time mothers and old females lay fewer eggs. Like any of the other Crocodylian species, temperature determines the sex of the offspring. Eggs hatched at 34 °C or more become males while those hatched at 30 °C or lower become females (Joanen 1982). Nests built on wet marsh will be cooler and produce females while those built on leaves will be warmer and produce males. The incubation period of American alligators is 62 to 66 days (Lance 1989). The mother will stay near the nest this whole time, and will eat some of the eggs occasionally (Hunt 1987). When the young are ready to hatch, they will make a unique hatchling sound and just like other crocodylians, the mother will quickly dig them out and carry them to the water in her mouth (Lance 1989). The hatchlings are an average 26.4 cm long and weigh 68 g right after hatching (Goodwin & Marion 1978). Young alligators mostly feed on invertebrates such as insects, snails and worms but also eat frogs and small fish (Hunt 1982). In addition, they are preyed upon by large fish, birds, raccoons and even other adult alligator (Hunt 1982). While on the water, they stay together in pods, which make it easy for the mother to guard and protect them. Mother alligators eventually become more aggressive towards their own offspring. Such behavior encourages them to leave her side and become independent. Young alligators

grow 3 to 8 inches a year and reach adulthood when they are 1.8 m long. An alligator can have a life span of 30 to 50 years.

The **Cuvier's dwarf caiman** (*Paleosuchus palpebrosus*) is found in Bolivia, Brazil, Colombia, Ecuador, Paraguay, Peru, Surinam and Venezuela (Ross 1992), living primarily near streams. Males measure 1.3 to 1.5 m and females up to 1.2 m (Choi 2004) with an average adult typically weighing 6 to 7 kg. Both juveniles and adults eat fish, amphibians and invertebrates, with juveniles feeding on smaller fish (Ross 1989). Members of this species hide in burrows during the day (Choi 2004), tend to be found singly or in pairs and become mature at age 10.

There is no Cuvier's dwarf caiman breeding season. They may nest year around but this is dependent on location (Choi 2004). Both males and females take part in nest building with females laying 10 to 25 eggs (70g each) on a mounded nest constructed of vegetation and mud, and eggs hatching within 90 days after being laid. During the nesting period, both parents become defensive and guard their eggs at all costs, with the females particularly always alert, remaining near the nest and reacting to any stimulus. Males do not regularly stay near the female during the hatching or post-hatching period. Adult females open the nest and help hatchlings reach the water (Campos et. al 2012). Hatchlings have a coating of mucus on them which may delay them from entering the water until this has dried, so they stay around the nest for several days (Choi 2004). Older juveniles (no more than 21 months old) may be found together in the same group with juveniles from the current nesting season under the care of an adult. Females remain with the hatchling group for only a few weeks before

the hatchlings disperse. Females rarely return to their nests to search for young, but can recognize them by smell.

The **Smooth-fronted caiman** (*Paleosuchus trigonatus*) is a small crocodylian native to the Amazon and Orinoco Basins with males growing to 1.7 to 2.3 m long and females rarely growing past 1.4 m (Ross 1989; Villareal 2003). Members of this species inhabit small streams in forests and for that reason are rarely seen in open areas or basking in the sun (Magnusson 1991). During the day they hide in underwater burrows, hollow logs or under fallen trees (Ross 1989). Adults mainly feed on porcupines, snakes, birds and lizards, and less so on fish or mollusks.

Females and males reach maturity and start to breed at 11 years and 20 years respectively and do not breed annually (Magnusson 1991; Villareal 2003). At the end of the dry season, females build mound nests out of leaves and earth (Ross 1989) but can also use old nests. Females lay 10 to 15 eggs, which they cover with more leaves and earth. Females remain near and protect the nest during the 115 day incubation period. When the eggs hatch, they transport hatchlings to a nursery area and stay with them for a mere 7-14 days, after which time the hatchlings naturally disperse (Campos et. al 2012; Magnusson & Lima 1991; Villareal 2003). Hatchlings feed on insects at first then gradually increase their prey as they grow (Ross 1989).

The **Broad-snouted caiman** (*Caiman latirostris*) is found in Brazil, northern Argentina, Uruguay, Paraguay and Bolivia (Rayburn 2011). This species lives in freshwater marshes, swamps and mangroves, but can also be found in still or very slow moving

waters and in human-made cow ponds (Verdade et al 2010). Adults normally reach 2 to 2.5 m in length (Rayburn 2011), (with old males possibly reaching 3.5 m), typically weigh 29.2 to 62 kg, and feed on small invertebrates, turtles and snails (Borteiro et al 2009). Broad-snouted caimans have a lifespan of 22 years in captivity (Rayburn 2011).

Females are responsible for nest building and lay 18 to 50 eggs at a time, with incubation periods lasting 70 days (Verdade et al 2010; Rayburn 2011). Female offspring develop at and above 32°C and male offspring at or lower than 31°C (Lang 1989). During this time, females are very protective and guard the nest with some assistance from the males. When ready to emerge, hatchlings weighing roughly 30g at birth, start calling from within and the mother will take the egg in her jaw to help it crack. Young of this species feed mostly on insects and as they grow, increase their prey variety to birds, fish and other reptiles.

The **Yacare caiman** (*Caiman yacare*) is found in South America (Cintra 1988). Average adult males grow to 2 or 2.5 m in length (with the occasional 3 m individual) and average females grow to 1.4 m long (Mourão et. al 1996). Males and females range in weights of up to 58 kg and 14 to 23 kg respectively, and their diet consists of fish and birds.

Mating occurs in the dry season for this species (Cintra 1988) in contrast to nest building (small mounds constructed of leaves and twigs) and egg laying (18 to 38 eggs) occurring in the wet season. Average incubation period is 70 days long and females exhibit defensive behavior while guarding the nest. When the hatching time arrives, mothers help hatchlings get out of the egg. Hatchlings length and weight varies from 22

to 27 cm and 41 to 57 g, respectively.

The **Spectacled caiman** (*Caiman crocodilus*) is found in much of Central and South America (Terry 2010), and although tolerant of salt water, live in lowland wetlands and rivers. Average adults are 1.5 to 2.1 m long with females being smaller, and tend to weigh 7 and 58 kg. Like other caimans they eat insects, crustaceans, and mollusks and only larger individuals will eat fish and water snails. This species has a lifespan of 30 to 40 years.

The spectacled caiman reaches sexual maturity between 4 to 7 years old (Terry 2010). They gather and mate during the wet season and females, sometimes aided by males, build mound nests made of dense vegetation. Females lay up to 40 eggs (Thorbjarnarson 1994), with each weighing 38 to 85 g. Like any other crocodylian species, the sex of the developing offspring is nest temperature dependent (Terry 2010). Incubation lasts 65 to 104 days and when the eggs hatch, both parents help hatchlings get out of the shells. Hatchlings tend to be 21 to 25 cm long and 35 to 49 g in weight (Allsteadt 1994). Females form crèches in which one female will take care of her own young as well as those of other females (Terry 2010). Hatchlings stay close to the female and sometimes even within the male's territory for 12 to 18 months, receiving care and protection until they disperse (Terry 2010, Velasco & Ayarzagüena 2010).

The **Black caiman** (*Melanosuchus niger*) lives along slow-moving rivers, lakes, seasonally flooded savannas of the Amazon basin, and in other South American freshwater habitats (Thorbjarnarson 2007). Mature females measure 2.5 to 3.35 m and

weigh 95 to 100 kg (Villamarín-Jurado & Suarez 2007). Black caimans prey on a variety of fish, reptiles, birds and mammals.

At the end of the dry season, females build a mound nest made of soil and vegetation (Herron et. al 1990), and lay 30 to 60 eggs (maximum of 65 eggs), with each large egg averaging 144 g in weight (Villamarín-Jurado & Suarez 2007). Females guard their nests aggressively (Herron et. al 1990) with hatching occurring 42 to 90 days after eggs are laid. Females help hatchlings break out of the egg with their teeth, then transport them in the jaw to the water where they form pods and stay close. These pods may consist of hatchlings from other nests. Females look after their hatchlings for several months but the young are largely independent and thus most of them do not survive to maturity.

II. Family Crocodylidae

American crocodiles (*Crocodylus acutus*) can be found from Florida to northern Peru (Thorbjarnarson et. al 2006). Male American crocodiles are about 4.3 meters long while the females are 3 m long and weigh 173 kg. Females first reproduce when they are 2.1 m long (Platt & Thorbjarnarson 2000).

American crocodiles breed in late fall or early winter (Ogden 1978). Mature females begin building the nests in February or March. These are made near the water out of sand, mud, and dead vegetation (Lutz et.al 1984). Depending on the size of the female, she will lay 15 to 56 eggs in a nest and may cover the eggs with dead vegetation or leave them uncovered. The eggs are white, elongated and are 8cm long and 5cm wide with a porous shell (Ogden 1978). The incubation period lasts 75 to 80

days. Again, sex of the offspring is dependent on the nest temperature. Both parents ferociously guard the nest, especially females. During the hatching process, babies emit soft, grunt-like croaks. Mothers respond by opening the nest, if it was covered, and aiding hatchlings out of the eggs either right there at the nest site or in the water (Lutz et.al 1984). Mothers carry hatchlings in the mouth to the water. The hatchlings are about 22 cm in length and weigh about 60 g (Platt & Thorbjarnarson 2000), and actively hunt within a few days of hatching (Lutz et.al 1984). The mother, however, will care for them weeks after they have hatched, providing them transportation and attention (Ogden 1978). Hatchlings become independent within five weeks. Most of them will not survive as they become the prey of birds and large fish. Those that survive grow rapidly and feed on insects, fish, frogs and in some cases, one another.

Orinoco crocodiles (*Crocodylus intermedius*) are found in freshwater environments such as the Orinoco River in Colombia and Venezuela (Thorbjarnarson & Hernández 1993). Males are about 4.1 m in length and 380 kg in weight while females are slightly smaller at about 3.6 m and 225 kg (Greer 1974). Orinoco crocodiles prey on a variety of reptiles, birds and mammals, including caimans on occasion (Ross 1998).

Orinoco crocodiles reproduce in the dry season when the water level is low (Thorbjarnarson & Hernandez 1993). They dig holes in the sand when ready to lay their eggs. The female digs the nest and lays about 40 eggs. Each egg weighs an average of 111.07g (Antelo 2010), with incubation periods lasting about 3 months. Mothers guard their nest vigilantly. Young crocodiles hatch during the night, will call to their mother, and these mothers dig them out of the nest and carry them to the water in her mouth.

They are about 28.6 cm and 66.9 g in weight (Antelo 2010). Males grow faster than females. It is known that in captivity, both sexes help to feed the young by bringing and dismembering the prey near them. The female will defend pods of juveniles for over 3 years (Ross 1998).

Freshwater crocodiles (*Crocodylus johnstoni*) are endemic to Australia (Webb 1988). Unlike the dangerous saltwater crocodile, these crocodiles are known to be shy. They are relatively small with males growing 2.3 to 3 m long and females reaching a maximum size of 2.1 m. Males commonly weigh around 70 kg while females weigh about 40 kg. The diet of the adults consists of fish, birds, bats, reptiles and amphibians. This species lives for up to 50 years (Tucker 1997).

Freshwater crocodiles are hole-nesters (Somaweera 2012). The female lays about 12 eggs in holes during the Australian dry season (usually in August) and these eggs hatch at the beginning of the wet season (November/December). Unlike other species, the crocodiles do not defend their nests during the incubation period. From one to five days before hatching, the young begin to call from within the eggs. Such sound stimulates hatching in siblings and also signals for adults to open the nest. However, it is not known if the adult that opens a given nest is the respective parent. Adults will help hatchlings by breaking through the eggshell. Hatchlings measure about 24 cm, and once they are out of the nest, the adult picks one hatchling at a time and carries it to the water. Unlike reports on the *A. mississippiensis* and *C. johnstoni*, this species is not known to accidentally swallow her eggs as the young are attempting to hatch (Somaweera 2012).

Philippine crocodiles (*Crocodylus mindorensis*) are small, freshwater crocodiles endemic to the Philippines (Van Weerd & van der Ploeg 2003) and live in rivers, creeks, ponds and marshes (van Weerd 2010). They average 1.5 m in length, with females a bit smaller than males. As juveniles their diet consists of shrimps, dragonflies, small fish and snails. Larger crocodiles feed on all these in addition to large fish, wild and domestic pigs, dogs, civet cats, snakes and water birds. Both sexes reach maturity at 1.5 m and 15 kg (van Weerd 2010).

Females build nests consisting of dried leaves, twigs, bamboo leaves and soil during the dry season, and situate these nests near the river. After females lay eggs, both male and female crocodiles take turns guarding the nest. The female crocodile usually visits the nest during the late afternoons and early mornings. Mean clutch size in the wild is 20.1 eggs but in captivity the clutch averages 26 eggs. Like the other crocodylian species, Philippine crocodiles exhibit temperature-dependent sex determination, with females being produced at 30°C to 31°C and males at 33°C. Philippine crocodiles are very aggressive towards each other. During their second year, juveniles establish individual territories through aggressive interactions.

Morelet's crocodiles (*Crocodylus moreletii*) are found in the Atlantic regions of Mexico, Belize and Guatemala (Abercrombie et. al 1980) and mainly reside in fresh waters (Platt & Thorbjarnarson 2000). Adults average 2.2 to 3 m in length (Abercrombie et. al 1980). Females weigh around 58.1 kg (Hurley 2005). Their diet consists of small mammals, birds, and reptiles (Platt & Thorbjarnarson 2000). Morelet's crocodiles have a lifespan

of 80 years (Hurley 2005).

Breeding in this species occurs between April and June, right before the wet season (Platt et. al 2008). Unlike other species which build mound and hole nests, Morelet's crocodiles are known to only build mound nests located near the water or on floating vegetation. Females lay 20 to 45 eggs with mean egg length and width being 57.0 to 98.2 mm and 35.4 to 49.0 mm, respectively. Nests can contain eggs from more than one female. Females protect the nests from predators during the incubation period which last about 80 days. When ready to emerge from the egg, hatchlings begin to vocalize and the mother responds rapidly. Hatchlings are about 23 cm long and weigh about 31.9 grams (Hurley 2005). Once out of the egg, females carry their young to the water and will carry multiple hatchlings at a time in her mouth (Hunt 1987). Hatchlings form pods while in the water, and may remain intact for up to 2 years. Once in the water, both parents protect the young aggressively. They would respond to distress calls made by the hatchlings if they get captured (Platt et. al 2008). However, adults also threaten and attack young crocodiles, especially during egg incubation and hatching periods (Hunt 1977). Hatchlings mainly feed on fish and insects until they become bigger and more capable of bringing down larger prey.

Nile crocodiles (*Crocodylus niloticus*) are endemic to Africa (Ross 1989). They inhabit both fresh and saltwater, but are rarely found in the latter. Male crocodiles usually measure from 3.5 to 5 m long and mature female measure 2.5 to 3.8 m (B Cott 1961). The size of their prey depends mostly on the size of the crocodile itself. Hatchlings usually feed on small fish, frogs, insects and small aquatic invertebrates (Ross 1989).

Juveniles and sub-adults feed on the previously mentioned organisms, as well as on birds, turtles, snakes, and small to mid-sized mammals, such as various monkeys, and porcupines. Adults prefer to feed on larger fish like catfish and freshwater bass but they also consume birds, reptiles and mammals such as antelopes, in addition to prey consumed also by the younger specimens (B Cott 1961). Nile crocodiles also prey on humans far more often than other crocodylian species (Ross 1989). Males reach maturity when they are about 3 m long while females become mature when they are 2 to 2.5 m long (Kofron 1990) and this takes roughly 10 years for either sex under normal conditions. This species can live up to 80 years.

About two months after mating, females lay about 16 to 80 eggs (Pooley & Gans 1976) with nesting occurring in November or December. Females prefer to build their nests near sandy shores, dry stream beds, or riverbanks (Modha 1967) and dig a hole a few meters from the bank. Multiple females may choose to nest close together. Female Nile crocodiles bury their eggs in sand (Guggisberg 1972) as opposed to incubation in rotting vegetation. Both parents fiercely guard the nest during incubation by attacking anything approaching their eggs (Pooley 1977). The female only leaves the nest if she needs to cool off the heat (Pooley 1977). Nile crocodiles have temperature-dependent sex determination.

When ready to hatch, the young ones start to make a high-pitched chirping noise that stimulate the mother to rip open the nest (Magnusson 1980). Both parents may help the hatchlings get out of the eggs by gently picking up the eggs in their mouths, and roll them between their tongue and the upper palate (Modha 1967). Once out of the egg, females may lead the hatchlings to water, or even carry multiple hatchlings in her

mouth (Hunt 1987). Hatchlings are about 30 cm long at birth and weigh 52.3 to 83.9 g (Modha 1967). If there are multiple nests in the same area, the mothers may form a crèche to protect the hatchlings. To keep them safe, the mothers may choose to keep their offspring in their mouth (Pooley 1977). She can also carry them on her back to avoid them from being eaten by turtles or water snakes.

New Guinea crocodiles (*Crocodylus novaeguineae*) are found on the island of New Guinea (Ross 1989). This species of crocodile is relatively small and even though tolerant of saltwater, are rarely found in such environments. Instead they inhabit freshwater swamps and lakes. Males and females grow to a length of up to 3.5 m and 2.7 m respectively (Ross 1992). Females become sexually mature at about 1.6 to 2 m long and males at about 2.5 meters. They are mostly active at night when they eat (Jerome Montague 1983) with adults mostly feeding on fish, crabs, frogs, snakes, birds, and bats (Ross 1989). This species has an average life span of 25 years (Tran 2013).

The population in the northern parts of New Guinea breeds during the dry season (Cox 2010). Females make floating nests composed of vegetation (Tran 2013). Clutch sizes range between 22 and 45 eggs (Ross 1992); with each egg weighing about 86 g (Hall 1985). In the south, however, breeding occurs in the wet season (Cox 2010). Similar nests made of vegetation are built and larger but fewer eggs are laid (Tran 2013). At both locations, mothers stay close to the nest during the averaged 80 day incubation period (Ross 1992). When the hatchlings (averaging 29 cm in length) emerge, both parents transport young inside their mouth into the water (Hall 1985; Tran 2013). Hatchlings feed on aquatic insects, frogs, fish, and snails (Ross 1989) and communicate via different vocalizations even while still in the egg (Tran 2013). When in

danger, a warning sound emitted by one alerts the others and hatchlings will all dive to the bottom of the water. Distress noises of young stimulate adults and these become involved in overexcited activity; rushing towards the juvenile, beating about in the water and slapping their heads down on the surface.

The **Mugger crocodile** (*Crocodylus palustris*) is found throughout the Indian subcontinent and near-by countries (Ross 1989). Freshwater lakes, ponds, sluggish rivers, swamps and marshes make up the majority of their habitat (Da Silva & Lenin 2010). Males grow to be 4 m to 4.5 m in length (Ross 1989). Females become sexually mature at 1.8 to 2 m long and weigh about 200 kg. These crocodiles' diet consists of fish, reptiles, birds and mammals (Ross 1989). They are not as aggressive as some other species, and have a life span of 28 to 40+ years (Lammy 1999).

Females dig holes in the sand at the opening of or inside their burrows and lay 25 to 35 eggs with each weighing 85 g. Like other crocodylian species, incubation temperatures determine the sex of the offspring (Ross 1989; Whitaker and Whitaker 1989). Average incubation is 55 to 75 days, during which time mothers aggressively defend nests (Da Silva & Lenin 2010; Ross 1989). At the end of incubation, both parents excavate the nest in response to the (31 cm long) hatchlings' call, and they transport and guard the young to and in the water (Lammy 1999; Ross 1989). The male is known to take his parent role so serious that he will chase away any crocodile including the own mother. Hatchlings remain in groups with the adults until about one year, after which they disperse (Lammy 1999).

The **Saltwater crocodile** (*Crocodylus porosus*) can be found in coastal waters between Northern Australia and the southern coast of India (Ross 1989). Although these crocodiles can live in salt water, their habitat usually consists of mangrove swamps, estuaries, lagoons, and rivers. They are the largest of all living reptiles with males reaching to sizes of up to 6.7 m and weighing as much as 2,000 kg (Erickson 2012). However, an adult male saltwater crocodile is more commonly 4.3 to 5.2 m long and weighs 400 to 1,000 kg. Females are approximately 3 m and 1000 kg. Prey selection of this species is based on availability and size; the larger they are the greater the prey variety (Ross 1989). Saltwater crocodiles have a life span of up to 70 years with some possibly exceeding 100 years ("Saltwater crocodile" 2008).

Saltwater crocodiles mate during the wet season (Ross 1989). Females select a site along rivers or freshwater areas to construct a nest, a mound of mud and vegetation. She then lays 40 to 80 eggs. As in all of the other species, hatchling sex is nest temperature dependent (Wayman 2002). Both parents defend the nest but the female guards it at all times during the 80 to 98 days incubation period. When the hatchlings are ready to hatch they start yelping and the mother excavates the nest, rolls the eggs in her mouth to help them get out and then transport them in her mouth to the water. She stays with them for at least two months and then the young ones will naturally disperse (Webb, Messel & Magnusson 1977). Newly hatched saltwater crocodiles measure about 32 cm long and weigh an average of 90 g (Brien et. al 2013). Males reach sexual maturity at around 3.3 m and 16 years of age, while females reaching sexual maturity at 2.1 m and 12 to 14 years of age (Wayman 2002). Hatchlings feed on smaller animals including small fish, frogs, insects and small aquatic

invertebrates (Grigg et. al 1980).

The **Cuban crocodile** (*Crocodylus rhombifer*) is a small but aggressive species of crocodile found only in Cuba's Zapata Swamp and the Isle of Youth (de Sola 1930). The Zapata Swamp habitat is very similar to that of the Floridan Everglades. They inhabit freshwater environment such as swamps, marshes, and rivers and rarely swim in salt water (Targarona 2010). Adults measure 2.1 to 2.3 m in length on average and weigh 70 to 80 kg (Targarona 2008). Large males, however, can reach to 3.5 m in length and weigh 215 kg or more (Targarona 2008). Most females begin reproducing when they are 6 to 7 years old (Targarona 2010). Like other crocodilians, their diet consists of small fish, arthropods, crustaceans, small mammals, and turtles (de Sola 1930). The lifespan of the Cuban crocodile is unknown but may live up to 75 years in zoos ("Cuban Crocodile" 2000)

The Cuban crocodile breeding season overlaps with that of the American crocodile by a few days in the month of January (Varona 1966). Little is known about the reproduction habits of these crocodiles. Nonetheless, their nests have been described in the past as holes dug in the ground, filled with dirt and vegetation (Targarona 2010). Subsequent research indicates however that they construct mounds, usually made of peat (Targarona 2010). Females tend to lay 25 eggs in captivity and 15 eggs in the wild (Targarona 2010). Each egg weighs about 104 g, with hatching taking place in August and early September (Ramos 2000; Thorbjarnarson 1996).

The **Siamese crocodile** (*Crocodylus siamensis*) is a small freshwater crocodile native

to Indonesia, Brunei, East Malaysia, Laos, Cambodia, Burma, Thailand, and Vietnam (Platt 2000). Adults average 2.1 m in length and 40 to 70 kg in weight. The largest female measures 3.2 m and weighs 150 kg while large males can reach 4 m and weigh 350 kg. Adults feed on fish, amphibians, reptiles and small mammals and have a lifespan of more than 60 years (Ross 1989; Siamese crocodile 2014).

It has been observed that while in captivity, Siamese crocodiles deposit eggs during the dry season (Platt et. al 2006). Females build mound-nests out of scraped-up plant debris mixed with mud and lay 20 to 50 eggs, 106.9 g each, which are guarded until they hatch (Platt et. al 2012; Thorbjarnarson 1996). The incubation period is 60 to 80 days, with females helping the young get out of the eggs and then carrying them to the water in the jaw.

The **African slender-snouted crocodile** (*Mecistops cataphractus*) is native to freshwater habitats in central and western Africa (Waitkuwait 1989). This is a medium sized crocodile, with adults measuring 3 to 4 m and weighing 125 to 230 kg. Slender-snouted crocodiles are sexually mature when they reach 2.0 to 2.5 m in length at 10 to 15 years of age (Lavinder & Pennington 2012). Their slender snout is used for catching prey, which consists mainly of fish, snakes, amphibians and crustaceans. This species is not usually found in groups, except during their breeding season (Abercrombie 1978). They have a lifespan of at least 40 years (Lavinder & Pennington 2012).

During the wet season, females constructs a mound nest out of plant matter on the banks of rivers and lay an average (13 to 27 range) of 16 very large eggs (relative to body size) about a week after building the nest (Abercrombie 1978). The incubation

period lasts over 110 days (Waitkuwait 1989). Females remain close to the nest, but do not defend it with the same vigor as some other species of crocodilians. Once the eggs begin to hatch and the young start chirping, mothers break open the nest, assist in the hatching process and hatchlings disperse across the flooded forest floor (Abercrombie 1978). Hatchlings are roughly 31 cm long. They will stay near the nest for as long as two weeks, with both parents defending and caring for them during this time (Lavinder & Pennington 2012; Waitkuwait 1989).

The **Dwarf crocodile** (*Osteolaemus tetraspis*) is endemic to Central and West Africa, with adults averaging 1.5 m in length, and the largest growing to 1.9 m (Kofron 1994; Waitkuwait 1989). Largest females and males may weigh up to 40 kg and 80 kg respectively, with both reaching sexual maturity at age 5. Dwarf crocodiles feed on vertebrates and large invertebrates (Eaton 2010). They are slow, timid and nocturnal (digging burrows to hide and rest during the day), only interact during their breeding season and may live to 50 years.

During the wet season females build nest mounds near the water, and lay 15 eggs (each weighing about 64g) which incubate for 85 to 105 days (Hara & Kikuchi 1978; Kofron 1994; Waitkuwait 1989). Mothers aggressively guard the nest and will watch over the hatchlings for many months after hatching (Campos et. al 2012; Waitkuwait 1989). Newly born dwarf crocodiles measure 28 cm and weigh 47 g (Hara & Kikuchi 1978; Waitkuwait 1989).

III. Family Gavialidae

The **gharial** (*Gavialis gangeticus*) is found in the northern part of the Indian subcontinent and inhabits freshwater habitat such as rivers with fast flowing currents (Bouchard 2009; Ross 1989), with fish being the primary constituent of their diet. They can reach lengths of 6.5 m with females always being smaller than males and weigh 160 to 180 kg. Females become mature at 8 years of age and 3 m in length.

These hole-nesters breed once per year, with mating and nesting occurring during the dry season. Females lay 28 to 43 eggs, each weighing about 156 g and having an incubation period of roughly 80 days (Bouchard 2009; Ross 1989). Females visit and guard eggs during the night but remain in the water during the day. Females and males excavate the nest during hatchling, but do not pick up the 18 cm long young. Females protect hatchlings for several weeks after hatchling. Males do not protect them but do tolerate them nearby.

The **false gharial** (*Tomistoma schlegelii*) is native to Indonesia, Malaysia and Brunei (Foster 2013), residing in freshwater habitats such as swamps, lakes, streams and slow-moving rivers. Adults measure 4 to 5 m and weight 90 to 210 kg. Like other crocodylians males are larger than females, both sexes become mature at about 20 years of age, and have a life span of 60 to 80 years. They mostly prey on fish due to the structure of their snout but small vertebrates may be included if present (Revol 1995).

False gharials breed twice a year (Foster 2013), with nesting taking place in the rainy season. Females construct mound-nests and lay 20 to 60 very large eggs weighing up to 155 g each. Young hatch after 90 days of incubation and males have no

parental investment beyond fertilization. Females however sit on top of nest mounds and will defend these. Females also may help to excavate nests before or during hatching. Unlike other crocodylians, they do not move hatchlings in their jaw to the water.

METHODS

My null hypothesis was that hatchling quality (weight in g) was not correlated to hatchling number. My working hypothesis (the Smith-Fretwell hypothesis) was that hatchling size was negatively correlated with hatchling number (more hatchlings would result in smaller hatchlings). Offspring number, offspring body size/weight, and female body size/weight for each crocodylian species were obtained from numerous research studies (see Introduction). These data were analyzed to determine relationships between mother and offspring traits. When a range of body sizes was given for offspring and reproductive females for a single species, the high number was selected. Similarly, when a range of offspring number per clutch was given per species, the high number was also selected. The maximum sizes were selected because we were looking for trends in offspring quality and quantity at the extreme. Data are summarized in the table below.

Table 1: Mother and offspring traits by species.

Groups	Species name	Egg Number/ Nest	Hatchling Size (cm)	Hatchling Size (g)	Breeder Size (cm)	Breeder Size (g)	Breeder Longevity	Offspring Quality	Log Breeder Size (cm)
A	Chinese alligator (Alligator sinensis)	40	21	30	170	36000	70	0.00083 3	2.23
A	American alligator (Alligator mississippiensis)	50	26	68	300	295000	50	0.00023 1	2.47
C	American crocodile (Crocodylus acutus)	56	22	60	300	173000		0.00034 7	2.47
C	Orinocco crocodile (Crocodylus intermedius)	40	37	129	360	225000	80	0.00057 3	2.55
C	Freshwater crocodile (Crocodylus johnsoni)	12	24	51	210	40000	50	0.00127 5	2.32
C	Phillipine crocodile (Crocodylus mindorensis)	26			150	15000			2.17
C	Morelet's crocodile (Crocodylus moreletii)	45	23	50	300	58100	80	0.00086 1	2.47
C	Nile crocodile (Crocodylus niloticus)	80	30		380	550000	80		2.57
C	New Guinea crocodile (Crocodylus novaeguineae)	45	29	85	270		25		2.43

C	Mugger crocodile (<i>Crocodylus palustris</i>)	35	31	85	200	200000	28	0.000425	2.30
C	Saltwater crocodile (<i>Crocodylus porosus</i>)	80	32	90	300	1000000	70	0.00009	2.47
C	Cuban crocodile (<i>Crocodylus rhombifer</i>)	25	33	104	230	80000	75	0.0013	2.36172784
C	Siamese crocodile (<i>Crocodylus siamensis</i>)	50	33.5	106.9	320	150000	80	0.000713	2.50514998
C	African slender-snouted crocodile (<i>Mecistops [Crocodylus] cataphractus</i>)	27	31		400	230000	50		2.60205999
C	Schneider's Dwarf crocodile (<i>Osteolaemus tetraspis</i>)	15	28		140	40000			2.14612804
a	Cuvierf's Dwarf caiman (<i>Paleosuchus palpebrosus</i>)	25	23	50	120	7000		0.007143	2.07918125
a	Smooth-Fronted caiman (<i>Paleosuchus trigonatus</i>)	15	23	50	140	15000		0.003333	2.14612804
a	Broad-snouted caiman a(<i>Caiman latirostris</i>)	60	21	30	250	62000	22	0.000484	2.39794001

a	Yacare caiman (Caiman yacare)	38	27	57	140	23000		0.00247 8	2.14612 804
a	Spectacled caiman (Caiman crocodilus)	40	25	49	210	40000		0.00122 5	2.32221 929
a	Black caiman (Melanosuchus niger)	65	38	144	335	100000		0.00144	2.52504 481
G	Gharial (Gavialis gangeticus)	43	37	130	450	181000		0.00071 8	2.65321 251
G	False gharial (Tomistoma schlegelii)	60	40	160	400	90000	80	0.00177 8	2.60205 999

RESULTS

The number of eggs per nest did not vary significantly by family group (Fig. 1a; Oneway ANOVA: $F_{2,22} = 0.24$; $p = 0.786$). The longevity of the breeder did not vary significantly by family group (Fig. 1b; Oneway ANOVA: $F_{2,22} = 0.91$; $p = 0.429$). The length of the breeder varied significantly by family group (Fig. 1c; Oneway ANOVA: $F_{2,22} = 6.0$; $p = 0.0089$). Hatchling length varied significantly by family group (Fig. 1d; Oneway ANOVA: $F_{2,22} = 7.1$; $p = 0.0082$).

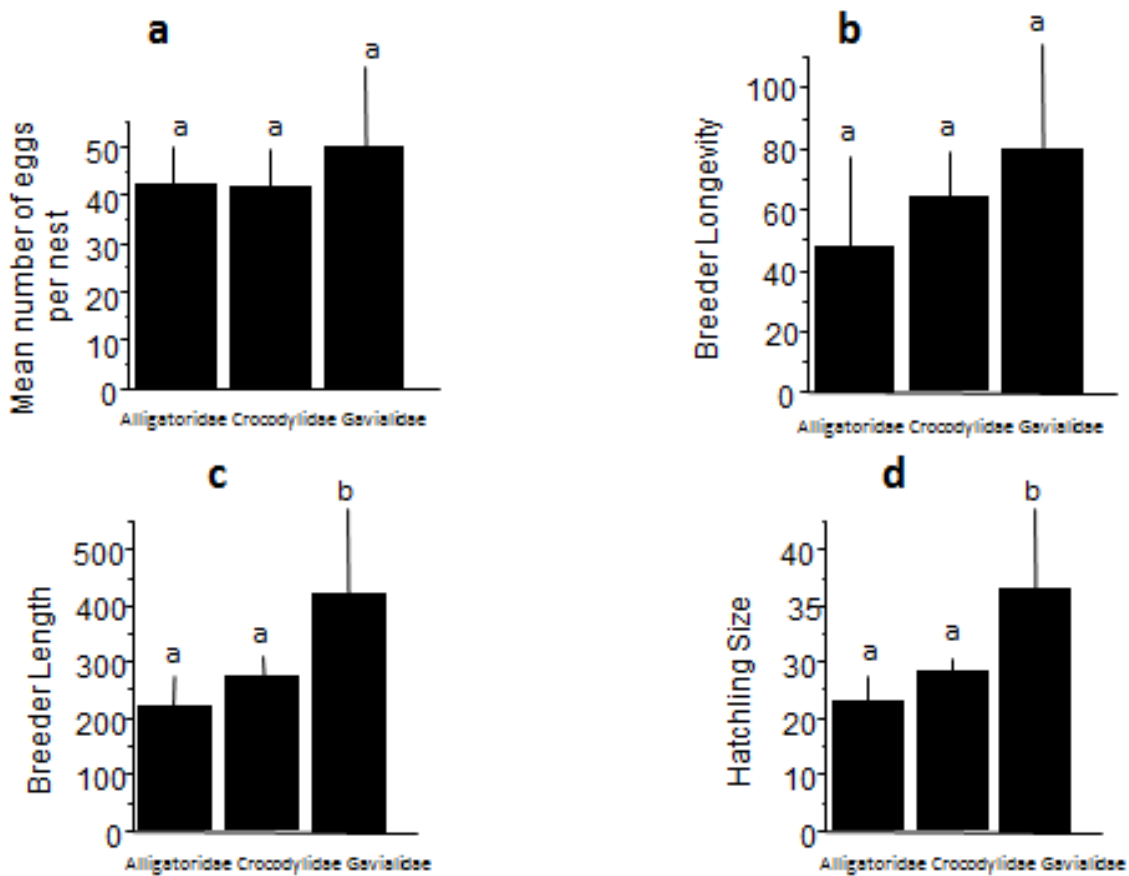


Figure 1: Maternal investment variables by three families within the order Crocodylia.

(a) Mean number of eggs per nest. (b) Breeder longevity. (c) Breeder length. (d) Hatchling size

The number of eggs per nest was not significantly correlated with hatchling size (Fig. 2a; Regression: $R^2 = 0.088$; $p = 0.264$). Although there appears to be a correlation between breeder size and hatchling size, the correlation was not statistically significant (Fig. 2b; Regression: $R^2 = 0.211$; $p = 0.073$). When analyzing just the crocodiles, there was a slightly negative correlation between breeder size and hatchling size but this was not statistically significant (Fig. 2c; Regression: $R^2 = 0.012$; $p = 0.833$). When analyzing the crocodiles again, there was a correlation between breeder size and egg number per nest, the larger the breeder the more eggs they have (Fig. 2d; Regression: $R^2 = 0.62$; $p = 0.0023$). When analyzing all groups of breeders, there was a positive correlation between the number of eggs per nest and the breeder size (Fig. 2e; Regression: $R^2 = 0.38$; $p = 0.0018$). There was a positive correlation between the breeder size and the hatchling size (Fig. 2f; Regression: $R^2 = 0.36$; $p = 0.0029$). There was no correlation between the breeder size and its longevity (Fig. 2g; Regression: $R^2 = 0.15$; $p = 0.172$).

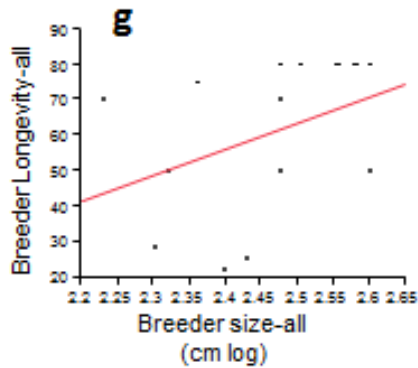
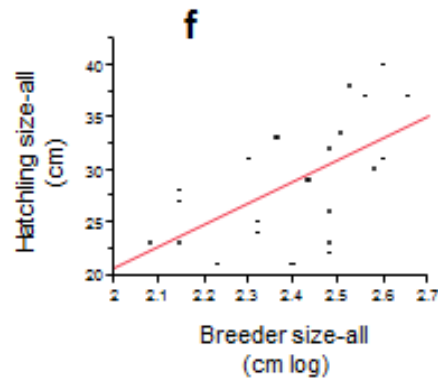
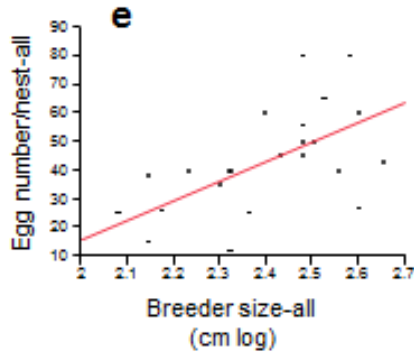
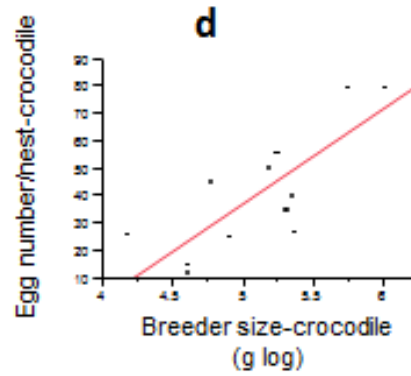
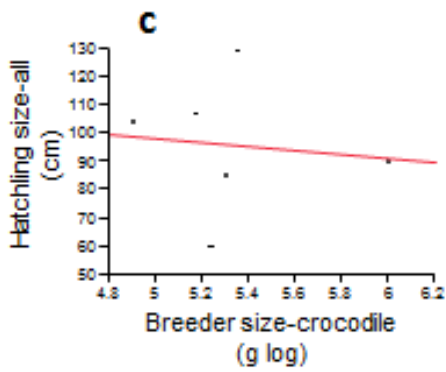
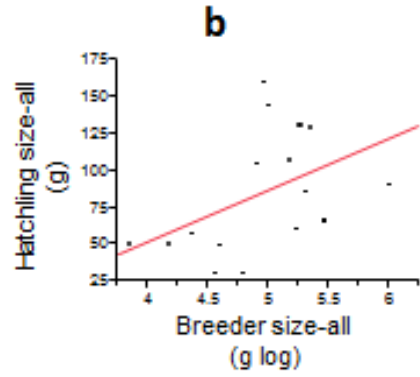
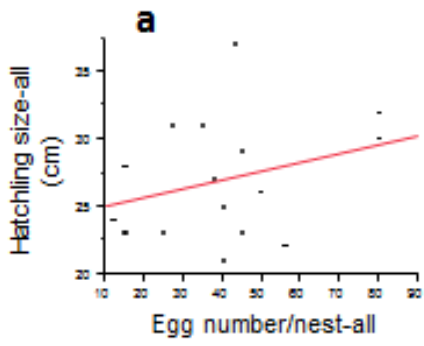


Figure 2: Relationship of maternal investment variables. (a) Hatching size (cm) vs. Egg number per nest for all crocodilians. (b) Hatching size (g) vs. Breeder size (g log) for all crocodilians. (c) Hatching size (cm) vs. Breeder size (g log) for the family Crocodylidae only. (d) Egg number per nest vs. Breeder size (g log) for the family Crocodylidae only. (e) Egg number per nest vs. Breeder size (cm log) for all crocodilians. (f) Hatching size (cm) vs. Breeder size (cm log) for all crocodilians. (g) Breeder longevity vs. Breeder size (cm log) for all crocodilians.

When analyzing maternal investments of the species within the order Crocodylia, according to the alternative model, I found that the hatchlings of crocodilians, as a group, are vulnerable to predation more than they are vulnerable to starvation (Fig. 3).

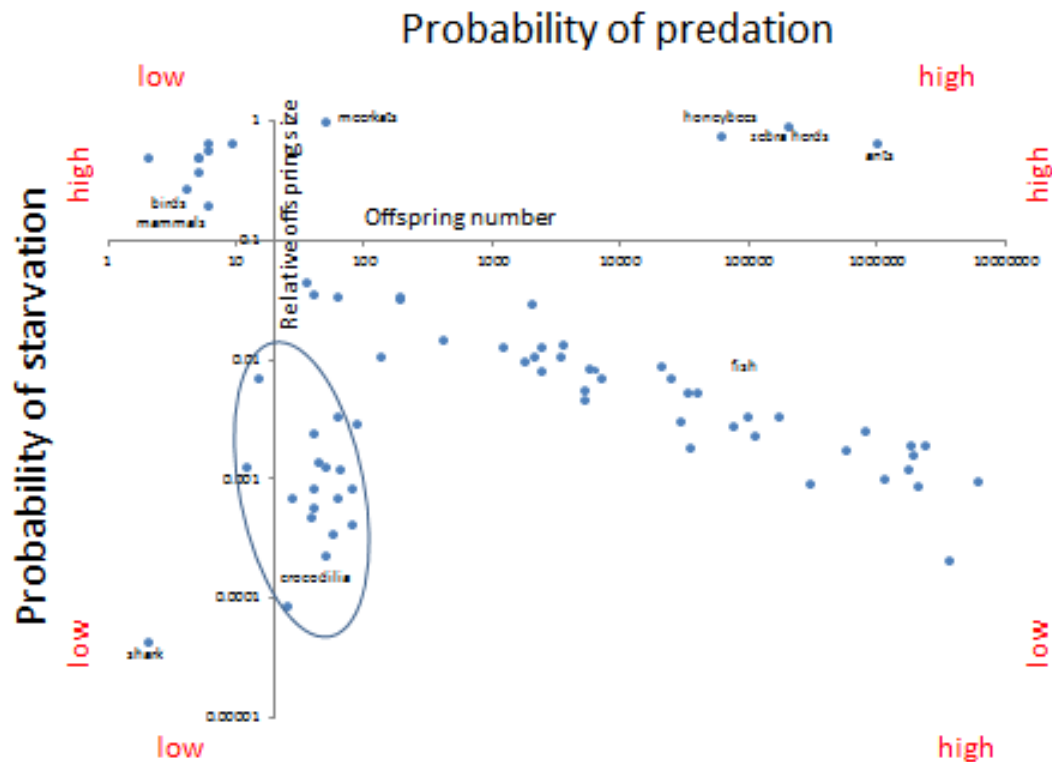


Figure 3: Maternal investments for a number of animal groups. Data inside the oval were the investments of the order Crocodylia. Other data are from alternate sources (Cassill, manuscript in preparation). To determine maternal investments per species using the alternative model, data on offspring quantity and relative offspring quality were plotted. The alternative model (Cassill, unpublished data) assumes that predation selects for large clutch size and starvation selects for large hatchling size and extended parental care.

DISCUSSION

In this study, it was found that egg number per clutch, hatchling size, breeder size and longevity did not vary among the three family groups within the order Crocodylia. I speculate that the fact that adults continue to grow throughout their lifetime is a confounding factor that interferes with viable patterns. When analyzing differences among species (not just family groups), it was found that larger breeders produced more eggs per clutch and larger hatchlings. This finding contradicts the Smith-Fretwell model and supports the alternative model hypothesis that egg number per clutch and hatchling sizes per clutch are independent variables.

The Smith-Fretwell model of maternal investment suggests there is a tradeoff between offspring quality and offspring quantity. Mothers who invest more in offspring quantity will produce smaller hatchlings. Likewise, mothers who invest in larger offspring, eggs or hatchlings must sacrifice offspring number.

In the final analysis, hatchlings were about the same size regardless of the

number of eggs produced. Thus, we need a different model to explain maternal investment patterns in the order Crocodylia. The alternative maternal investment model (Cassill, unpublished data) has the potential to explain offspring quality and quantity based on environmental factors. Future studies on maternal investment must include not only the number of offspring per clutch but the size (length or weight) of offspring per clutch as well.

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