2010

The Evolution of the Family

Benjamin E. Hardisty

The Evolution of the Family

by

Benjamin Hardisty,

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Environmental Science, Policy and
Geography
College of Arts and Sciences
University of South Florida—St. Petersburg

Major Professor: Deby Lee Cassill, PhD.
Erika Asano, PhD.
Alison Watkins, PhD.

Date of Approval:
July 7, 2010

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

The Evolution of the Family

Benjamin Hardisty

ABSTRACT

Biological levels of complexity usually begin with the cell and extend forward to tissues, organs, organ systems, organisms, populations, community, and end with ecosystems. The family is a unit of biological complexity is missing. As a result, the evolution of altruism and cooperation from a natural selection perspective has not been produced. In the following chapters, I argue that the family is a unit of biological complexity will illuminate such mysteries as the evolution of eusociality, theories of lifetime fitness—sometimes referred to as Lifetime Reproductive Success (LRS)—cultural learning and its importance as a parallel mechanism of inheritance, finally, the resolution of evolutionary arms races. The key insight offered here is that the formation of family groups may offer an alternative to past models of group formation in organisms as diverse as snakes and humans, cultural evolution in humans and other primates and arms races in marine organisms. Each of the attempts to model the evolution of altruism and cooperation has been unsuccessful because they have ignored the fundamental reality that an extended period of parental investment combined with cooperative brood care has led to some of the most ecologically dominant organisms on earth: humans, social insects and birds.

INTRODUCTION: FOCUS ON THE FAMILY

For the past three years, though I am originally a philosopher by training, I have

been reading and thinking about the biology of social groups and aggregations. In my

attempt to answer the question of why we have groups at all when solitary foragers and

pair-bonded animals can be, and are, ecologically successful in that they fulfill their basic

life-history functions generation after generation, I have been led to the primacy of one

idea above all. This idea is that life in family units and extended family units, i.e.,

cooperative breeding of varying degrees of "cooperativeness," is what has produced some

of the most ecologically dominant species in the history of life. By using the term

"dominant" I allude to the fact that these candidate species can live in a variety of

environments, successfully reproduce generation after generation, and overcome

extremely challenging ecological conditions, when necessary, by migrating and

colonizing new habitats, or by out-competing neighboring groups of similar species, and

often by out-competing totally different species. Often, these species also engage what is

called eco-system engineering or "niche construction." In particular, the species to which

I am referring to include humans, social insects and birds.

The family is one unit of biological complexity that has scarcely been analyzed in

an evolutionary context (Clutton-Brock 1991; Hrdy 1999; Forbes 2005). For example,

while Clutton-Brock (1991) discussed a variety of data and hypotheses on parental

investment in multiple phyla, it contained no information about why families might have

formed in the first place. Hrdy's (1999) book contained a long discussion of female

lactation in primates in general, and in humans in particular, and she argued that humans

have always been cooperative breeders, a no doubt controversial position on human

evolution. She briefly alludes to the idea that keeping multiple males around to protect

their offspring may have led to the first family units in primates. However, she never

spells out this position clearly beyond her use of the cooperative breeding concept and

her comparison of human families with eusocial insects and eusocial naked mole-rats.

She did speculate, however, that humans may represent something special in evolution

because we possess some of the most beneficial traits of the social insects (cooperative

care of brood, life in extended family units and group foraging) and of primates (large

brains, complex social alliances and pair-bonding).

Forbes (2005), in his *A Natural History of Families*, has anticipated some of my

thinking, particularly his thesis that at least in a large number of species of birds—

solitary, pair-bonded and cooperative breeders included—breeders seem to be create a

"disposable caste." That is, breeders in these species, which includes both synchronous

and asynchronous egg laying species, always overproduce offspring and typically only

the first to hatch survives to adulthood and successfully reproduces. Occasionally, when

environmental conditions are exceptionally good, several baby birds in a single nest live

to adulthood and start families of their own, but most often the last birds to hatch are

killed by their older sibling/s or their mother, are forcefully ejected from the nest and fall

to their death, or are simply allowed to starve to death. Thus, Forbes believes that in

birds, families have arisen as a bet-hedging strategy to protect against uncertain resource

cycles. In ants, Cassill (2002) argues that queens produce a disposable caste of sterile

offspring that protect the queen and her fertile offspring from starvation and predation. In addition to producing sterile offspring, ant queens overproduce fertile offspring and bias their size such that only a few of the largest are likely to mate and survive long enough to produce their own family (Cassill et al. 2007).

In the following chapters, I argue that the family is a unit of biological complexity whose study can illuminate such mysteries as the evolution of eusociality, theories of lifetime fitness—sometimes referred to as Lifetime Reproductive Success—cultural learning and its importance as a parallel mechanism of inheritance, group formation and, finally, evolutionary arms races. In particular, I believe that the evolution of the family is one of the greatest uncelebrated events in the history of life on Earth. The family can accomplish what solitary foragers cannot: it can be an anti-predation strategy, a resource accumulation strategy and a strategy by which breeders can focus on producing genetic variability by utilizing cooperative care of brood *or* over production of offspring. The formation of family groups thus offers an alternative to past thinking about social insects, group formation in organisms as diverse as snakes and humans, cultural evolution in humans and other primates and arms races in marine organisms. All of these questions have been addressed before (social evolution in insects: Darwin 1859; Hamilton 1964; Hamilton 1967; Wilson 1971; Michener 1974; Wilson 1975; Oster and Wilson 1979; Wilson and Sober 1989; Holldobler and Wilson 1990; Holldobler and Wilson 1995; Stern and Foster 1996; Queller et al. 2000; Griffin and West 2002; Wilson 2005; Foster et al. 2006; Heikki and Bargum 2007; Wilson and Wilson 2007; mechanisms of group formation: Wynne-Edwards 1963; Wynne-Edwards 1965; Williams 1966; Hamilton 1971; Connor 1986; Clements and Stephens 1995; Connor 1995a; Connor 1995b; Connor

1995c; Wilson 1997; Wilson and Dugatkin 1997; Landa 1998; Sober and Wilson 1998; Duffy et al. 2000; Cassill 2002b; Duffy 2003; Cassill and Watkins 2004; Cassill 2005; Cassill 2006; Teyssedre et al. 2006; Cassill et al 2007; Field 2008; Landa 2008; Cassill and Watkins 2010; Cassill et al. 2010; the evolution of cultural behavior in: Dawkins 1976; Boesch and Boesch 1989; Boesch and Boesch 1990; Boesch 1994; Stanford et al. 1994; Stanford 1996; Smolker et al. 1997; Reader and Laland 2001; Boesch 2002; Biro et al. 2003; Ridley 2003; Lonsdorf et al. 2004; Hayashi et al. 2005; Krutzen et al. 2005; Richerson and Boyd 2005; Whiten 2005; Whiten et al. 2005; Laland and Sterelny 2006; Hopper et al. 2007; Laland et al. 2007; Lycett et al. 2007; Pruetz and Bertolani 2007; Whiten et al. 2007; Madden 2008; Sanz and Morgan 2009; Sergeant and Mann 2009; and arms races in: Vermeij 1973; Dawkins 1976; Stanley 1977; Vermeij 1977; Vermeij 1978; Signor and Brett 1984; Vermeij 1987; Allmon et al. 1990; Oji 1996; McClintock et al. 1999; Vermeij 1999; Bambach et al. 2002; Amano and Vermeij 2003; Baumiller and Gahn 2004; Dietl et al. 2004; Vermeij 2004; Grey et al. 2005; Kowalewski et al. 2005; Reinhold and Kelley 2005; Vermeij 2005; Aberhan et al. 2006; Amano 2006; Harper 2006; Kelley and Hansen 2006; Kowalewski et al. 2006; Madin et al. 2006; Roopnarine et al. 2006; Vermeij 2006a; Vermeij 2006b; Vermeij and Dietl 2006; Wilson and Taylor 2006; Amano and Jenkins 2007; Holland 2007; Huntley and Kowalewski 2007; Vermeij 2007; Vermeij and Williams 2007; Baumiller et al. 2008; Stanley 2008; Vermeij 2008; Vermeij et al. 2008. Each of the past attempts to address these questions has certainly offered some insight into the diverse ways that evolution plays out, but each attempt has been unsuccessful, I believe, because they have ignored the fundamental reality that a drastically extended period of parental investment (Trivers 1974) and the formation of

4

family units have led to some of the most ecologically dominant organisms on earth:

social insects and humans.

CHAPTER 1: EUSOCIALITY REEXAMINED FROM THE PERSPECTIVE OF THE

FAMILY

Introduction

Eusociality is a term that describes social invertebrates such as ants, bees, wasps,

termites, some aphids, some thrips (Batra 1966; Wilson 1971; Crespi 1992; Stern and

Foster 1996) and social shrimps (Duffy et al. 2000; Duffy 2003). Three criteria define

eusociality: overlapping generations in which parents, offspring and siblings all reside in

one domicile or territory; cooperative rearing of young by individuals other than a parent

(for example, this would include aunts, uncles and siblings, as well as unrelated

individuals in the community or colony); and a reproductive division of labor with fertile

breeders and sterile helpers (Wilson 1971; Foster and Ratnieks 2005).

I have proposed (Hardisty and Cassill 2010a) that eusociality, once considered

exotic and rare, will be found to be widespread when attention is paid to the *family* as a

unit of biological organization (also see Sherman et al. 1995). First, it is not unusual to

find social vertebrate families with one breeder and her offspring being reared by

facultative-sterile helpers such as prepubescent siblings (for example, see Hagen and

Barrett 2009), unmated aunts/uncles, grandparents, and other homosexual relatives.

Second, 24-hour care for offspring, a result of polyphasic wake/sleep cycles by helpers

(Cassill et al. 2009), provides offspring survival benefits as well as breeder fitness

benefits. Finally, there are several social vertebrate species that I believe meet this extended eusociality criteria (Hardisty and Cassill 2010).

Background

A typical social insect family consists of a queen and her offspring (Wilson 1971). The queen's offspring are either sterile or fertile. As adults, sterile offspring stay at home, caring for their mother and rearing their siblings while fertile offspring disperse from home, mate and begin their own families (Wilson 1971). Social insect families that coexist within a single nest resemble social vertebrates that coexist within a single domicile or territory such as lions, wolves, elephants, chimpanzees and humans (Wilson 1975). Others rear their offspring in isolation from each other and resemble vertebrates such as mice, eagles, lions and bears (Wilson 1975).

The discovery of eusociality in the naked mole-rat (*Heterocephalus glaber*) shocked the social insect world and extended eusociality from its insect focus to include a single species of vertebrate (Jarvis 1981). Naked mole-rats possess overlapping generations living under the same roof and a reproductive division of labor that includes queens and sterile helpers. In each family, the queen is the only breeder (Jarvis and Sherman 2002). The queen's offspring (most sterile helpers) forage, tunnel, help rear siblings and defend the queen, her mates and her pups against non-colony members. Naked mole-rats also exhibit caste dimorphism, though to a lesser degree than social insects as breeders are typically only 30% larger than non-breeders (Jarvis and Sherman 2002).

Compared to social vertebrate families, social insect families differ significantly in family size, variation in body size and fertility ratios. For example, a single ant queen can live up to forty-five years, depending on the species, and produce millions of offspring during her lifespan (Hölldobler and Wilson 1995). In contrast, social vertebrate breeders typically produce only tens of offspring (often far fewer) during their lifespan. Body size can vary 10-fold to 500-fold between fertile and sterile ants; whereas in humans that difference would be comparable to producing children that mature at weights ranging from 100 lbs to 50,000 lbs (Wilson 1971). Lastly, in ants the ratio of sterile to fertile adults within a family is 20:1 (Cassill 2002); whereas in vertebrates, the ratio of facultative-sterile helpers to fertile breeders within a family might be 4:1. Thus, the eusocial criteria (over-lapping generations, cooperative breeding and sterile helpers) do exist in vertebrate families.

Foster and Ratnieks (2005) proposed that *Homo sapiens* be classified as eusocial and Barber (2004) argued that we might consider nuns and priests as a caste sterile of helpers at large. I believe that human families also fit the eusociality criteria: we possess overlapping generations under the same roof, cooperative care of young *and* a facultative-sterile caste of helpers in the form of prepubescent juveniles, servants and post-menopausal women such as aunts and grandmothers, who devote some of their resources to help rear someone else's offspring (Hardisty and Cassill 2010a). It has been shown, for example, that when grandmothers help out (Hill and Hurtado 1991; Hawkes et al. 1997; Hawkes et al. 1998; Voland and Beise 2002; Hawkes 2003; Hawkes 2004), daughters breed earlier, more frequently and more successfully (Lahdenpera et al. 2004; Shanley et al. 2007; Sear and Mace 2008).

New Ground

I also proposed another trait that eusocial families such as ants, naked mole-rats and humans, have in common: polyphasic wake/sleep cycles (Hardisty and Cassill 2010a). In the red imported fire ant, *Solenopsis invicta*, queens are active fifteen hours a day and sleep the remaining nine hours, in naps averaging six minutes; workers are active nineteen hours a day and sleep five hours in naps averaging one minute (Cassill et al. 2009). As a result, 80% of the colony's workers are available around the clock to complete any task at any time, no matter how large or small. Naked mole-rats also exhibit polyphasic wake/sleep cycles (Davis-Walton and Sherman 1994) and helpers are available to complete tasks 24 hours a day in their colonies as well. Thus, for both the fire ant and the naked mole-rat, olfactory communication has allowed them to thrive in subterranean habitats. Without the need for sunlight to forage, mate and rear a family, there is no need for a circadian clock. The innovations of electricity and artificial heat released humans from circadian and seasonal activity cycles and we are now able to work 24 hours a day year round in lighted and heated homes, offices and factories. The greater number of available work hours for adults has generated a further need for family members—facultative-sterile helpers—to help rear offspring. If family members are not available, 'nannies' or regulated cooperative-care facilities are available (Allen 2003). Because 24-hour care for young by facultative-sterile helpers—human or otherwise—is such a successful parental adaptation, it is no surprise that eusocial species often dominate prime real estate within their habitats.

Conclusion

Some researchers would like to narrow the definition of eusociality specifically to exclude vertebrates (Crespi and Yanega 1995; *contra* Sherman et al. 1995; Burda et al. 2000; Foster and Ratnieks 2005). However, I propose (Hardisty and Cassill 2010a) that the definition be expanded to include social vertebrate families consisting of one or more reproductive females, their offspring and other non-reproductive helpers such as unmated aunts/uncles, grandparents and nannies that help rear the reproductive female's offspring.

With this extension, a variety of social vertebrates could be thought of as eusocial: the Florida scrub jay *Aphelocoma coerulescens* (Foster and Ratnieks 2005; Wilson 1975), the Mexican jay *A. ultramarines*, the black-tailed prairie dog *Cynomys ludovicianus*, the meerkat *Suricata suricatta*, the African elephant *Loxodonta africana*, the hamadryas baboon *Papio hamadryas*, the eastern mountain gorilla *Gorilla gorilla beringei*, the spotted hyena *Crocuta crocuta* (Wilson 1975), the short-finned pilot whale *Globicephala macrorhynchus*, the orca *Orcinus orca* and the sperm whale *Physeter macroecaphalus* (McAuliffe and Whitehead 2005). A broader definition of eusociality provides biologists an opportunity to compare the conditions that select for helpers, whether they are facultative-sterile as in humans, elephants and whales, or obligate-sterile, as in ants, bees and naked mole-rats. The intent here is to further the debate begun by Foster and Ratnieks (2005) with the goal of better understanding the evolution of the extended family.

CHAPTER 2: A 4-D MODEL OF FITNESS AND THE PRODUCTION OF
OFFSPRING SKEW AS AN EVOLUTIONARY STRATEGY TO COPE WITH
FLUCTUATING ENVIRONMENTS

Introduction

Advocates of individual selection, group selection and kin selection have been
battling each other for decades—typically it has taken the form of one group promoting
their model of altruism over all the other alternative models (Hamilton 1964; Trivers
1971; Dawkins 1976; Axelrod and Hamilton 1981; Connor 1986; Connor 1995a; Connor
1995b; Connor 1995c; Wilson 2005; Foster et al. 2006; Jansen and van Baalen 2006;
Heikki and Bargum 2007; Wilson and Wilson 2007; Landa 2008 and Wilson 2008).
However to date, none of these models have provided a truly unified solution to the
problem of altruism among both family members *and* among non-kin group members.

In this chapter, drawing heavily on other collaborative work (Cassill and Hardisty
2010), I will describe the limitations of individual fitness, group fitness and inclusive
fitness to explain the mechanisms by which altruism evolves and show how a 4-
Dimensional model (referred to hereafter as "the 4-D model") of biological fitness can
overcome the limitations of the above models.

In a nutshell, the limitations of the previous approaches to the study of altruism are
that their definitions of 'fitness' are incomplete; offspring survival is assumed to be

11

random when it is often far from random; lastly, each way of thinking about fitness

assumes that individuals interact with each other in an environmental vacuum when they

do not. Next, I show how the 4-D model calculates fitness retroactively, from a parent's

perspective, based on the number of offspring that survive long enough to become

breeders themselves. A key assumption of the 4-D model is that offspring survival is

biased, that is, skewed due to diverse pre and post-zygotic mechanisms of parental

investment. The model also assumes that both altruistic *and* selfish interactions are

largely influenced by environmental risks, such as cycles of resource scarcity and

predation.

In the following sections, I describe offspring skew, parental lifetime fitness and,

finally, explain how a Darwinian selection environment optimizes parental lifetime

fitness when parents produce both altruistic *and* selfish offspring.

Offspring Skew

Two centuries ago, Charles Darwin (1859) published his theory of natural selection to

explain the world's great diversity of species. Today, one of the last great challenges left

for theoretical biology is to explain *behavioral* diversity, especially the evolution of

altruistic and self-serving behavior. Before revealing a possible solution to the enigma of

altruism, two key factors that lubricate the process of evolution must be reviewed. The

first factor is offspring overproduction (Malthus 1803). Parents overproduce offspring

whenever possible because most will die young from natural selection events such as

accidents, injury, disease, desiccation, starvation or predation. Of the few that survive to

maturity, some mate and become the next generation of breeders; others, particularly males, never mate at all and die without passing their genes on.

The second key factor is offspring diversity (Ghiselin 1974). One specific pattern to offspring diversity is offspring skew. Skew in offspring size, motivation, fertility, gender or behavior, increases the probability that some offspring will die whereas others will mature into the next generation of breeders. During periods of scarce food or high predation or both of these conditions, the smallest, youngest and least aggressive are likely to die first, effectively reducing the number of offspring to a state of equilibrium with the reduced carrying capacity of the environment. The major point here is that death among offspring is *not* random. Later, some reasons are offered as to why skew in offspring survival might be adaptive. But first I explain the mechanisms by which offspring survival is skewed.

Offspring Skew by Nature or Nature

Pre-birth (i.e. pre-zygotic) mechanisms for generating offspring skew involve the fusion of diverse gametes (eggs with sperm) during sexual reproduction (Cassill and Hardisty 2010). In addition, offspring skew is generated by gene shuffling during the processes of meiotic cell division.

During meiosis, forty-six chromosomes pair up in random orientation; half are inherited from an offspring's mother and half from its father. During this process each pair of chromosomes, a maternal chromosome and a paternal chromosome, joins independently of the other pairs. The maternal chromosome is sometimes on the top and the paternal chromosome is sometimes on the bottom—or vice versa. After pairing up,

the maternal and paternal chromosomes can exchange sequences of genes with each other in a process called chromosomal crossover. At the same time, transposons, or "jumping genes" change location within the same chromosome in a process called transposition (McClintock 1950; McClintock 1953). Another mechanism for generating skew in offspring survival is gene mutation, where single nucleotides within genes and even whole genes themselves, are deleted from the chromosome or added in at random locations during crossover.

To grasp the ease with which chromosomes and genes to are mixed to generate offspring skew, imagine that a deck of cards represents the two sets of chromosomes inherited from our parents; twenty-six chromosomes are inherited from each parent—fifty-two chromosomes total (which is close to our forty-six chromosomes) (Cassill and Hardisty 2010). The black suites, ordered Ace through King, represent the chromosomes inherited from our father and the red suites, ordered Ace through King, represent the chromosomes inherited from our mother. Now shuffle this deck of 52 cards seven or more times to ensure random assortment (Aldous and Diaconis 1986) and deal the cards into two piles. The two piles represent the formation of our eggs or sperm containing only one copy of each chromosome, inherited from our father or our mother. What are the odds of exactly duplicating the original order of cards—with black cards inherited from our father in one pile and red cards inherited from our mother in the other pile—and in the original order, Ace through King? The odds are effectively zero. Reshuffle and re-deal the same deck of cards a billion times, representing the number of different sperm or eggs that we produce. What are the odds of exactly duplicating, even once, the original order of cards—with black suites in one pile and red suites in the other pile, and in the

14

original order Ace through King? The odds are still so small as to be effectively zero.
The point of this example is that even without a single gene mutation offspring diversity
is produced through the random pairing up of maternal and paternal chromosomes during
meiosis (Cassill and Hardisty 2010).

A skew in offspring survival is sometimes generated by variation in the quality of
food ingested by offspring after birth or hatching (Cassill and Hardisty 2010). For
example, in wild and domestic hogs, the quality and quantity of milk produced differs
among a sow's tits (Graves 1984; Newberry and Wood-Gush 1985; Andersen et al. 2000;
Fernandez-Llario and Mateos-Quesada 2005; Drake et al. 2008). The mother's apical
(forward) tits produce higher quality milk in greater quantity. As a result, piglets
suckling on the distal tits develop more slowly and are significantly smaller than piglets
suckling on the apical tits. The skew in tit quality creates a skew in piglet quality leading
to a non-random rate of survival (Cassill and Hardisty 2010). Thus, smaller piglets are
far less likely to survive birth and predation than larger piglets (Graves 1984; Andersen et
al. 2000; Marchant et al. 2000; Fernandez-Llario and Mateos-Quesada 2005; Kranendonk
et al. 2007; Roehe et al. 2009).

In some fish, particularly annuals that breed and die in one year, mothers skew the
rate of development of embryos by varying the quality and quantity of egg yolk (i.e.
developmental polymorphism). Eggs spawned and fertilized on the same day hatch
anywhere from 40 days to 320 days later (Wourms 1973). This developmental skew will
guarantee that some portion of the fry hatch under favorable conditions and thus survive
to maturity despite the unpredictability of rain, temperature, food availability and
predators as they grow and develop (Cassill and Hardisty 2010).

'Group' Skew by Nature and Nurture

Imagine a time in our history 150,000 years ago, in which a group of our ancestors is foraging for food (Cassill and Hardisty 2010). Further imagine that a hungry carnivore stalks the group and begins a chase. Humans run as a group toward shelter or deep water to avoid the jaws of death. However, they do not need to run faster than the carnivore pursuing them. They only need to run faster than one of their *own group members* (Williams 1966) or one of their *own family members* (Hardisty and Cassill 2010). The youngest, or oldest, is most likely to become the carnivore's dinner. The others survive. Moreover, they will survive whether all of the group members are related or not (Cassill and Watkins 2004; Cassill and Watkins 2009; Cassill and Hardisty 2010; Cassill et al. 2010).

Whether by nature or nurture, when parents produce a caste of disposable offspring, and those offspring join large groups of *unrelated* individuals, predators need not evolve into faster runners (see also Chapter 5). Thus, the larger group members are guaranteed to survive, mate and produce the next generation of skewed offspring that will join large groups. Thus, the aggregation of individual s into "selfish-herds" (Hamilton 1971; Landa 1998) is one way both families *and* groups of organisms with low dispersal rates could evolve.

Not only is group skew good for the parent's lineage, it is good for the predator as well. Without the next generation of prey, there would be no next generation of predators.

In human families, skew is established one-at-a-time by continuous mating among parents and by delayed development of offspring. Thus, human families consist of a few

adults and a few children of variable age, size, fertility and ability. Because human

families are relatively small, families often cluster together, forming large groups of

unrelated members that provide sufficient safety-in-numbers against omnipresent

predators (Cassill 2002a; Cassill 2002b; Cassill and Watkins 2004; Cassill 2006; Cassill

et al. 2009; Cassill and Watkins 2010; Cassill et al. 2010) and the ability to engage in

ecosystem engineering and construct multiple, resilient dwellings that can house large

extended families (Hardisty and Cassill 2010a).

Parents of other species skew the ratio of altruists and self-serving offspring one-at-a-

time. For example, zebra, wildebeests and antelope cluster together into herds and mate

in synchrony (Wilson 1975). During the spring, they give birth all at once. With so

many breeders birthing at the same time, predators are overwhelmed and able to kill only

a few—again the youngest or oldest. The survivors grow, mature, mate and give birth in

an ongoing cycle of life. In addition, per Chapter 1, above, there is often an incentive for

the family group to make sure that it's *only* the youngest offspring that get killed by

predators (Forbes 2005; also see: Driver and Humphries (1988) for data on predation

rates in many large carnivores).

The point here is that the skew in unrelated members of large groups likely has its

origin in offspring skew. The conduit by which groups maintain a skewed membership

in each generation is through each member's parents who, in the previous generation,

skewed offspring abilities, size or behavior.

Conceptualizing **'**Fitness'

In evolutionary biology, 'fitness' is a measure of an individual's success in breeding and propagating copies of its genes into the next generation's offspring (for example, Dawkins (1976) defines evolution as a change in gene frequencies over time). Because data on the total number of *surviving* offspring over a parent's lifetime are difficult to acquire (Betzig 2008: 8), biologists have relied on proxies such as annual clutch size or the probability of offspring survival. As I will argue (Cassill and Hardisty 2010) in the next several sections, these proxies have blinded biologists to the power of Darwinian selection to solve the enigma of altruism.

Individual fitness, the most popular of the natural selection metrics, measures the success of organisms in spreading their genes into the next generation of offspring (Betzig 2008: 8). Individual fitness, also referred to as direct fitness, is measured in two ways: by a typical metric based on parental fitness; and sometimes by an atypical metric based on hypothetical offspring fitness. Typical fitness values are based *solely* on the number of offspring that a parent produces in one breeding season—such as clutch size. Other acceptable, atypical, values of fitness are those assigned to offspring based on the probability that each will survive, mature and mate *in the future*.

The inability of individual fitness metrics to explain altruism usually lies in their assumptions (Hardisty and Cassill 2010e). Typical individual fitness assumes that survival among a parent's offspring is random (Oster and Wilson 1979); thus, biologists only need to measure the annual number of offspring produced—such as clutch size—to estimate a parent's individual fitness.

In contrast, atypical fitness is a metric awarded to offspring based on the rate of offspring survival from previous generations (i.e., Type I and II survivorship curves, Fisher 1930). Because it is projected from past trend data, atypical fitness is a prediction of offspring survival *in the future*, not a fait accompli. Moreover, atypical offspring fitness is a measure of survival, not reproduction. This is an important distinction because even when offspring survive to maturity, many never breed (Cassill and Hardisty 2010).

In summary, neither typical nor atypical individual fitness can explain altruism (Cassill and Hardisty 2010). For example, if an ant dies helping another ant, the fitness of its parent (typical fitness) declines by some increment. If an offspring dies helping a stranger, its fitness (atypical fitness) is thus zero. Consequently, other metrics, such as inclusive fitness and group fitness, were developed to fill the void created by the inability of typical and atypical fitness metrics to explain the origin of altruism (Cassill and Hardisty 2010).

Limitations of Inclusive Fitness

In an attempt to explain altruistic behavior, Hamilton (Hamilton 1964; Hamilton 1967) developed a fitness metric he called "inclusive fitness" by extending the atypical fitness metric described in the previous section. Hamilton focused his model on the idea of some hypothetical altruists helping other altruists in the hopes that some altruists would survive and propagate their genes, if only the very gene or genes that made them behave altruistically to begin with. To understand the limitations of Hamilton's inclusive

fitness metric, I discuss below four essential tenets that must be met for inclusiveness to be valid.

According to inclusive fitness, offspring are either altruistic or selfish; they cannot be both. This tenet ignores the reality that organisms are fully capable of altruistic *and* selfish behavior, depending on the circumstances (Trivers 1971; Cassill and Watkins 2004; Cassill 2006; Teyssedre et al. 2006; Cassill et al. 2007; Cassill et al. 2009; Cassill and Watkins 2010; Cassill et al. 2010). For example, workers in the fire ant, *Solenopsis invicta*, are known for their willingness to share food with nestmates. What is little appreciated, however, is that these same ants *always* retain sufficient food in their storage crop for their own use to keep themselves alive and energized for weeks and even months (Cassill and Tschinkel 1999). Indeed, half of an ant's dry body mass is fat reserves (Tschinkel 2006) accumulated by absorbing what is needed before sharing. Ants share only when they have food in excess of the amount that they need to survive. Thus, even one of the most altruistic animals known to science behaves in its own best interest first, and *in another's best interest second*.

Another example of the duality of animal behavior is the Shedao pit viper (Cassill et al. 2010; see: Chapter 3). Pit viper breeders produce offspring that help themselves when the opportunity arises *and also* help non-kin neighbors when the opportunity arises. A simulated study of pit vipers showed that breeders realize *three times* greater lifetime fitness (number of surviving offspring over ten breeding years) relative to breeders whose offspring help only themselves, and not neighbors. These same breeders realize *twenty-three times* greater lifetime fitness relative to breeders whose offspring help only

neighbors and do not help themselves when the opportunities arises (Cassill et al. 2010). Clearly, self-interested and helping behaviors *both* improve offspring survival.

The 4-D model recognizes that humans and other animals help themselves *and* they help others depending on the immediate circumstances and their ability to help. For example, animals often share food, territory or other resources in return for appeasing potentially aggressive neighbors or in return for joining large groups to gain safety in numbers when a predator lurks nearby (Cassill 2006; Cassill and Watkins 2004; Cassill and Watkins 2010; Cassill et al. 2010).

A second requirement of Hamilton's inclusive fitness is that acts of altruism among offspring must not affect their parent's fitness; otherwise parental fitness can explain altruism (Cassill 2006). Any help offered to a sibling where the benefit to the sibling is greater than the cost to the altruist (i.e. "Hamilton's rule"), automatically increases their parent's fitness; hence, parental fitness can explain altruism instead and an essential requirement of inclusive fitness is violated.

A third requirement of inclusive fitness is that diploid parents must produce a 1:1 ratio of altruistic to selfish offspring (note: this does not refer to sex ratios). A 1:1 ratio is rarely found in nature. For example, among siblings in the fire ant, *Solenopsis invicta*, the numeric ratio of altruistic sterile offspring (workers and soldiers) to self-serving fertile offspring (males and future queens) over a year is 20:1 (Cassill 2002a). In honeybees, the ratio is typically much greater than 1,000:1 (Michener 1974). In wasps, the ratio ranges from 4:1 to 50:1 (Field et al. 2000; Queller et al. 2000). In naked mole rats, the ratio averages about 70:1 (Holmes et al. 2007) with a high of 285:1 (Brett et al.

1991). In meerkats, the ratio ranges from 2:1 to 30:1 (Clutton-Brock et al. 2001). In vervet monkeys, the ratio averages 4:1 (Seyfarth and Cheney 1984).

A fourth requirement of inclusive fitness is that death is assumed to be random among offspring. In other words, altruists are no more likely to die by desiccation, starvation or predators than selfish offspring. This requirement ignores the reality that survival among offspring is far from random (Darwin 1859; Driver and Humphries 1988; Hrdy 1999; Forbes 2005; Cassill 2006). Thus, offspring skew produces disposable, easy-to-catch piglets as bait for predators, effectively suppressing the predator-prey arms race. Over evolutionary time (Vermeij 1987; Vermeij and Dietl 2006), the prey-predator relationship plateaus and stabilizes rather than escalating (Hardisty and Cassill 2010d).

In summary, Hamilton's (1964) inclusive fitness construct has inspired a large number of artificial puzzles, such as the Prisoner's Dilemma (Trivers 1971; Axelrod and Hamilton 1981), upon which hundreds of mathematical modelers have sharpened their skills. However, because of its highly constrained requirements (especially the requirement that altruistic actions *must not affect the fitness* of the altruist's parents and that *survival is random* among altruistic and self-serving siblings), inclusive fitness is incapable of solving the evolution of altruism in complex, natural systems (see also Connor 1986; Clements and Stephens 1995; Connor 1995a; Connor 1995b, Connor 1995c; Cassill 2006; Field 2008; Cassill et al. 2009; Cassill et al. 2010).

Limitations of Group Fitness

Group selection, with its group fitness construct, was developed to solve the enigma of altruistic behavior among unrelated individuals in cohesive groups such as herds of zebra or schools of fish (Wynne-Edwards 1963; Wynne-Edwards 1965; Wilson and Sober 1989; Wilson 1997; Wilson and Dugatkin 1997; Landa 1998; Sober and Wilson 1998; Wilson 2005; Wilson and Wilson 2007; Landa 2008). Group selection gets it almost right by recognizing that groups with more altruists can survive longer than groups with fewer altruists when in direct resource competition with each other, especially when dispersal rates are low (Sober and Wilson 1998; Landa 2008).

However, group selection models often assume that group members vary in ability and survival because of nurture (i.e. nutritional differences during development), not nature (e.g., Wilson and Sober 1989; Wilson 1997; Wilson and Dugatkin 1997; Sober and Wilson 1998). In other words, altruistic behavior has no *underlying heritable* behavior. Without a heritable behavior, groups with a successful a ratio of altruists to self-serving members, such as the 20:1 ratio found in fire ants (Cassill 2002), *cannot* reproduce the next generation of groups with the *same* ratio. Without a heritability mechanism, group selection is equivalent to a train with hundreds of fully-loaded cars sitting on a track facing the future, but missing the engine needed to move it forward into the next generation (Cassill and Hardisty 2010).

In summary, group selection is a one-dimensional (1-D) model that fails to solve the evolution of altruism. As will be shown in the next section, a 4-D model that unifies 'parental lifetime fitness' and 'offspring skew' provides the appropriate lens through

23

which we can begin to make sense of the evolution of altruistic *and* self-serving behavior (Cassill and Hardisty 2010).

A Better Approach: Parental Lifetime Fitness

The problem with individual fitness metrics, typical and atypical (i.e. clutch size or the probability of offspring survival), is not that they are wrong. Rather, the problem is that these individual fitness metrics are *incomplete*. Individual fitness must be calculated from data involving at least two generations: the parent and its offspring. In addition, individual fitness must be calculated based on a parent's *lifetime* reproductive effort, not just its annual litter size (Cassill 2002). Parental lifetime fitness, defined as the 'sum total of offspring that survive and mature into breeders over a parent's lifetime,' meets these two criteria. To clarify, parental lifetime fitness is a retro-generational metric (Figure 2.1). Offspring must survive and mate *before* their parents' fitness can be calculated to give us a complete picture.
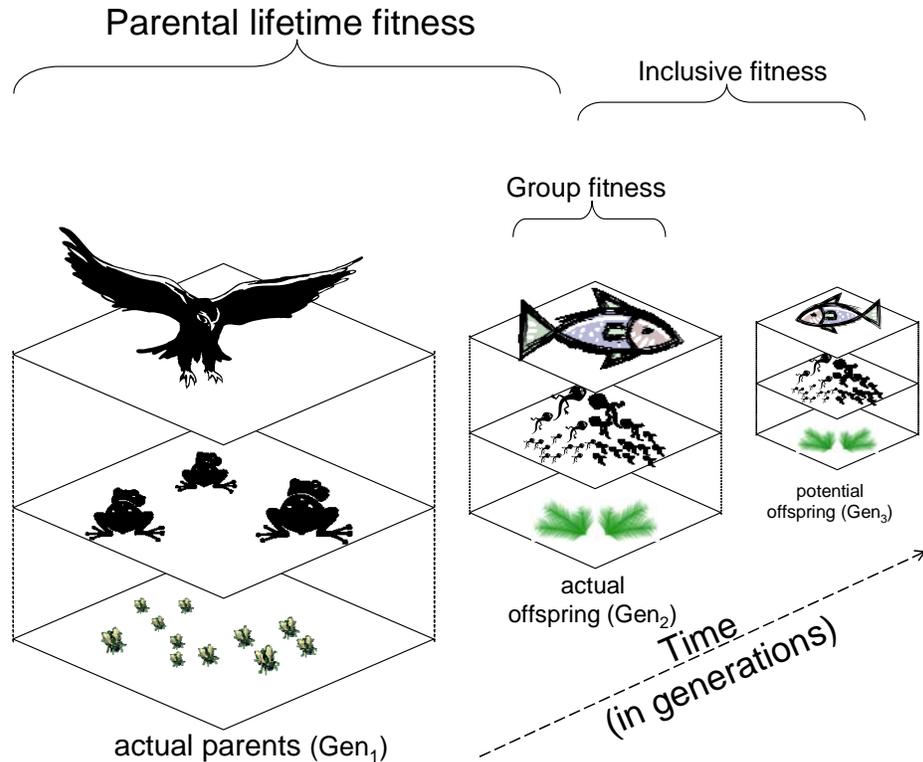
Figure 2.1 Parental Lifetime Fitness: A 4-D natural selection model for the evolution of both altruistic and self-serving behavior. The focal animal, its prey and its predators, comprise the three spatial dimensions. Three generations comprises the fourth dimension of time. In generation 1, frog parents prey on insects and are preyed on by hawks. In generation 2, tadpoles 'prey' on algae, and are preyed on by fish. The third generation is fiction, based on the assumption that some of the tadpoles in generation 2 will mature to adults, mate and produce tadpoles of their own. **Parental lifetime fitness**: In the 4-D model, the parental lifetime fitness metric is a retro-generational construct. The number of *surviving* tadpoles, those that successfully metamorphose into adult frogs in generation 2, determines the fitness of parental frogs in generation 1. **Group fitness**: Group selection's group fitness metric is a 1-D, intra-generational construct based on the number of survivors in a population of tadpoles. How group fitness is passed into the next generation of groups is not resolved. **Inclusive fitness:** Kin selection's inclusive fitness metric is an idealized, future-generation, probability construct. The ideal number of tadpoles that might be produced in Generation 3 by an ideal number of tadpoles that were saved by a related altruistic tadpole in the Generation 2 is determined by the probability (Hamilton's 'r' coefficient) that the altruistic tadpole and its surviving altruistic sibling in the Generation 2 shared altruistic genes by descent from a common relative, a parent, in the Generation 1 (Figure: Cassill and Hardisty 2010).

To further appreciate the power of a parental lifetime fitness perspective to solve the

enigma of altruism let us consider a frog. Adults are known to survive four to forty

years, depending on the species (Snider and Bowler 1992). Each breeding season, adults produce batches of eggs that number from dozens to hundreds, depending on the species (Savage 2002). Imagine that one frog breeder survives ten years and produces an average of 100 eggs each year. That frog's individual fitness, measured as clutch size, would be '100.' If, on average, only one tadpole survives to metamorphose each year, the tadpole's individual fitness would be '0.01', the rate of tadpole survival to maturity, and the parent frog's lifetime fitness is '10' (one tadpole per year survives to maturity). Further imagine that, once a tadpole matures, the probability of its breeding successfully is 0.5 (an estimate). We can now calculate the parent's lifetime fitness as '5' (10 x 100 x 0.01 x 0.5).

Equation 1 (from: Cassill and Hardisty 2010): the Cassill-Hardisty Fitness Metric

Parental lifetime fitness: $f_l = lnp_sp_b$

l = parental lifespan;

n = annual clutch size of parent;

p_s = probability of offspring surviving to maturity;

p_b = probability of mature offspring eventually breeding

From an evolutionary perspective, the most meaningful of the fitness metrics presented here is not 100. It is not 0.01. It is not 10. It is 5. Five of the original frog's offspring survived and matured into breeders. The point of this toy example is to show that typical and atypical fitness metrics are *both* important components of lifetime fitness, but do not, by themselves, reveal how altruistic genes perpetuate themselves over many generations.

If we agree that parental lifetime fitness is the best metric by which to assess the spread of genes in populations over generations, we are ready to consider a 4-D natural selection model for solving the enigma of altruism. The 4-D model specifies environmental conditions that favor parents who not only overproduce offspring, but also skew the overproduction of offspring into altruistic and self-serving offspring. Skewing offspring size and behavior (which the model assumes will be correlated traits: see Michener 1974; Seyfarth and Cheney 1984; Brett et al. 1991; Field et al. 2000; Queller et al. 2000; Clutton-Brock et al. 2001; Cassill 2002a; Holmes et al. 2007) guarantees that some offspring will survive the bust and boom of unpredictable environments to become the next generation of breeders.

The Darwinian Selection Environment

Environmental factors such as the number of predators, the availability of shelters and cycles in food availability divides all offspring into two categories: those who survive to maturity and breed, and those who do not (Cassill and Hardisty 2010). When the dominant environmental risk involves finding food in patches shaped by spatial or seasonal gaps in food availability, nature selects for parents who produce gluttonous offspring that store excess fat or storage protein to survive periods of scarcity (Ghiselin 1974; Wheeler and Buck 1995; Wheeler et al. 2000). When the dominant risk involves avoiding predators, nature selects for parents who produce many offspring, overwhelming predators with large numbers (Hamilton 1971). When animals face both risks, gaps in food availability *and* predators, nature selects for parents who produce two types of offspring: a few gluttonous offspring *and* many small, disposable offspring

(Figure 2.2). Over many generations, the risks of starvation and predation shape the

genetic mechanisms that skew offspring size, ability, fertility or behavior to guarantee

that some offspring survive and become breeders, thus maximizing their parent's lifetime

fitness.
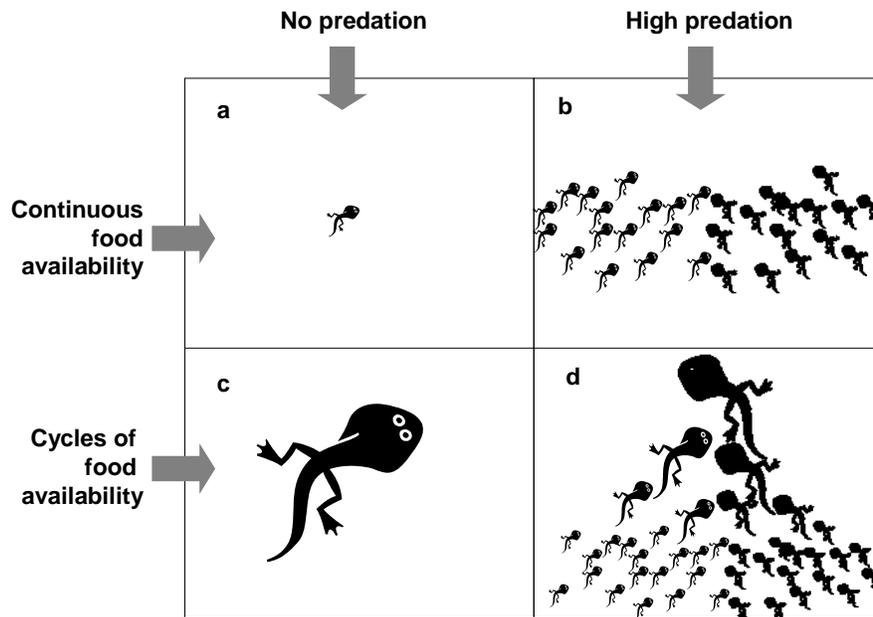
Figure 2.2 4-D Model of Natural Selection: The ratio of altruistic to self-serving offspring
depends on the degree of risk associated with finding food and avoiding predators. (a) If the risk
of predation and starvation is zero; offspring survival will be high; clutch size and offspring body
size will be small. (b) If the risk of predation is high, parents can optimize their fitness by
increasing clutch size to ensure that some will survive the jaws of death. (c) If the risk of finding
food is high, parents can optimize their fitness by producing large-bodied, well-provisioned
offspring to survive gaps in food availability. (d) If families must cope with both predation *and*
gaps in food, parents can optimize their lifetime fitness by skewing offspring body size so that
body size and clutch size are large (Figure: Cassill and Watkins 2004; Cassill 2006; Cassill and
Hardisty 2010).

The 4-D model is based on the assumption that, in high risk environments, parents

who skew the ratio of altruistic to self-serving offspring increase their lifetime fitness

relative to parents who produce only self-serving offspring (Cassill 2002a; Cassill 2002b;

Cassill and Watkins 2004; Cassill et al. 2007; Cassill and Watkins 2010; Cassill et al. 2010).

To better understand the benefit of skewing offspring quality and quantity from a parent's perspective, an analogy is in order. Imagine that the resources needed by a frog to produce tadpoles are equal to one American dollar (Figure 2.3) (Cassill and Hardisty 2010). If the frog produces only large offspring, she can invest her dollar *equally* into two tadpoles sufficiently well-provisioned to survive gaps in food and mature into breeders. Alternatively, a frog can invest *unequally* and skew clutch size without compromising her ability to produce at least one large offspring. To accomplish this feat, our hypothetical frog could create one 50-cent tadpole and surround it with two 25-cent tadpoles, or five 10-cent tadpoles, or fifty 1-cent tadpoles, or any other number of tadpoles of variable size as needed to buffer the larger, 50-cent tadpoles from predators (Cassill and Hardisty 2010).
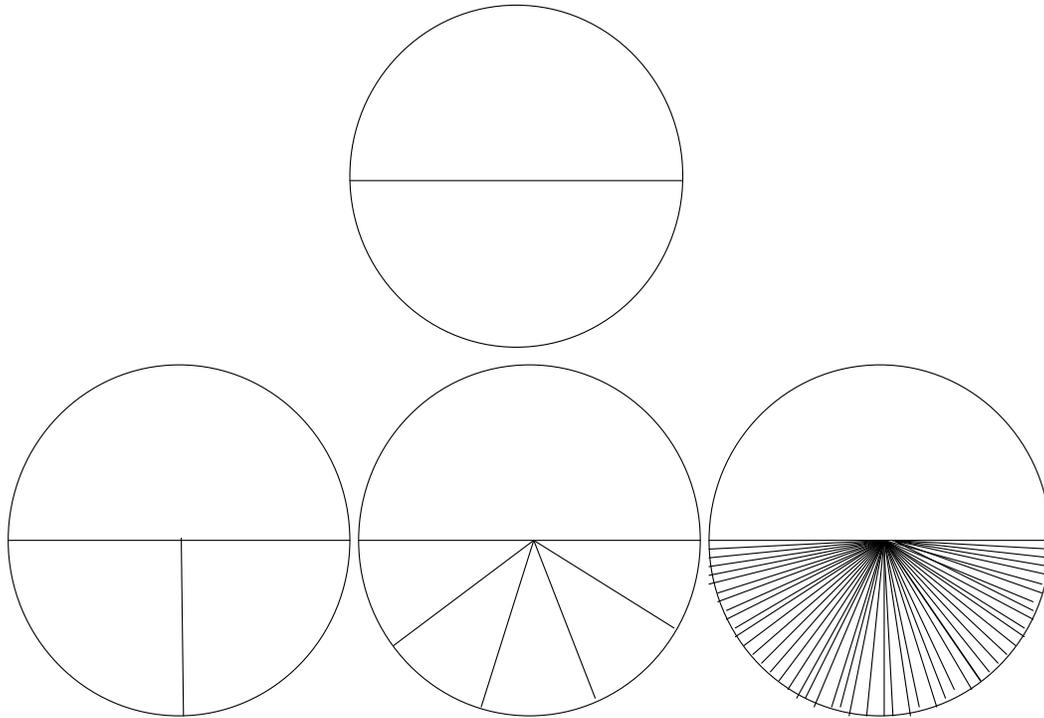
Figure 2.3 Partitioning Offspring Quality and Quantity: instead of producing two equally large offspring, a parent can produce one large offspring and then skew the remaining resources into 2, 5, 50 or any other number of smaller offspring to protect the large offspring from predators. The number and size will be shaped by predators and food availability respectively. The point of this graph is to show how easily different ratios of altruistic to self-serving offspring can be produced if parents skew (i.e. diversify) the allocation of resources. Moreover, offspring skew is not as strict a trade-off as assumed by Smith and Fretwell (1974) and subsequent models. Parents *can* increase clutch size without compromising maximum body size (figure: Cassill and Hardisty 2010; also see: Forbes 2005 for some alternatives to Smith-Fretwell models).

The point of our analogy is that our imaginary frog has more flexible options than the classic Smith-Fretwell scheme for dramatically increasing the probability that at least one tadpole matures and breeds to carry on her parental lineage. An important point here is that skewing the quality of offspring reduces the number of large offspring—but does not eliminate them altogether. Parents can produce a few self-serving offspring *and* many altruistic offspring. The ratio or degree of skew evolves over generations depending on

the risks of starvation and predation (Cassill and Hardisty 2010). Thus, the model

predicts that environments of high predation and low food abundance should produce lots

of small organisms, such as fire ants and sea turtles, which is exactly what we see.

Offspring skew in body size or behavior can be measured with two metrics: a ratio

coefficient or an asymmetry coefficient. Ratios of altruistic to self-interested offspring

are simple count data. Asymmetry, measured using the Gini coefficient, is continuous

data based on body mass or the probability of behaving altruistically. With the Gini

coefficient, a standardized metric for quantifying variation in the degree of offspring

skew is available; the relationship between offspring skew and a number of important

variables can be compared and contrasted within and among species (Figure 2.4).
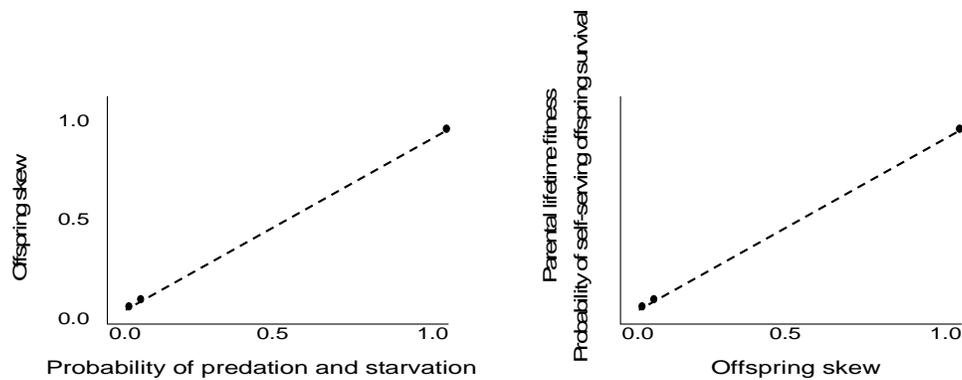
Figure 2.4 Offspring Skew: (as measured by the Gini coefficient) calculated from offspring ratios

in Figure 2.3. The 4-D model predicts a *positive relationship* between offspring skew and the

probability of predation or starvation, parental lifetime fitness and the probability of survival of

self-serving offspring (figure: Cassill and Hardisty 2010).

In summary, just as natural selection shapes life history traits such as clutch size or body size (Stearns 1992), so too does natural selection shape the degree of skew in altruistic to self-serving offspring (Cassill and Hardisty 2010). Each life history parameter depends on the risks associated with finding shelter, finding food, finding mates, successfully mating and avoiding predators (Hardisty and Cassill 2010e).

When Relatives are Altruists

Do relatives help each other? Of course they do. The point I make here is that Hamilton's (1964) highly constrained, gene-centric inclusive fitness metric is not needed to explain why (see also: Cassill 2006; Hardisty and Cassill 2010e). Instead, Ghiselin's (1974) parental exploitation model opens the door to an answer. Ghiselin got it almost right when he reported that mother-nature does not pack the lunch boxes of her offspring equally. Our 4-D model extends Ghiselin's parental exploitation model by describing the optimal pattern of unequal allocation—it is skewed (Cassill 2002a; Cassill 2002b; Cassill 2006; Hardisty and Cassill 2010d).

If lunch boxes were packed equally, generation after generation, offspring might do well in years of abundance, but could die all-at-once during an extreme shortage of food. To avoid a situation in which offspring die all-at-once, mother-nature skews the distribution of resources among offspring (Cassill 2002a; Cassill 2002b; Cassill 2005; Cassill and Watkins 2004; Cassill et al. 2007; Cassill and Watkins 2010; Cassill et al. 2010). A skewed resource distribution means that the smallest die preferentially until the size of the group shrinks and reaches equilibrium with the reduced levels of resources or sated predators. In other words, when environmental risks are low, seven of eight piglets

survive to maturity; when environmental risks are high, one of eight piglets survives to maturity (Cassill and Hardisty 2010; also see: Cassill et al. 2010).

When Neighbors are Altruists

In his attempt to solve the enigma of altruism, Hamilton got it almost right with his selfish herd model (Hamilton 1971; also see: Landa 1998; Landa 2008). Individual offspring hide in a large crowd to protect themselves and it matters not at all whether group members are related or unrelated. Hamilton's model is extended by the 4-D by awarding the survival of herd members to their parent's lifetime fitness rather than to the individuals themselves.

In groups, individuals need not expend excess energy out-swimming, out-running or out-flying a predator; they only need to swim a little faster than another fish (Landa 1998), run a little faster than another zebra or fly a little faster than another bird to survive (Williams 1966). The one left behind become the predator's lunch (Figure 2.5). Those that are faster than their neighbors gain an increment of survival that is awarded as an increment of potential fitness to their *parents*.
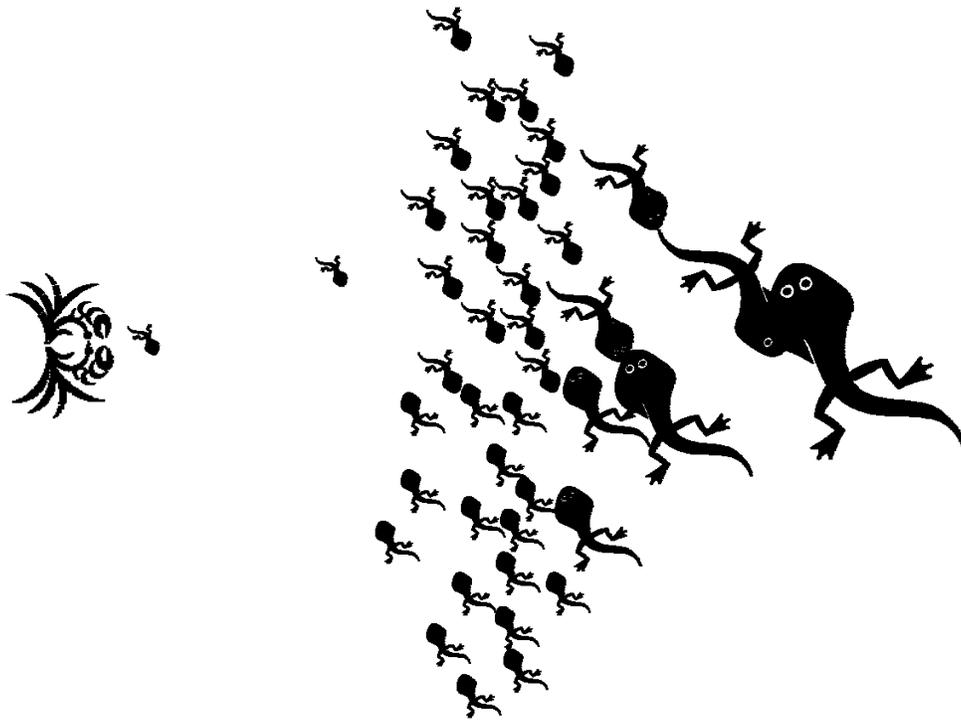
Figure 2.5 Offspring Skew and Within-Group Competition: the 4-D model explains why competitions among offspring or non-kin group members are not always lethal. A competitor does not want to kill his opponent; otherwise he loses an increment of group size and reduces his ability to hide in a crowd. An individual only wants to *weaken* his opponent and gain a position of status within the group, away from the vulnerable edge. Thus, competition is less about being the best and more about *not* being the worst (figure: Cassill and Hardisty 2010).

In the final analysis, the selfish herd construct is an important component of our 4-D model (see also: Landa 1998). If offspring disperse first and then form groups later in life—as is the case with some species of birds, dolphins, elephants, fish, hyenas, whales, lions, some primates, some sharks and wolves—group members are unlikely to be related. Alternatively, small families with one offspring might merge together to form larger groups of unrelated members (Cassill et al. 2007) such as prides of lions, packs of wolves or pods of whales. Either way, in high risk environments, when individuals gain an increment of survival by joining groups, their parents gain a potential increment of fitness (Cassill and Watkins 2004; Cassill and Watkins 2010; Cassill and Hardisty 2010).

Altruists Exist at Multiple Levels of Organization

A multilevel selection perspective is an important and useful concept in biology (Field 2008; Landa 2008; Landa and Wilson 2008), but it needs to be associated with a 4-D model rather than group selection (see: Limitations of Group Fitness). Indeed, the tenets of the 4-D model can be applied at every level of biological organization from molecules to cells to organisms to families to societies. Each level of biology has its own challenges for finding sources of energy and avoiding predators such as viruses, bacteria, carnivores or armies.

For example, by skewing the function of nucleic acid sequences, the probability that an invading virus will disrupt a functional gene is low (Cassill 2005). By skewing piglet development, easy-to-catch runts shield the more developed piglets from the jaws of death (Graves 1984; Andersen et al. 2000; Marchant et al. 2000; Puppe and Tuchscherer 2000; Fernandez-Llario and Mateos-Quesada 2005; Kranendonk et al. 2007; Drake et al. 2008; Roehe et al. 2009).

The important point is that, at each level of complexity, organic agents diversify their offspring to cope with their own challenges. Their goal is not to win the race by producing highly adapted offspring; rather, their goal is to avoid extinction by producing diverse offspring. According to the 4-D model, the most successful diversification pattern is skew—whether it is body size, ability, fertility, motivation or behavior. At each level of organization, skew allows organic units to cluster into hierarchies and create the next level of biological complexity. Without the survival guarantee that offspring skew provides, biological complexity as we know it would not have evolved.

CHAPTER 3: THE 4-D FITNESS MODEL APPLIED TO FAMILIES OF SNAKES

Introduction

The Shedao pit viper, *Gloydius shedaoensis*, is the only species of snake found on the
island of Shedao, located in the Bohai Sea off the northeastern coast of China (Li 1995)
(Cassill et al. 2010). In scientific circles, the Shedao pit viper is known for its 'accidental
altruism' (Shine et al. 2002a). Small pit vipers, juveniles, expend venom killing birds
that are too large to swallow. However, the bird carcasses are not wasted; instead, they
are quickly scavenged by large, neighboring adults. Large adult pit vipers kill raptorial
sparrowhawks that prey on juvenile snakes, but which pose no threat to the adults. The
adults do not swallow the sparrowhawks, thus the hawks are not a source of nutrients for
the snakes. That the juveniles kill songbirds that are too large to swallow and the adults
kill hawks that are no threat to themselves has been classified as altruism because there
are apparent costs in venom with no immediate benefit in food. These behaviors have
been labeled 'accidental' as the origin of adults killing hawks is most likely the retention
of juvenile defense behavior, and the origin of juveniles killing large birds is most likely
a practice behavior wherein juveniles strike at and kill any songbird that flies within
striking distance but swallow only those that are small enough (Cassill et al. 2010).

These behaviors could have 'atrophied' over evolutionary time, and yet they have not.
We hypothesized that these behaviors have remained in the gene pool because there are

immediate survival benefits to offspring that have not been accounted for by current models of natural selection (Cassill et al. 2010).

In the following sections, the behavioral ecology of the Shedao pit viper will be detailed, as well as how the 4-D model was used to perform a computer simulation which compared the lifetime fitness of pit viper breeders with altruistic and selfish genotypes. In particular, we wanted to know whether it could pay pit viper mothers to have offspring which were selfish part of the time when hunting, but also altruistic part of the time when hunting. Finally, the straightforwardness and simplicity with which the 4-D model of natural selection explains the evolution of mutualism and altruism from a breeder exploitation perspective is discussed (see also: Ghiselin 1974; Cassill 2006).

A Den of Snakes

Shedao is a small island located 13 km off the northeast coast of China. The island is one of many that provide a rest stop for large populations of songbirds that migrate to and from their Siberian breeding sites (Li 1995). For two weeks each spring and fall, thousands of songbirds, passerines ranging in size from finches to ravens, temporarily inhabit the island of Shedao. In addition to these migratory birds, Shedao is inhabited year-round by the pit viper, *G. shedaoensis*, one of a few snake species worldwide known to feed on birds from birth (Shine 1983). The snakes are inactive most of the year, but emerge from terrestrial shelters to ambush songbirds during migration periods (Sun 1990)

During each migration period, the songbirds are so abundant that there is no need for Shedao pit vipers to compete with each other for food. Indeed, the Shedao pit viper lives at extremely high densities in relatively open habitat (approximately one snake per square

meter at prime ambush sites) without aggression toward each other (Shine et al. 2002b), even when the snakes are in physical contact on the same or adjacent branches from which they ambush songbirds.

Shedao pit vipers feed twice a year in gluttonous quantities, swallowing three or more birds a day during the bird migration period. Their venom is more toxic than that of most vipers as evidenced by the observation that birds die within seconds of being bitten (Zhao et al. 1979). Despite its high toxicity, venom is limited in supply. Ten to fifteen days are needed to fully replenish a snake's supply (Li 1995). The dynamics of venom injection are not well known. Current studies suggest that the snakes do not meter the rate and amount of venom injected in their prey in proportion to prey size or type (Young et al. 2002). Thus, if the Shedao pit viper is unable to kill a sufficient number of prey because it wasted venom on prey it could not swallow or predate predators that were no threat as it would risk dying of starvation before the next songbird migration.

Shine and colleagues (2002a) labeled the behavior of the small, gape-limited juvenile pit vipers altruistic because the juveniles often expend venom killing songbirds that are too large for them to swallow. Large songbird carcasses are abandoned by the juveniles, but not wasted. Within twenty-four hours, prey carcasses are scavenged by neighboring adults. Adult pit vipers on the island of Shedao have no natural predators. Despite their immunity from predation, adults viciously attack and kill the sparrowhawk, *Accipiter nisus,* which preys only on the small juvenile pit vipers (Shine et al. 2002a).

In summary, juvenile pit vipers enhance the survival of adults by providing them free meals and adults enhance the survival of juveniles by protecting them from predatory sparrowhawks. Because neighboring pit vipers are not likely to be siblings (littermates

disperse throughout the island after hatching) the altruistic behavior of the Shedao pit

viper toward neighbors thus does not fit into a kin selection model (Shine et al. 2002a).

Therein lays the pit viper's enigma. How are we to explain the accidental altruism of this

snake species? In the next section, we describe how the four-dimensional (4-D) model

offers a feasible pathway for the pit viper's altruism to evolve due to natural selection

processes.

A Den of Selection Models

In an "eat or be eaten" world, not only do organisms interact with each other, they

must constantly search for food and at the same time 'look over their shoulders' to avoid

predators (see Figure 3.1). Few game models incorporate all three levels of interactions

when describing animal behavior. However, the 4-D model (Cassill 2006; Cassill and

Watkins 2009; Cassill and Hardisty 2010) takes into account three levels of interaction:

offspring x offspring interactions; offspring x predator interactions and offspring x prey

interactions. In addition, the 4-D model also takes into account two generations of

conspecifics: breeders and their surviving offspring. The quantity 'surviving offspring' is

emphasized because, when calculating parental fitness, we should not 'count our eggs

before they hatch.' Counting the number of 'surviving offspring' is the most appropriate

metric for quantifying a breeder's lifetime fitness.
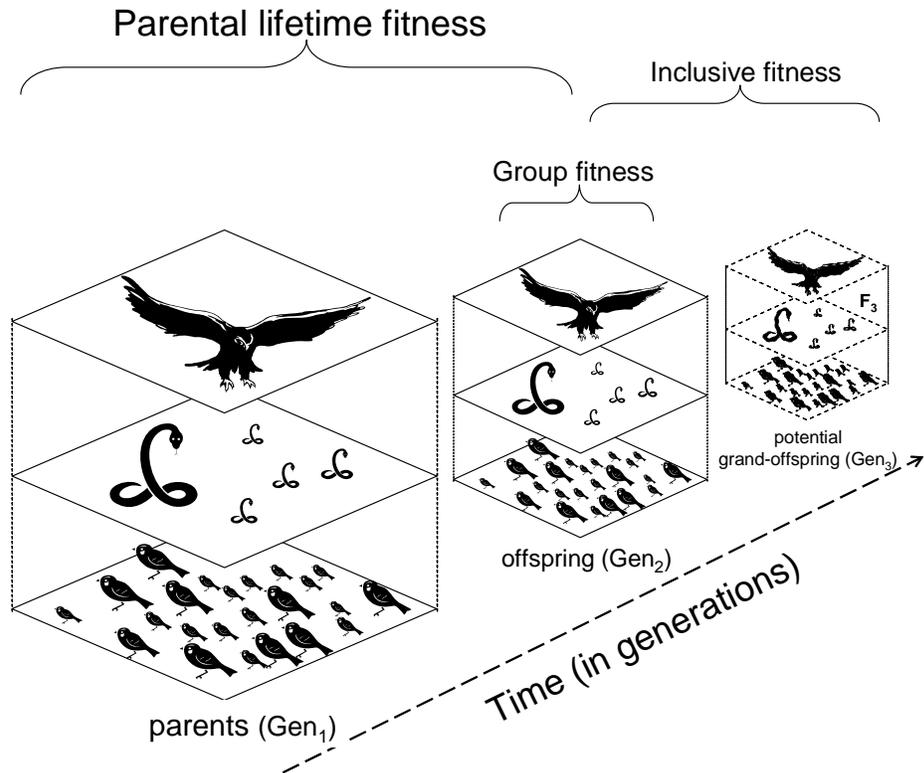
Figure 3.1 Fitness Calculations in a 4-D Natural Selection Environment: Pit vipers, their prey and their predators comprise the three levels of interaction; time in the form of generations comprises the fourth dimension. In the 4-D model, direct fitness is a retro-generational construct based on parental lifetime fitness. The number of "surviving" pit viper offspring in Generation 2 is the quantitative measure for the lifetime fitness of breeders in Generation 1. Offspring survival depends on their interactions with predators, prey and conspecifics. In group selection, group fitness is a one-dimensional (1-D) intra-generation construct. The number of surviving offspring within the same generation determines mean group fitness. The probability of offspring survival, rather than individual reproduction, is the quantitative measure for fitness. Kin selection employs inclusive fitness. According to inclusive fitness, an ideal number of relatives must be produced in Generation 3 by an ideal number of surviving relatives of an altruistic organism in Generation 2. The ideal number is determined by the probability that the altruist and its surviving relatives in Generation 2 shared genes by descent from a common ancestor in Generation 1. Inclusive fitness is predicated on the probability of 'future' reproduction by altruistic offspring saved by an altruistic relative who, in actuality, may or may not live to reproduce (Figure: Cassill 2006; Cassill et al. 2010).

Unlike kin selection, the 4-D model awards the benefits of offspring survival

retro-actively, back to their *parents*, and not to the offspring themselves. Another

difference is that kin selection assumes offspring survival is random whereas the 4-D

model assumes offspring survival is biased in a skewed pattern. From conception, some

offspring are simply more likely to survive and reproduce than others (see also: Ghiselin 1974).
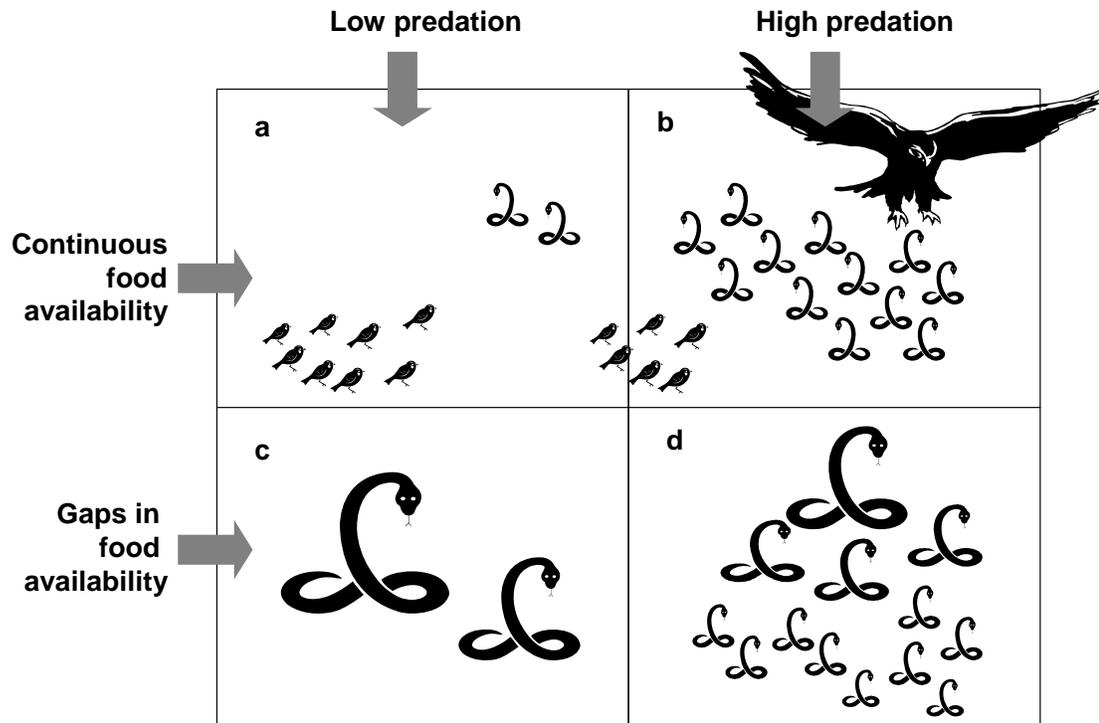
Figure 3.2 Predictions of the 4-D Model: (a) When food is continuous and predators are rare, breeders produce a few, small offspring. (b) When food is continuous and predators are many, breeders produce many, small offspring. (c) When food cycles between abundant and scarce and predators are rare, breeders produce a few, large, well-provisioned offspring. (d) When food cycles between abundant and scarce, and predators are many, breeders produce a few large offspring that will survive scarcity *and* many small offspring to buffer the larger offspring from predators. Skewing offspring size or behavior also has the advantage of de-escalating the arms-race between predator and prey. Small offspring are sacrificed so that predators need never evolve to be fast enough or large enough to kill large offspring (Figure: Cassill et al. 2010).

When the risks of death by predation and starvation are high, the 4-D model predicts that breeders can increase their lifetime fitness by skewing offspring morphology or behavior (Figure 3.2d). Litter size or clutch size is selected for based on rates of

predation. The degree of skew, which can be measured by the Gini coefficient, in offspring quality is selected for based on the duration of cycles of food scarcity (Figure 3.2).

In this study, we simulated the altruistic behaviors of the Shedao pit viper in their natural habitat. We hypothesized that breeders with offspring that were both altruistic *and* selfish (help oneself *and* help others as the opportunities arise) would realize greater lifetime fitness than breeders with pure-altruistic offspring (help only others, not oneself) or pure-selfish offspring (help only oneself, not others). Our series of computer simulated experiments were based on the known biology of the Shedao pit viper. In the next section, we describe the snake's biology and the algorithms of the simulated experiment based on their behavior and their environment. Although facts about the biology of the pit viper, *G. shedaoensis,* are accumulating, our knowledge of this island snake is still limited and thus we cannot consider our simulation "perfect" but still the results do offer some encouragement to the theory that offspring skew is an appropriate explanation for Shedao pit viper predation behavior.

A Den of Simulated Pit Vipers

Shedao pit viper juveniles are approximately one-tenth the weight of adults (Wüster et al. 2005). The head and jaw gape of juveniles is one-third the size of adults. The relatively large gape of juveniles is likely an adaptation to accommodate avian prey at an early age (Sun et al. 2002). The longevity of pit viper breeders is unknown. The mean litter size of the Shedao pit viper is five (range 2 to 9; n = 18; Sun et al. 2002).

Littermates disperse randomly about the island. Once they establish a shelter and a nearby ambush site, snakes are faithful to those spots (Shine et al. 2002b).

During a single two-week bird migration through Shedao, a research team collected 25 snake-bitten birds that were dying, but not yet dead (5 hawks and 20 songbirds; Shine et al. 2002a). The ratio of dying songbirds to predatory hawks was 4:1. The ratio of large to small songbirds was 4:1. The number of snakes in the area was estimated at ~180. Thus, the ratio of hawks to snakes was about 3:100. In this sample, hawks were over-represented because, after a strike, hawks are always rejected, whereas few songbirds are rejected. In addition, the sample's ratio of large to small songbirds was overly large as small birds are rarely rejected; instead they are swallowed. In addition, because snakes do not allocate venom according to prey size, larger birds might not get the same proportional dose as smaller birds (Young et al. 2002); thus larger birds would take longer to die before being swallowed. In summary, the ratio of hawks to snakes is likely to be greater than 3:100 and the ratio of large to small songbird prey is likely to be less than 1:1.

In this section, we describe the algorithms of our computer simulation based on the known biology of the Shedao pit viper. The simulated ratio of hawks to songbirds and the ratio of small to large songbirds were similar to natural populations. In addition, several parameters in the simulation were standardized to reduce random variation so we could better quantify the effect of altruistic behaviors on offspring survival. Offspring survival was awarded to their parents, the breeders, in the form of lifetime fitness.

Our objective was to quantify the survival of pit viper offspring when they had to interact at three levels: with each other, with hawk predators, and with songbird prey over

ten bird migration cycles (Figure 3.1), each type of interaction occurring over time. By definition, altruistic interactions incur a cost to the donor; at the same time, altruistic interactions produce a benefit to the recipient. Our overall objective was to determine if the benefits of altruistic interactions were greater than the costs. If so, then the lifetime fitness of their *parents* would increase, revealing a simple pathway, via natural selection, for the evolution of altruistic and selfish behaviors.

Our computer simulation consisted of an island of 400 cells (a 20 x 20 cell grid). Environmental conditions and behavioral parameters mimicked the biology of the Shedao pit viper. The question we wanted to answer was whether our 4-D natural selection model could explain the evolution of altruistic behavior among juvenile and adult offspring. A description of the simulation parameters follows.

Lifetime Fitness for Pit Viper Breeders

Each simulated breeder produced four offspring per year for ten breeding cycles. The maximum lifetime fitness for each simulated pit viper breeder was 40 offspring. If small juvenile offspring survived the first year (Table 3.1; Column 1), they transformed into large non-breeding adult offspring. The lifetime fitness per breeder was calculated as the total number of *surviving* juvenile and non-breeding adult offspring at the end of the ten breeding cycles.

TABLE 3.1 (Table: Cassill et al. 2010): Survival Algorithms and Correlated Genotypes for Juvenile and Adult Pit Vipers

1	**Juveniles**	Must ingest two small songbirds per migration.
2	**Altruistic juveniles**	Kill only large songbirds. Do not swallow.
3	**Selfish juveniles**	Kill and swallow only small songbirds.
4	**Flexible juveniles**	Kill large and small songbirds. Swallow only small songbirds.
5	**Adults**	Must ingest two large songbirds, or one large and two small songbirds per migration.
6	**Altruistic adults**	Kill only hawks. Do not swallow them.
7	**Selfish adults**	Kill and swallow songbirds of any size. Do not kill hawks.
8	**Flexible adults**	Kill and swallow songbirds of any size. Kill hawks, but do not swallow them.

Pit Viper Parental Genotype

Simulated pit viper breeders were programmed with diverse behavioral genotypes, two pure and four flexible. In the 100% selfish genotype (Table 1, Rows 3 & 7), juvenile snakes did not kill large birds; adult snakes did not kill hawks. In the 100% altruistic genotype, (Table 3.1, Rows 2 & 6), juvenile snakes killed only large songbirds for neighbors, but did not kill small songbirds for themselves; adult snakes killed only hawks to protect juveniles, but did not kill songbirds for themselves. In the flexible genotypes, the probability of altruistic behavior varied (0.25, 0.5, 0.75, 1.0). A flexible 1.0 genotype

meant that snakes behaved altruistically every time an opportunity presented itself to do so; and, they behaved selfishly every time an opportunity presented itself. Pit vipers with intermediate genotypes (i.e. 0.25, 0.5 and 0.75) were considered "moody." Sometimes they were altruistic when the opportunity arose, sometimes they were not, depending on the probability level set for altruism.

Controls were "no hawks present" for the 100% flexible altruistic genotype (1.0) and "no hawks present" for the 100% selfish genotype (0.0). In the figures and text, data for "no hawk" controls were labeled with an asterisk (1.0* and 0.0*).

Pit Viper Breeder Location and Offspring Dispersal

Seven pit viper breeders were randomly located on the island; each occupied one of the 400 cells (mature males were assumed, and not included in the simulation). Each pit viper breeder produced four juvenile offspring each breeding season for ten years. Offspring randomly dispersed to unoccupied cells on the island. Once they entered a cell, they stayed in that cell for the rest of their lifetime (maximum ten years if they did not starve or get killed by the hawk). If all offspring survived (i.e. 7 breeders x 4 offspring/breeder/year x 10 years = 280 snakes), 70% of the island's 400 cells would be occupied.

Breeder Diversity

To test the influence of heterogeneous behavior among neighbors, an additional treatment included a mix of breeder genotypes on the island. Seven breeders and their

offspring representing six genotypes were randomly distributed on the island for each of the 100 replicates.

Songbird Dispersal

Each breeding season, after simulated juvenile pit vipers hatched and randomly dispersed from the parent's cell to unoccupied cells on the simulated island, 800 simulated songbirds migrated to the island over two weeks. During the first week, 400 songbirds, in a ratio of 1:1 small to large birds, flew onto the island and landed randomly, one bird per cell, until the island cells were saturated. If a cell contained a pit viper, the songbird was struck and killed, but not necessarily eaten. At the end of the first week, surviving songbirds flew from the island to the mainland and a second wave of 400 birds flew to the island (1:1 ratio of small to large songbirds), randomly saturating the island's cells as before. During the two-week songbird migration, each pit viper was guaranteed an opportunity to kill two birds--2 small birds, 2 large birds, or 1 small and 1 large bird. If adult snakes were not able to ingest at least 2 large songbirds, they died. If juveniles were not able to ingest 2 small songbirds, they died. If a juvenile killed a large songbird, it was ingested by the nearest adult snake.

Hawk Dispersal

After two waves of simulated songbirds had migrated to and from the simulated island, seven hawks (one for each pit viper breeder on the island) migrated onto the island at randomly selected cells and then flew to the nearest pit viper offspring. If the pit viper was a juvenile, the hawk killed and ate it. The hawk then flew off the island, but returned

the next year (Table 3.1). If the pit viper was an adult, there were two outcomes, depending on the pit viper's genotype. If the adult's genotype, or "mood," was altruistic, the hawk was killed, but not eaten. If the adult's genotype was selfish, the hawk lived and returned to the island the following year. On a perfect island, with all 280 pit viper offspring surviving for ten years along with the seven hawks, the ratio would be ~ 3:100 (7/280), similar to the estimated ratio of hawks to Shedao pit vipers (Shine et al. 2002a).

Simulation Design and Data Analysis

We had two independent variables: breeder genotypes (six treatments), and population diversity (two treatments, homogeneous or heterogeneous populations). We repeated each run 100 times. The dependent variable was the lifetime fitness for each pit viper breeder over 10 breeding seasons (6 genotypes x 100 runs each = 600 breeder lifetime fitness outcomes). Controls without predation (1.0* and 0.0*) were run and analyzed independently. Lifetime fitness data per genotype were normally distributed (Pearson's skew index); thus data were analyzed with multi-factor ANOVA, t-tests or regression using JMP IN statistical software (Sall et al. 2005).

A Den of Altruistic *and* Selfish Individuals

Breeder genotype had a significant effect on their lifetime fitness (multi-factor ANOVA: $F_{4,595} = 100.48$; $p<0.0001$; Figure 3.3a). Breeders with behaviorally flexible genotypes realized 23 times the fitness of breeders with pure altruistic genotypes and 3 times the fitness of breeders with pure selfish genotypes.

Prey sharing among pit viper offspring accounted for 78.5% of the observed variance in breeder fitness (0.0* vs 1.0*: $t_{98} = -26.9$; p<0.0001; Figure 3.3a). Killing the predatory hawk accounted for 21.2% of the observed variance in breeder fitness (0.0* vs 0.0: $t_{98} = -7.31$; p<0.0001; Figure 3.3a). When a larger number of juvenile offspring survived to mature into large adults, hawks were killed significantly sooner, eliminating predation on future litters of offspring and thus increasing breeder lifetime fitness (Figure 3.3b).
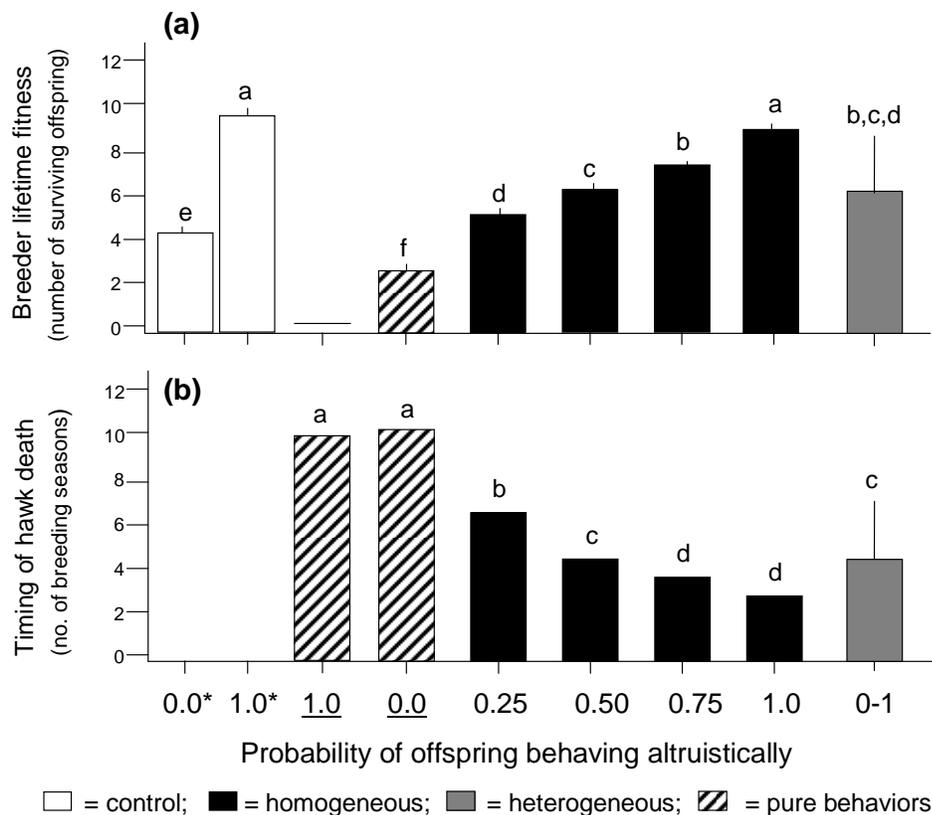
Figure 3.3 Offspring Genotype versus Offspring Survival: In populations of pit vipers with pure altruistic genotypes (striped 1.0), juveniles killed large birds for adults, but not small birds for themselves; adults killed hawks that prey on juveniles but did not kill birds for themselves. (a) Not surprising, all offspring died of starvation before maturing to non-reproductive adults; thus their parent's lifetime fitness was zero. Pure altruistic genotypes are not sustainable over many generations. (b) Also not surprising, without at least one juvenile maturing into an adult that could kill hawks, hawks survived ten years.

In populations of pit vipers with pure selfish genotypes (striped 0.0), juveniles killed small birds for themselves but not large birds for adults; adults killed large birds for themselves, but not hawks that prey on juvenile snakes. (a) Breeder lifetime fitness was low. (b) Hawk survival was high. Relative to behaviorally flexible genotypes, pure selfish genotypes would not be sustainable over many generations.

In populations of behaviorally flexible genotypes (black 0.25-1.0), juveniles killed small birds for themselves and large birds for neighboring adults when opportunities arose; adults killed small and large birds for themselves and they killed hawks that prey on juveniles when the opportunities arose. The greater the probability that snakes would behave altruistically when the opportunities arose, the longer they survived, thus (a) increasing their parent's lifetime fitness, and (b) decreasing hawk survival. *Not only were snakes helping others through 'accidental' acts of kindness, others were helping them.*

In heterogeneous populations of genotypes (gray 0-1), breeder fitness (a) and hawk survival (b) were intermediate relative to homogeneous populations. Hawks survived longer when pit viper breeders were selfish rather than altruistic. Hawks reduced juvenile offspring survival (Figure: Cassill et al. 2010).

50

The relationship between the timing of a hawk's death and a snake's lifetime fitness

(number of surviving offspring) was significant (Regression: breeder fitness = 8.84 –

0.53 hawk death; R^2 = 0.435; p<0.001; Figure 3.4). When adult snakes killed hawks,

more juvenile snakes survived, resulting in an increase in their parent's lifetime fitness.
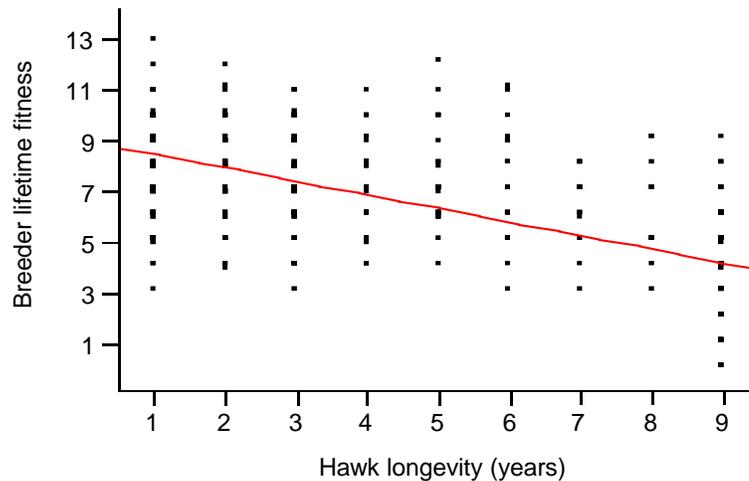
Figure 3.4 Predator Mortality versus Breeder Fitness: When adult offspring behaved selfishly, hawks lived longer and killed a larger number of juvenile offspring. As a result, the mean lifetime fitness of breeders declined (Figure: Cassill et al. 2010).

Why Animals Help Themselves First and Others After

The lifetime fitness of pit viper breeders whose offspring helped themselves *and*

others, related or unrelated, increased *three-fold* relative to pit viper breeders whose

selfish offspring helped only themselves *and twenty-three-fold* relative to pit viper

breeders whose altruistic offspring helped only others. These results reveal that altruism

can evolve as a part of a flexible repertoire of behaviors. Not only were altruistic and

51

selfish snakes occasionally helping others, they were occasionally receiving help from other snakes. Thus, the accidental altruism of the Shedao pit viper is better explained as opportunistic mutualism.

The 4-D model closes the loop left open by other models by awarding the benefits of altruistic behavior among offspring to their parents, not to the offspring themselves (Cassill 2006; Cassill and Hardisty 2010). Second, the 4-D model introduces realism by simulating individuals with flexible behaviors. If we open our thinking to the nuances of the choices that animals make, we are more likely to discover the elegant solutions that have evolved for surviving in complex environments. With the 4-D perspective, we can model animals based on the reality that gene possession does not always mean gene expression. Just because an organism has a gene for altruism does not mean that it will ever be expressed. The dislinkage between gene possession and gene expression is well documented in developmental biology for phenotypic plasticity (e.g. West-Eberhard 1989; West-Eberhard 2003; Banerji & Morin 2009). Here, we see that the gene possession-expression dislinkage may apply to behavior as well. Organisms may be capable of selfish *and* altruistic behaviors, depending on their ecological circumstances. Organisms might cooperate in one circumstance, but not in another depending on factors such as season, time of day or temperature, and on the traits of the other individual such as its health, status, age or sex.

We posited (Cassill and Hardisty 2010) that breeders might skew the behavior of their offspring as a type of "bet-hedging" strategy to guarantee that some offspring survive risky environments (Seger and Brockmann 1987; Philippi and Seger 1989; Landa 1998; Landa 1999; Gifford 2000; Cassill 2002a; Cassill 2002b; Cassill et al. 2007). There are

52

some opportunities to modify current bet-hedging models (Cohen 1966; Cohen 1968; Seger and Brockmann 1987; Philippi and Seger 1989; Hopper 1999) to fit the 4-D model but it should be noted that the 4-D model is a bet-hedging strategy where the parent is *maximizing* lifetime reproductive success (e.g. this model makes good on "the individual-as-maximizing-agent" analogy: Grafen 1999), rather than *minimizing* the variance in *annual* reproductive success (i.e., Cohen 1966; Cohen 1968; Gillespie 1977; Seger and Brockmann 1987; Philippi and Seger 1989; Hopper 1999; Beaumont et al. 2009; Rees et al. 2010; Ripa et al. 2010).

When viewed through a 4-D lens, different forms of reciprocity can also be explained. According to a 4-D model perspective, pseudo-reciprocity (Connor 1986; Connor 1995a; Connor 1995b; Connor 1995c) and reciprocal altruism (Trivers 1971) are mutualisms with differences in the timing, content and intent of payback (Connor 1995a; Connor 1995b; Connor 1995c). In the Shedao pit viper, adults were better fed by protecting juveniles and juveniles were better protected by feeding adults. In both cases, offspring survival increased because neighbors helped neighbors, resulting in increased lifetime fitness for their parents.

In summary, if we enhance our models to include the biology and ecology of animals, we are likely to find that cooperation among conspecifics is far more ubiquitous than we ever imagined (see also Simberloff 1982; Lewin 1983; Lewin and Lewin 1983). In addition, the Shedao pit vipers may also shed some light on the evolution of the family. For by having both friends *and* potential competitors around, the Shedao pit vipers are also inadvertently ensuring their own survival by 'safety in numbers.'

CHAPTER 4: MEMES AS AN ALTERNATIVE FORM OF INFORMATION

TRANSMISSION FROM MOTHER TO OFFSPRING

Animal Tool-Use

In *The Selfish Gene*, Richard Dawkins (1976) defined a discrete unit of cultural

inheritance he called the meme. Dawkins' intention was to conceptualize units of culture

so that the evolution of culture could be scientifically studied. Although memes are an

interesting 'qualitative' construct, they have not yet matured into a 'quantitative'

construct. In this chapter, I will describe a conceptual framework by which scientists can

quantify memes (Hardisty and Cassill 2010b). Memes and genes are parallel systems by

which organisms increase their lifetime fitness (see also Odling-Smee et al. 2003; Whiten

2005). By illuminating the influence of memes on an animal's lifetime fitness, we thus

illuminate the link between the evolution of culture and the evolution of species.

According to Dawkins (1976), memes must share three properties with genes:

longevity, fecundity and copying fidelity. Longevity refers to the lifespan of a meme.

Fecundity refers to the rate of spread of a meme. Copying-fidelity refers to how

accurately a meme is replicated. There is also a fourth property: memes must—like

genes—affect an organism's lifetime fitness (Hardisty and Cassill 2010b; Hardisty and

Cassill 2010c). In other words, the presence of a meme must, on average, improve the

survival or reproductive success of the organism that replicates it. Dawkins (1976) had

claimed that memes us their carriers to replicate like viruses but I believe that this is incorrect or at the least impossible to operationalize given the current state of neurobiology. In the following sections, I will describe some studies that have the potential to link a type of meme—tool-use—to an organism's lifetime fitness (Hardisty and Cassill 2010b; Hardisty and Cassill 2010c). The novel examples of tool-use in dolphins, chimpanzees and bowerbirds are presented as a first attempt to link the benefits of memes to animals' fitness (Hardisty and Cassill 2010b). I will also show how the 4-D model allows us to take into account the effect of a meme on an organism's fitness.

Animal Tool-Use as a Meme

Sterelny (2006) extended the meme concept by noting that memes can be categorized into different levels of 'fitness.' According to Sterelny, a high fitness meme should result in an artifact that is physically enduring, made from easy to find materials and easy to reverse-engineer. Animal tools may thus be considered to constitute an excellent example of a meme (Hardisty and Cassill 2010b; Hardisty and Cassill 2010c). A tool is an object held in the hand, foot or mouth that is manipulated to gain some immediate goal (Boesch and Boesch 1990). With the discovery of tool-use among a number of animals, we now have the opportunity to conduct long-term field studies to determine the effects of tool-use memes on an organism's lifetime fitness (see Figure 4.1) (Hardisty and Cassill 2010b). Long-term studies of memes such as tool-use on an organism's lifetime fitness may confirm that 'nature *and* nurture,' in the form of memes and genes, interact to determine survival and reproductive success (Ridley 2003).

Starvation

Internal nutrient storage
Chase and capture
Filter feeding
Foraging
Ambush

External nutrient storage
Tools of capture/harvesting
Agriculture/Farming
Genetic engineering
Hybrid breeding

genes memes

Learned avoidance

Chance

genes   genes

Accidents --------- animal --------- Catastrophes

memes   memes

Safety tools
Safety rules
Teaching avoidance

Dams
Locks
Sea walls
Constructed shelters
Constructed roads

genes memes

Speed
Spines
Thick fur
Thick shells
Camouflage
Hide in a crowd
Status to gain center of crowd

Weapons
Armor
Motes
Rafts
Constructed shelters
Cultural status symbols

Predation

Figure 4.1 Genes and Memes, Parallel Inheritance Systems: According to Darwin's theory of natural selection, many organisms die by natural causes including starvation, predation, accidents or catastrophes. Nature selects for genes that increase the survival rate of juveniles or the reproductive success of adults. Likewise, culture selects for memes that enhance the survival rate of juveniles or the reproductive success of adults. Tool-use by dolphins, chimpanzees and bowerbirds are each an example of a meme likely to enhance lifetime fitness. Long-term studies are needed to confirm the conjecture (Figure: Hardisty and Cassill 2010b).

Studies of dolphins have revealed multiple examples of tool-use, making them prime candidates for studying memes (Hardisty and Cassill 2010b). Dolphins have been observed using prey items to dislodge and catch other prey items in the wild (Anderson 2002), scrapers to dislodge seaweed in captivity (Anderson 2002), and sponges while foraging in the wild (Smolker et al. 1997; Krutzen et al. 2005; Sargeant and Mann 2009). Krutzen et al. (2005) found that females in wild populations of bottlenose dolphins, *Tursiops*, stick their snouts into sponges, presumably to prevent injury while foraging on

the ocean bottom. Sponging is a meme that female dolphins teach to their female

offspring, but not usually to their male offspring. A study on the lifetime fitness of

spongers relative to non-spongers could provide an example of how the origin and

evolution of culture parallels the origin and evolution of species (Hardisty and Cassill

2010b).

Chimpanzees also use tools regularly for multiple tasks (Hardisty and Cassill 2010b).

Tool-use varies between the sexes, among families and among groups. The most

commonly observed tool-uses by chimpanzees are fishing for insects or honey, cracking

nuts, and hunting (Boesch and Boesch 1990; Biro et al. 2003; Lonsdorf et al. 2007;

Lycett et al. 2007; Pruetz and Bertolani 2007; Sanz and Morgan 2009; McGrew 2010).

At one location, chimpanzees employ stone hammers and anvils to open one species of

nut, whereas at a different location, wooden hammers, stone hammers, root anvils and

stone anvils are used in various combinations to crack open three species of nuts.

Differences in nutcracking techniques are not genetic differences between populations,

but are cultural differences (Lycett et al. 2007). "Cultural zones" formed when chimps

were trained in new foraging tasks using tools and then allowed to teach their

conspecifics the newly learned techniques (Biro et al. 2003; Whiten et al. 2005; Hopper

et al. 2007; Whiten et al. 2007). Chimpanzees exhibit tool-use preferences based on sex,

perceived status and age (Lonsdorf et al. 2004; Whiten et al. 2005; Pruetz and Bertolani

2007). Long-term comparative studies on the effects of tool-use versus non-tool-use on

chimpanzee lifetime fitness would further legitimize memes (Hardisty and Cassill

2010b).

Bowerbirds can be argued to possess cultures (Madden 2008), thus bowerbirds are an attractive study system for memes (Hardisty and Cassill 2010b). Bowers take three general forms: tooth-billed bowerbirds clear and decorate courts, but do not build a structure; avenue bowers build two or four walls into an "avenue" and surround it with decorations; and maypole bowers build a central pillar, or "maypole," to which they attach twigs (Madden 2008). Sometimes bowerbirds paint their bower's avenue walls by masticating plant material, carbon and saliva in their bill and spreading it on the walls. Some observers report that the male forms a brush with which to apply paint, though others suggest that only the bill is used. Bowers are constructed throughout the breeding season, usually by a single male, and are the display sites for attracting females. Females inspect bower components closely and mate with males who build the best bowers. Numbers of specific decorations, bower size and symmetry, vary between species and accurately predict male reproductive success. In all of these cases, male bowerbirds bring together natural elements to produce a construct that performs a function his body cannot (Madden 2008). Differences within and among bowerbird cultures could thus provide ideal conditions for both experimental and comparative studies linking tool-use memes to lifetime fitness (Hardisty and Cassill 2010b).

Quantifying the Connection between Memes and Lifetime Fitness

'Lifetime fitness' is central to the study of evolution. Hence, we must be able to quantify lifetime fitness before we can study the effects of memes on an organism's fitness (Hardisty and Cassill 2010b; Hardisty and Cassill 2010c). Although annual fitness is perhaps the most common metric, a more powerful metric may be 'breeder

58

lifetime fitness' (Hardisty and Cassill 2010b). Annual fitness, for example the number of

eggs laid by a bowerbird breeder during one breeding season, is a poor measure of fitness

because most chicks die before they breed, thus their genes are not passed on to the next

generation. The metric, 'breeder lifetime fitness,' (Equation 1, Chapter 2:**32**) measures

the number of offspring that survive to maturity over breeder lifetime. In the case of

bowerbirds, a breeder might produce twenty chicks during its lifetime with only two

maturing and breeding. Thus, the lifetime fitness of this hypothetical bowerbird is two,

not twenty.

Breeder lifetime fitness: $f_l = lnp_sp_b$

l = breeder lifespan;

n = annual clutch size of breeder;

p_s = probability of offspring surviving to maturity;

p_b = probability of mature offspring eventually breeding

If tool-use by a male bowerbird allows him to paint a bower faster or with more color,

and if the rate of building or the color intensity of the bower is more likely to attract a

female, then the probability of that male mating (p_b = probability of mature offspring

breeding) increases relative to a bowerbird that uses only its bill. The increase is

awarded, not to that male, but to its parent's lifetime fitness. If tool-use for food

gathering by a mated chimpanzee increases her longevity (l) or the survival of an infant

(p_s), those increments of survival are awarded to the mated chimpanzee, not the infant

(Hardisty and Cassill 2010b).

59

In summary, by quantifying the effects of memes, such as tool-use, on an animal's lifetime fitness, we can elucidate the importance of memes as a cultural force shaping the evolution of species (Hardisty and Cassill 2010b; Hardisty and Cassill 2010c).

Memes and the Ecological Niche

Above, I argued that successful memes should share a fourth property with successful genes: memes should affect an organism's lifetime fitness by improving survival or reproduction (Hardisty and Cassill 2010b). Here, I argue that another way to link memes to individual fitness is to think of tools of an organism's ecological niche (Hardisty and Cassill 2010c). Each tool or artifact an organism makes that extends its evolutionary lifespan or increases its reproductive output is a meme that is contributing directly to that organism's fitness.

Though Hutchinson is usually credited with providing one of the first modern definitions of the ecological niche (1958), scientists have debated the best way to quantify the term "niche" for experimentation (see Gause 1934; Odum 1953; Whittaker et al. 1973). I prefer Whittaker et al.'s (1973) definition of the niche as entailing all of the intracommunity relationships and habitat requirements of a species.

However, as has been pointed out by Odling-Smee et al. 2003 (see also Laland and Sterelny 2006; Laland et al. 2007), if we extend the ecological niche concept to include culturally inherited memes, then the tools that organisms use to modify their environments can play a crucial role in their lifetime fitness and the survival of their offspring (see also: O'Brien et al. 1994). Niche artifacts from which organisms can create tools for hunting can be linked explicitly to their fitness (Hardisty and Cassill

2010b; Hardisty and Cassill 2010c). This is because any tool an organism makes that increases its survivorship or reproductive success, when such tool-use is a learned ability, should increase the organism's fitness (Plotkin and Odling-Smee 1979, Plotkin 1988; Richerson and Boyd 2005; Laland et al. 2007; Kingsbury 2008). For example we humans have modified our own environment, dramatically reducing the risks of predation and starvation to an historic low (Laland et al. 2007). In response, human populations have grown exponentially, not because we experienced increase reproductive output, but mainly because we stopped dying like flies (Lomborg 2001).

Hunting Tools as 'Ready-to-go' Memes that Increase Breeder Fitness

For example, further studying tool construction and use in chimpanzee hunting, where tool-use is rare (Boesch and Boesch 1989; Pruetz and Bertolani 2007), bonobo hunting, where tool-use is more common (Surbeck and Hohmann 2008; Surbeck et al. 2009), and human hunting, where a variety of tools are used (Kaplan and Hill 1985; Frison 1989; Walker et al. 2002; Waguespack and Surovell 2003), should be instructive in allowing biologists to make comparisons of the fitness of habitual hunters versus non-habitual, or infrequent, hunters (Hardisty and Cassill 2010c).

It has been hypothesized that successful male hunters in both chimpanzees and humans have increased opportunities for copulation (Kaplan and Hill 1985; Stanford et al. 1994; Hill and Hurtado 1996; Stanford 1996). In bonobos, hunting may allow immatures and females access to high-quality meat they would not otherwise have the chance to eat (Surbeck et al. 2009). Furthermore, in humans (e.g., the Ache, Hiwi, Machiguenga, Piro, Etolo, Gidra, Hadza and !Xo cultures) and chimpanzees a long-term

period of learning that lasts several years above and beyond peak physical strength, is necessary to become a proficient hunter (Walker et al. 2002; Boesch 2002).

What links all of these examples to memes? The fact that hunting behaviors in chimpanzees, bonobos and humans exhibit cultural variations but may *also* be construed as enlarging the ecological niche of the organisms engaging in these behaviors (Hardisty and Cassill 2010c).

The Oldowan Industrial Complex (~2.6-1 Million years ago or Mya) may be the best example of a stable tool-use meme (Hardisty and Cassill 2010c), showing little variability throughout a large geographic area over a period of more than a million years. It is often considered the first period of human technological innovation, though there is some disagreement over just who the tool-makers were (Susman 1991; Ambrose 2001; Toth and Schick 2009). Oldowan tools consist of percussors, prepared cores, shaped pieces and stone flakes, and starting 1.5 Mya, large bifacial cutting tools produced by more sophisticated shaping techniques, and have been found in Africa, Europe and Asia (Ambrose 2001; Toth and Schick 2009). Furthermore, Oldowan tool source materials seem to have been selected on the basis of the durability of the rock to be shaped, rather than abundance (Braun et al. 2008; Braun et al. 2009). According to Toth and Schick (2009), typical Oldowan stone tool assemblages generally includes percussors (hammerstones, spheroids), simple core forms (choppers, discoids, polyhedrons, heavy-duty scrapers), retouched elements (scrapers, awls), and debitage (flakes and fragments). These tools were durable and their construction can be learned, though it is not particularly easy to master. They were often made from locally available materials, but source rocks were sometimes gathered from as far as 20 kilometers away. The tools also

were likely made in multiple stages, when gathered from far away sources, and served multiple purposes. There is some debate over whether some types of tools were used for hunting, animal scavenging or plant foraging activities and the answer is not entirely clear (Toth and Schick 2009). However, what is clear is that Oldowan tools varied little, other than in the material of construction, over more than 1 million years and could be considered an example of a very stable meme that spread out of Africa with our early hominin ancestors. What also seems clear is that human tools took some of the burden of mechanical processing of foodstuffs from our teeth, allowing them to grow smaller (Ambrose 2001; Plummer 2004). Finally, anthropologists have long considered the Oldowan tools the first definitive remains of material culture, or, in my view, cultural memes. It is strongly believed that associated animal remains typically found at Oldowan sites were consumed using Oldowan tools (Ambrose 2001; Plummer 2004; Dominguez-Rodrigo et al. 2005; Toth and Schick 2009).

The Clovis tool complex lasted from approximately 13.2 to 12.8 thousand years ago and Clovis big-game hunters may have been amongst the first Americans (Goebel et al. 2008). The culture is named for their durable weapons, typically found with mammoth kills and believed to be part of a tool kit (Goebel et al. 2008) used to support a big game hunting-specialist lifestyle (Waguespack and Surovell 2003) and easily reverse-engineered (Frison 1989). In studies using the carcasses of culled African elephants, reconstructed Clovis weapons were highly effective for killing and butchering big game (Frison 1989). Frison's reconstructions included making hide and meat cutters, throwing spears with chipped-stone points and atl-atls with javelins, also with chipped-stone points. Frison showed that Clovis spear points were durable and easy to reverse-

engineer. For example, one spear point was re-shaped no less than threes times due to breakage, and was used successfully throughout Frison's experiments. In summary, Clovis weapons fit all of Sterelny's (2006) criteria and when taken with their long period of use—several hundred years—thus also constitute a high-fitness meme.

Discussion and Conclusions

The study of culturally inherited memes should thus illuminate answers as to the mysterious forces that govern the origins and spread of new technologies in both human and non-human hunters (Hardisty and Cassill 2010c). An important computational study by Gavrilets and Vose (2006) operationalized memes as either invented or imitated strategies that males use to win competitions for mate access. There may be some truth to this idea, as the work of Reader and Laland (2001) shows. Reader and Laland found that primate innovation occurs most frequently in males, followed by adult females, immature males and immature females. Male chimpanzees innovate most frequently in the context of mating and courtship competition. Low-status males were most likely to display innovation (Reader and Laland 2001), perhaps because they were unsuccessful at imitating higher-status males (Gavrilets and Vose 2006), or because they were marginalized and prevented from getting high-quality food stuffs or mates (Reader and Laland 2001).

Hayashi et al. (2005) found that when captive chimps which had been raised in the laboratory were shown how to use the hammer and anvil system, 1 chimp was never able to figure it out, while 2 other chimps were able to learn it almost immediately. The

64

researchers speculated that only some chimps learn to use tools effectively in the wild because of differences in the ability to put sets of objects together in their minds.

Whatever the origin of new memes, we must study their ecological contexts in order to gain further insight into the forces that foster innovation and force some animals to construct tools to accomplish important tasks.

CHAPTER 5: EVOLUTIONARY ARMS-RACES IN MOLLUSKS DAMPED BY SELECTION FOR THE PRODUCTION OF SELFISH AND ALTRUISTIC OFFSPRING WITHIN FAMILIES

Introduction: the Escalation Hypothesis

This chapter concerns evolutionary arms races in the phylum Mollusca and demonstrates that the classical idea of an evolutionary arms race is only one way the struggle between predator and prey may play out over geological timescales. The phylum Mollusca is comprised of a large number of diversified species ranging from the highly mobile cephalopods through the moderately mobile gastropods and bivalves to the nearly immobile chitons. To describe the explosive diversification in Molluscan bauplans and the dramatic increase in species numbers that occurred during the Paleozoic, Mesozoic and Cenozoic eras, beginning approximately 670 million years ago, Geerat Vermeij (1977) coined the terms "Escalation Hypothesis" and "Mesozoic Marine Revolution". According to Vermeij's Escalation Hypothesis, the explosive increase in Mollusca species was a result of an arms race between predators and prey (e.g., Dietl et al. 2004; Harper 2006; Vermeij 2006; Vermeij and Dietl 2006; Stanley 2008). In other words, as prey evolved traits to better evade one kind of predator, predators evolved traits that increased their ability to kill prey. A predator-prey arms race is a classic example of directional selection (Figure 5.1) (Hardisty and Cassill 2010d).
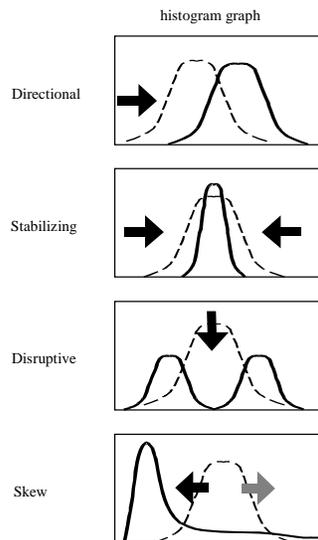
Figure 5.1 Stabilizing Selection for a Trait: a hypothetical population of bivalves with variation in shell thickness. A predator-prey arms race is a type of directional selection. Improved drilling ability in predators selects for prey with thicker shells. The production of offspring skew is a de-escalation strategy whereby the quality of offspring produced, every generation, by breeders is skewed (figure: Hardisty and Cassill 2010d).

   The predator-prey arms race has been cited as an important force in the life-history of

a number of marine species (Vermeij 1973; Vermeij 1977; Vermeij 1978; Abele et al.

1981; Vermeij 1987; Vermeij 2004; Vermeij 2007; Vermeij 2008). For example,

Vermeij's Escalation Hypothesis also applies to echinoderms and to some vertebrates.

Both groups comprise diverse sets of species with widely diversified means of

locomotion and shell-like skeletal adaptations. The echinoderms range from the

immobile hard-shelled corals to the semi-mobile soft hydra and migratory jellies. In

marine vertebrates, there are the relatively slow moving whales, with low metabolic rates,

as well as the fast moving, predatory seals and sharks. In terrestrial vertebrates, there are

the slow-moving, armored turtles and armadillos as well as the fast-moving cheetah, zebra, gazelles and birds.

In the following sections, I describe the predictions of Vermeij's Escalation Hypothesis and review the most cutting-edge evidence from the fossil record supporting those predictions. Finally, I offer offspring skew (also referred to as skew selection) (Cassill 2002a; Cassill 2002b; Cassill and Watkins 2004; Cassill 2006; Cassill et al. 2007; Cassill et al. 2010; Cassill and Hardisty 2010; Cassill and Watkins 2010; Hardisty and Cassill 2010d) as a model by which Mollusca and other animal phyla can be understood to 'strike back' and de-escalate predator-driven speciation events.

Predictions of the Escalation Hypothesis

The Escalation Hypothesis predicts that when a predator develops an adaptation that will allow it to compete more efficiently with other predators, the other predators will either evolve new adaptations or change their choice of prey, thus escalating speciation events and ultimately increasing species diversity (Vermeij 1978; Vermeij 1987; Vermeij 2004; Vermeij 2007; Vermeij et al. 2008). Examples of evolutionary innovations accelerated by predator-driven evolution are: increases in species diversity to foil both shell drilling and shell crushing predators (Vermeij 1973; Vermeij 1977; Vermeij 1978; Vermeij 1987; Baumiller and Gahn 2004; Dietl et al. 2004; Kelly and Hansen 2004; Vermeij 2004; Amano 2006; Kowalewski et al. 2006; Vermeij 2007; Vermeij 2008), walking ability in some species of crinoids (Meyer and Macurda 1977; Baumiller et al. 2008), chemical warfare in some marine species (McClintock et al. 1999; Harper 2006),

arm re-generation in crinoids (Baumiller and Gahn 2004; Baumiller et al. 2008) and hinged shells in bivalves (Harper 2006).

Finally, the Escalation Hypothesis predicts that when competitors and predators are the *most important*, or strongest, agents of natural selection, the incidence and expression of traits that enable individual organisms to cope with competitors and predators should increase within the same habitats over the course of time (Vermeij 1987). As a consequence, in periods of escalation, species that are unable to foil predators should either become extinct or be restricted to low-energy habitats where predators cannot follow. Evidence supporting these predictions is described below.

The Arms Race and Shell Crushing Predators

One of the predicted trends of the Escalation Hypothesis is that the relative abundance and power of shell-breaking predators in open oceans should increase. Supporting this predicted trend is the observation that the diversity of shell-crushing predators increased worldwide during the Mesozoic Marine Revolution. At the same time, Vermeij predicted that prey would evolve thicker armor or greater motility to escape predators. The fossil record shows that the incidence and expression of armor in gastropods, cephalopods, pelecypods, barnacles, epifaunal echinoids, encrusting calcareous algae and stemmed Paleozoic echinoderms increased (Vermeij 1987; Vermeij and Williams 2007). For example, opercular thickness of the shells of tropical gastropods in the family *Turbinidae* were significantly thicker than those of temperate turbinids. Other examples of such passive defenses include: apertural teeth, external tubercles and spines, extremely narrow or small apertures, glossy and/or slippery external

69

shells, making them hard for a predator to grip or hold in place and high spires in shells. It is also hypothesized that the hard, thick, spiral design of gastropod shells may have arisen in response to increased predation through geologic time, particularly during the Mesozoic Marine Revolution. As predicted by the Escalation Hypothesis, passive defenses are far more common among prey in the shallow, warm waters of the tropics where a larger number of predators abound.

Bivalves have evolved thicker shells as well. For example, the giant clam, *Tridacna squamosa*, is a free-living filter-feeder that resides atop the tropical ocean bottom rather than burrowing into the ocean's bottom and feeding from an extended siphon. Adult giant clams are unlikely to be crushed by predators because of their massive shell size. However, it was thought that juveniles were vulnerable to predation. Han et al. (2008) sought to determine if the scutes of juvenile giant clams provided a passive defense against crab attacks. Han and collaborators used the tools of physics to determine just how much mechanical force is necessary to crush a giant clam's shell and the difference in mechanical force that must be applied to adults' versus juvenile clams' shells to effect shell crushing. They also measured the *actual* crushing force of crabs' large claws. Their data showed that the scutes of juvenile giant clams do indeed serve a defensive function: they increase the thickness of clams' shells and hence damp the effective crushing force of predators' claws, jaws or beaks (Han et al. 2008).

The Arms Race and Shell Drilling Predators

Another prediction of the Escalation Hypothesis is that the incidence of repaired shells in gastropods, pelecypods and barnacles should increase over geological time, as should the abundance of drilling predators. Dietl et al. (2004) found that prior to the Plio-Pleistocene mass extinction two types of predators dominated the fossil record, edge-drilling and wall-drilling muricid snails. Just after the Plio-Pleistocene mass extinction, drilling attacks through the shell walls were more common. They concluded that prior to the mass extinction event, predation was more intense and shells were thicker; immediately after the mass extinction event, predation decreased and shells became thinner (Dietl et al. 2004).

Kelley and Hansen (2006) examined naticid gastropod predation from the Cretaceous to the Pleistocene. They compared "drilling frequency" and "prey effectiveness" in both class and taxa. Drilling frequency measured predator success. Prey effectiveness measured prey survival. While prey survival across taxa did not vary significantly, predator success did. Drilling frequencies changed smoothly and synchronously over time, supporting the hypothesis that predators can influence the morphology and behavior of their prey. Thus, predators responded to prey faster than prey responded to predators.

A significant study by Huntley and Kowalewski (2007) used entire collections from around the world and measured the percentage of failed predation attempts in each species. Their study confirmed the Escalation Hypothesis. Predation intensity rose dramatically in the early Paleozoic and continued to rise throughout. The Huntley and Kowalewski (2007) study generated numbers that were robust with respect to both multiple predation intensity metrics *and* multiple biodiversity metrics.

Amano and Jenkins (2007) found that drilling as a means of accessing prey tissue existed as long ago as the Eocene in deep, cold-water seeps near Hokkaido, Japan. Studying fossils, they concluded that not only had drilling occurred, but also that the drilling predators had elaborate chemical adaptations that allowed them to metabolize their prey without being poisoned by the deadly sulfides and other chemicals common in deep-water fauna. To access prey, predators had to adapt to cooler temperatures in deeper water and metabolize chemicals that had previously rendered deep-water chemosynthesizers off-limits. Further, the time scales involved in the Hokkaido study suggest that predators began looking for their "missing" prey in the Eocene, when they were forced to hunt these new chemoautotrophic bivalves that had escaped to the abyss. These data suggest that novel evolutionary adaptations began to appear just before Mid-Paleozoic Marine Revolution (Signor and Brett 1984), and might be pre-cursors to the escalated species diversification (i.e. adaptive radiation), during both the Mid-Paleozoic Marine Revolution and the Mesozoic Marine Revolution (Amano and Jenkins 2007).

Madin et al. (2006) suggested that the apparent coupling between predation intensity and species diversification was a statistical artifact—an effect of sampling bias. Hence, they claimed that the Escalation Hypothesis remained to be proven. Dietl and Vermeij (2006) responded that Madin and collaborators hadn't properly tested the theory. Because they tested the Escalation Hypothesis against whole clades, ecosystems, selection regimes and geographic zones, Madin and collaborators missed the relevant level of analysis: the interactions between individual organisms (also see Hardisty and Cassill 2010e). Dietl and Vermeij (2006) maintain that the Escalation Hypothesis must be tested at spatial scales relevant to organisms. Thus, global analyses such as Madin et

al.'s are generally flawed because of the great heterogeneity that occurs on spatio-temporal scales over geologic time.

An important point here is that Vermeij never claimed that predator-prey relations and predator-predator competition were the *only* forces driving evolutionary adaptation during the Mesozoic Marine Revolution or other important geologic time scales. His claim is that between-species predator-prey forces are *sometimes* more effective selection pressures than within-species competition forces over geologic time (Vermeij 1978; Vermeij 1987; also see Stanley 2008).

The Arms Race and Motile Predators

Another prediction of the Escalation Hypothesis is that locomotion in gastropods, cephalopods, pelecypods, echinoderms, fishes and land vertebrates should increase. In support of this prediction are studies on crinoids. As far back as the Carboniferous, stalked crinoids evolved a trait of shedding their stalks and crawling. Baumiller et al. (2008) solved the previously puzzling crawling crinoids by testing predation by the sea urchin *Calocidaris micans*. They found that, by shedding their stalks and crawling, crinoids avoided predation by slow moving marine predators. Ancient crinoids shed their more nutritious genital stalks and occasionally their distal stalks much as lizards shed their tails to avoid predation.

Kowalewski's collaborators, Aberhan et al. (2006), also found surprising trends in evolutionary diversification that supported the evolution of faster predators. These were: an increase in mobility across a broad range of taxa, declines in the number of free-living epifauna (with subsequent trends toward burrowing and fixing to substrates) and

increasing infaunalization of marine benthos. These trends were especially pronounced in the Paleotropics, often found to be the area of ocean with the most biological activity. Their study differed from many previous studies because it included data from all of the major marine benthic invertebrate groups (bivalves, gastropods, brachiopods, echinoids, corals and sponges) and analyzed global information about their evolutionary history at fine temporal scales. They found that predation pressures, as well as adaptations to resist predation, increased throughout the mid-Mesozoic (Aberhan et al. 2006). Their comprehensive study was a 'nail in the coffin' for theories competing against the Escalation Hypothesis.

The Arms Race and Deep-water Predators

    Another prediction of the Escalation Hypothesis was that the portion of formerly shallow-water marine groups adapted to deep, cold and dark waters should increase (Vermeij 1987). The stalked crinoids were once abundant in warm, shallow seas in the Paleozoic and early Mesozoic but underwent a dramatic habitat change during the late Mesozoic (Meyer and Macurda 1977). Stalked crinoids are now seldom found in less than 100 meters of water and 200 meter depth is the usual minimum at which they occur. The Escalation Hypothesis predicts that defenseless stalked crinoids escaped predators that arose in the new warm, shallow, high-energy habitats of the Mesozoic by adapting to cold, low-energy habitats. Lastly, rates of predation of stalked crinoids decrease as depth increases (Vermeij 2004; Stanley 2008). Indeed, rates of predation are so low in deep water stalked crinoids that they have lost their chemical defenses (McClintock et al. 1999). In addition, Amano and Vermeij (2003) found that an entire genus of gastropods

74

had shifted from warm water habitats to deep water habitats over evolutionary time (also see Oji 1996). Their shells had evolved from thick, ornamented scutes and opercula to thin scutes and opercula. Apparently, cold-water prey escaped predation by choosing deep, dark and cold habitats.

De-escalating Escalation: What the 4-D Model Tells Us about Arms Races

Vermeij (1999) has repeatedly argued that biologists need to measure the inequalities that exist at all levels of biological organization because these inequalities are "a nearly universal property of interactions among metabolizing entities" (Vermeij 1999:243). Vermeij also proposed that until biologists are able to quantify these asymmetries (see also Betzig's notion of incipient asymmetries versus acquired asymmetries, in Betzig 2008), they will not be able to account for the economic interactions in which all organisms participate (Vermeij 1999; Vermeij 2006b). Furthermore, he argued that until biologists model such inequalities, or asymmetries, they will be missing the fact that all organismal interactions take place within a matrix composed of predator, prey, and environment--no organism lives in a vacuum. I propose that offspring skew is such a model.

The production of offspring skew by parents is one of the four key predictions made by the 4-D model (Cassill 2002, 2005, 2006; Cassill et al. 2007; Cassill et al. 2010; Hardisty and Cassill 2010d). Here, I provide an overview of offspring skew and how it relates to the eternal struggle of both predator and prey for survival and reproduction, drawing on Hardisty and Cassill (2010d).

In an "eat or be eaten" world, not only do organisms interact with each other, they must constantly look over their shoulders to avoid predators as they search for food (Fig. 2). Few game theory models incorporate all three levels of interactions when describing the evolution of social behavior, but the 4-D model considers all three levels of interaction (each occurring over some timescale): offspring x offspring interactions; offspring x predator interactions and offspring x prey interactions. In addition, skew selection takes into account two generations of conspecifics: breeders and their surviving offspring. According to the 4-D model, unless offspring survive to maturity and produce their own offspring, they have zero fitness. Thus the 4-D model (Figure 5.1), is a significant break from kin selection, group selection and evolutionary game theory—all of which assume that offspring survival is equitable or random (Figure 5.2).
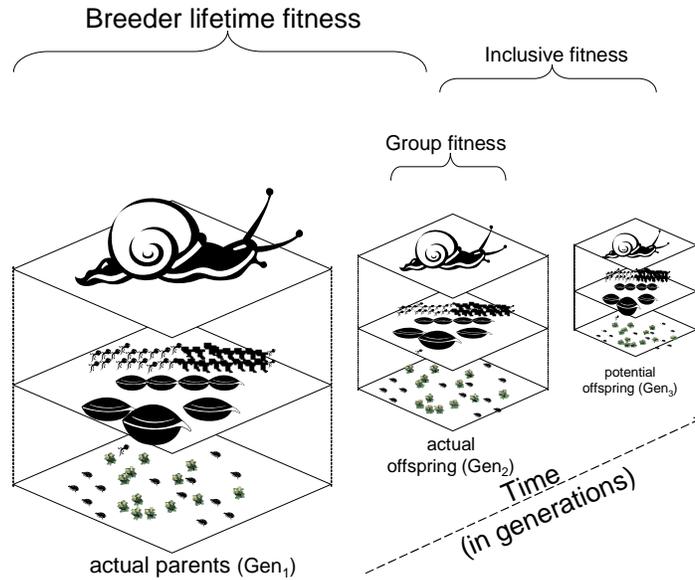
Figure 5.2 The 4-D Model and Marine Organisms: the focal animal, its prey and its predators, comprise the three spatial dimensions. Two generations, breeders and their offspring, comprise the fourth dimension of time. In Generation 1, bivalve breeders prey on zooplankton and are, in turn, preyed on by drilling gastropods. In Generation 2, bivalve offspring 'prey' on zooplankton, and are preyed on by drilling gastropods. **Breeder lifetime fitness**: In an offspring skew model, the breeder lifetime fitness metric is a retro-generational construct. The number of *surviving* bivalve offspring, those that successfully metamorphose into breeders in Generation 2, determines the fitness of breeder bivalves in Generation 1. **Group fitness**: Group selection's group fitness metric is a 1-D, intra-generational construct based on the number of survivors in a population of bivalves. Fitness is assigned to the Generation 2 'group' rather than Generation 1 breeders. Therefore, how group fitness is passed into the next generation of groups is not resolved. **Inclusive fitness:** Kin selection's inclusive fitness metric is an idealized, future-generation, probability construct. The ideal number of bivalves that "might" be produced in Generation 3 by an ideal number of bivalves in the Generation 2 is determined by the probability (Hamilton's 'r' coefficient) that the altruistic bivalve and its surviving altruistic siblings in the Generation 2 shared altruistic genes by descent from a common relative, a parent, in the Generation 1 (figure: Hardisty and Cassill 2010d).

Environmental factors such as the number of predators, the availability of shelters and cycles in food availability divide Molluscan offspring into two categories: those who survive to maturity and breed, and those who do not. When the dominant environmental risk involves finding food in patches shaped by spatial or seasonal gaps in food availability, nature selects for Molluscan breeders who produce gluttonous offspring that store excess fat or storage protein to survive periods of scarcity (Ghiselin 1974; Wheeler

and Buck 1995; Wheeler et al. 2000)—a K-selection strategy. When the dominant risk

involves avoiding predators, nature selects for breeders who produce many offspring,

overwhelming predators with large numbers (Hamilton 1971)—an r-selected strategy.

When Mollusca face both risks, gaps in food availability *and* predators, nature selects for

Molluscan mothers who produce two types of offspring: a few gluttonous offspring *and*

many small, disposable offspring—a combined r *and* K-selected strategy (see Figure 5.3

below). Over many generations, the risks of starvation and predation shape the genetic

mechanisms that skew offspring size, ability, fertility or behavior to guarantee that some

offspring survive and become breeders, thus maximizing their parent's lifetime fitness.
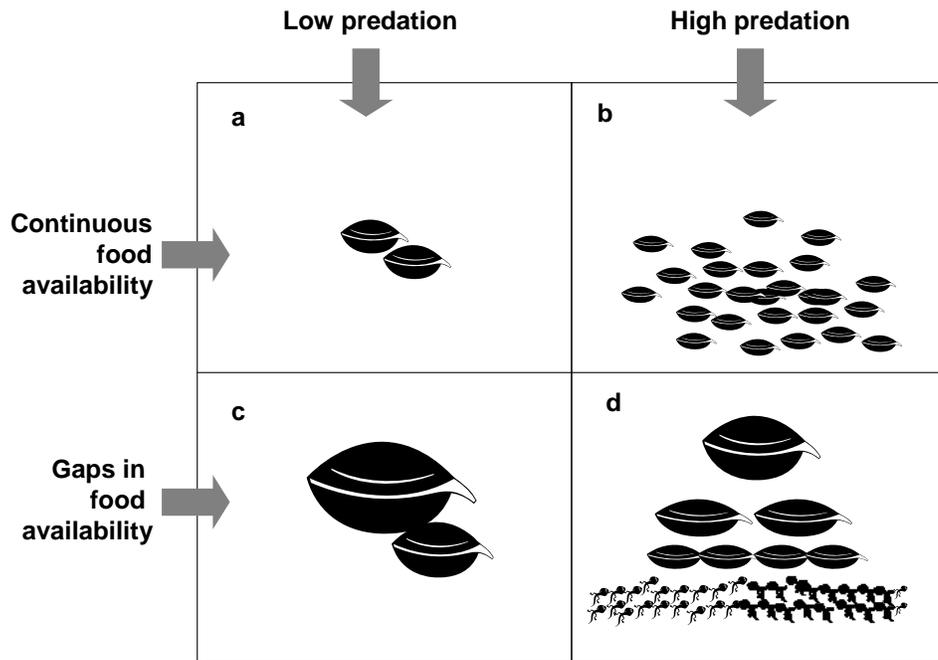
Figure 5.3 Predictions of the 4-D Model, Revisited: (a) When food is continuous and predators are rare, breeders produce one or two small-bodied offspring in their lifetime. (b) When food is continuous and predators are many, breeders produce many small offspring each breeding season—an r-selected reproductive strategy. (c) When food availability cycles between abundant and scarce and predators are rare, breeders produce a few, large, well-provisioned offspring—a K-selected reproductive strategy. (d) When food availability cycles between abundant and scarce, and predators are many, breeders produce a few large offspring that will survive scarcity *and* many small disposable offspring to buffer the larger offspring from predators—an offspring skew strategy. Skewing offspring quality has the advantage of de-escalating the arms-race between predator and prey. Small offspring are sacrificed so that predators need never evolve to be fast enough, strong enough or large enough to kill larger offspring (Figure: Hardisty and Cassill 2010d).

To further demonstrate the potential power of offspring skew as an explanation

for within and between-species diversity, I also mention several other cases that reveal

the fitness benefits of a skew-selected strategy. By skewing the fertility of her offspring

into a 20:1 ratio of sterile to fertile offspring, an ant queen enhances the odds that her

fertile daughters will successfully survive and carry on her genetic lineage (Cassill 2002a;

Cassill 2002b). Offspring skew also provides an explanation for the large ratio of junk to

functional DNA (Cassill 2005). By skewing the quality of genes relative to junk DNA, the probability that an invading virus will disrupt functional gene sequences is low. Finally, a large ratio of sluggish sperm buffer functional sperm from toxic microbes in the vagina as they make the ten-hour swim through the vagina, across the cervix, along the uterus and finally into the fallopian tubes where an egg awaits (Cassill 2005).

Conclusion

The 4-D model, with its offspring skew component, provides the missing link that connects the fossil evidence to genetic evidence, a prerequisite for any successful theory of evolution. One of the major conclusions we can draw from an offspring skew perspective is that, at each level of organizational and biological complexity, diverse offspring is essential to coping with environmental challenges (Cassill 2002a; Cassill 2002b; Cassill and Watkins 2004; Cassill and Watkins 2010; Cassill et al. 2007; Cassill et al. 2010). According to the 4-D model, the most successful diversification pattern is skew—be it skew of body size, ability, fertility, intelligence, motivation or behavior. In addition, though families are much less common in marine organisms than in terrestrial organisms, the existence of skew in offspring transmitted from mother to offspring may be the precursor to the crucial evolutionary step of keeping offspring close by after birth or hatching. For example, just such a process may be what sparked the evolution of colonial living in sponges, corals and jellies. Thus, arms races need not always carry on indefinitely, they may be resolved by the production of offspring with different trait values, some of which will be eaten while young, and some of which will live to reproduce.

CHAPTER 6: CONCLUSION: RESTORING THE FAMILY TO EVOLUTIONARY
BIOLOGY

Though the family has not always been given the respect it deserves from

biologists, I have shown that by considering the strategies used by breeders to perpetuate

themselves—such as colonial living in nuclear and extended family units in ants, naked

mole-rats and humans (Chapter 1); food sharing between adults and juveniles within and

between families in Shedao pit vipers (Chapter 3); the use of tools for tasks including

foraging and hunting in bonobos, bowerbirds, chimpanzees, dolphins and humans

(Chapter 4); and the production of skewed trait distributions in offspring (Chapters 2 and

5)—the study of the evolution of both altruistic and selfish behavior can be better

understood.

Though altruism and *cooperation* are often thought by biologists to be two

fundamentally different types of behavior, they both have one very important trait in

common: in both cases the donor is giving their time and energy to aid the survival or

reproduction of another individual, whether related or unrelated. If related, the donor was

traditionally thought to be helping their own genes (i.e., Hamilton's kin selection:

Hamilton 1964; Hamilton 1967) and, if unrelated, the donor was thought to be helping

the reproduction of an individual who they were reasonably sure would reciprocate at

some future time (i.e., Trivers' reciprocal altruism: Trivers 1971; Trivers 1974). What

both of these popular theories missed however is that one might help an individual to keep them around to help the donor reproduce (i.e., Hardisty and Cassill 2010), fight off predators or watch the recipient get eaten (i.e., Cassill and Watkins 2004; Cassill et al. 2007; Cassill and Watkins 2010; Cassill et al. 2010), or build a nest (Forbes 2005), or dwelling, to protect them both (Odling-Smee et al. 2003; Laland and Sterelny 2006; Laland et al. 2007). Thus, in the end the evolution of family illuminates some of what makes us human, and why it is that we love to help out others, even when not aware of what, if any, benefit we derive from such behavior. As long as a behavior exists, and has consequences for our survival or reproduction, then that behavior can be selected for or against. From aiding our relatives (Chapter 1), to catching food for them (Chapter 3), to building tools for foraging and hunting for ourselves and our families (Chapter 4), to coevolution (Chapter 5), an approach based on considering the problems that animals face in surviving (also see: Hardisty and Cassill 2010e), foraging and reproducing in unpredictable environments—a family perspective—can explain a wide variety of data and will hopefully explain more in the future.

LITERATURE CITED

Abele LG, Heck KL Jr., Simberloff DS, Vermeij GJ. 1981. Biogeography of crab claw
    size: assumptions and a null hypothesis. Systematic Zoology 30(4): 406-424.

Aberhan M, Kiessling W, Fursich FT. 2006. Testing the role of biological interactions in
    the evolution of mid-Mesozoic marine benthic ecosystems. Paleobiology 32: 259-
    277.

Aldous D, Diaconis P. 1986. Shuffling cards and stopping times. The American
    Mathematical Monthly 93:333-348.

Alexander RD. 1974. The evolution of social behavior. Annual Review of Ecology and
    Systematics 5:325-383.

Allmon WD, Nieh JC, Norris RD. 1990. Drilling and peeling of Turritelline gastropods
    since the late Cretaceous. Palaeontology 33: 595-611.

Ambrose SH. 2001. Paleolithic technology and human evolution. Science 291:1748-
    1753.

Andersen IL, Andenaes H, Boe KE, Jensen P, Bakken M. 2000. The effects of weight
    asymmetry and resource distribution on aggression in groups of unacquainted
    pigs. Applied Animal Behaviour Science 68:107-120.

Anderson JR. 2002. Gone fishing: tool use in animals. Biologist 49:15-18.

Allen SF. 2003. Working parents with young children: Cross-national comparisons of
    policies and programs in three countries. International Journal of Social Welfare
    12(4):261-273.

Amano K. 2006. Temporal patterns of naticid predation on *Glycymeris yessoensis*
    (Sowerby) during the late Cenozoic in Japan. PALOIS 21: 369-375.

Amano K, Jenkins RG. 2007. Eocene drill holes in cold-seep bivalves of Hokkaido,
    northern Japan. Marine Ecology 28: 108-114.

Amano K, Vermeij GJ. 2003. Evolutionary adaptation and geographic spread of the Cenozoic Buccinid genus *Lirabuccinum* in the North Pacific. Journal of Paleontology 77(5): 863-872.

Atkinson AB. 1970. On the measurement of inequality. Journal of Economic Theory 2:244-263.

Axelrod R, Hamilton WD. 1981. The evolution of cooperation. Science 211:1390-1396.

Bambach RK, Knoll AH, Sepkoski JJ Jr. 2002. Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm. Proceedings of the National Academy of Sciences of the USA 99: 6854-6859.

Banerji A, Morin PJ. 2009. Phenotypic plasticity, intraguild predation and anticannibal defenses in an enigmatic polymorphic ciliate. Functional Ecology 23:427-434.

Barber N. 2004. Kindness in Cruel World: the Evolution of Altruism. Amherst, New York: Prometheus Books.

Batra SWT. 1966. Nests and social behavior of halictine bees of India (Hymenoptera: Halictidae). Indian Journal of Entomology 28:375-393.

Baumiller TK, Gahn FJ. 2004. Testing predator-driven evolution with Paleozoic arm regeneration. Science 305: 1453-1455.

Baumiller TK, Mooi R, Messing CG. 2008. Urchins in the meadow: paleobiological and evolutionary implications of cidaroid predation on crinoids. Paleobiology, 34: 22-34.

Beaumont HJE, Gallie J, Kost C, Ferguson GC, Rainey PB. 2009. Experimental evolution of bet-hedging. Nature 462:90-94.

Bendel RB, Higgins SS, Teberg JE, Pyke DA. 1989. Comparison of skewness coefficient, coefficient of variation, and Gini coefficient as inequality measures within populations. Oecologia 78:394-400.

Betzig LL. 2008. Despotism and Differential Reproduction: A Darwinian View of History. New Brunswick (NJ): Aldine Transactions.

Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C., Matsuzawa T. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. Animal Cognition 6:213-223.

Blackmore S. 1999. The Meme Machine. New York: Oxford University Press.

Boesch C. 1994. Cooperative hunting in wild chimpanzees. Animal Behaviour 48:653-667.

Boesch C. 2002. Cooperative hunting roles among Tai chimpanzees. Human Nature 13(1):27-46.

Boesch C, Boesch H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. American Journal of Physical Anthropology 78:547-573.

Boesch C, Boesch H. 1990. Tool use and tool making in wild chimpanzees. Folia Primatologica 54:86-99.

Bonan GB. 1988. The size structure of theoretical plant populations: spatial patterns and neighborhood effects. Ecology 69:1721-1730.

Bonan GB. 1991. Density effects on the size structure of annual plant populations: an indication of neighborhood competition. Annals of Botany 68:341-347.

Braun DR, Plummer T, Ditchfield P, Ferraro JV, Maina D, Bishop LC and Potts R. 2008. Oldowan behavior and raw material transport: perspectives from the Kanjera formation. Journal of Archaeological Science 35:2329-2345.

Braun DR, Plummer T, Ferraro JV, Ditchfield P, Bishop LC. 2009. Raw material quality and Oldowan hominin toolstone preferences: evidence from Kanjera South, Kenya. Journal of Archaeological Science 36:1605-1614.

Brett RA, Sherman PW, Jarvis JUM, Alexander RD. 1991. In: Sherman PW, Jarvis JUM, Alexander RD, editors. The Biology of the Naked Mole-Rat. Princeton: Princeton University Press. p. 97–136.

Burda H, Honeycutt RL, Begall S, Locker-Grutjen O, Scharff A. 2000. Are naked and common mole-rats eusocial and if so, why? Behavioral Ecology and Sociobiology 47(5):293-303.

Cassill D, Watkins A. 2010. The evolution of cooperative hierarchies through natural selection processes. Journal of Bioeconomics 12:29-42.

Cassill DL. 2002a. Skew selection: nature favors a trickle-down distribution of resources in ants. Journal of Bioeconomics 5:83-96.

Cassill DL. 2002b. Yoyo-bang: A risk aversion investment strategy by a perennial insect society. Oecologia 132:150-158.

Cassill DL. 2005. The social gene. Journal of Bioeconomics 7:73-84.

Cassill DL. 2006. Why skew selection, a model of parental exploitation, should replace kin selection. Journal of Bioeconomics 8:101-119.

Cassill DL, Brown S, Swick D, Yanev G. 2009. Polyphasic wake/sleep episodes in the fire ant, *Solenopsis invicta*. Journal of Insect Behavior 4:313-323.

Cassill DL and Hardisty BE. 2010. A 4-D model trumps kin selection on the evolution of altruism (unpublished manuscript).

Cassill DL, Hardisty BE, Watkins A. 2010. A 4-D natural selection model solves the enigma of altruism in the Shedao pit viper. Journal of Bioeconomics (in press).

Cassill DL, Kuriachan I, Vinson SB. 2007. A test of two skew models to explain cooperative breeding among unrelated individuals. Journal of Bioeconomics 9:19-37.

Cassill DL, Tschinkel WR. 1999. Task selection by workers of the fire ant, *Solenopsis invicta.* Behavioral Ecology and Sociobiology 45:301-310.

Cassill DL, Watkins A. 2004. Mogul games: In defense of inequality as an evolutionary strategy to cope with multiple agents of selection. In: Koppl R editor. Advances in Austrian Economics. Norwell (MA): Kluwer Academic Publisher. p. 35-59.

Clements KC, Stephens DW. 1995. Testing models of non-kin cooperation: mutualism and the Prisoner's dilemma. Animal Behavior 50:527-535.

Clutton-Brock TH. 1991. The Evolution of Parental Care. Princeton: Princeton University Press.

Clutton-Brock TH, Brotherton PNM, Russell AF, O'Riain MJ, Gaynor D, Kansky R, Griffin AS, Manser MB, Sharpe L, McIlrath GM, Small T, Moss A, Monfort S. 2001. Cooperation, conflict, and concession in meerkats groups. Science 291:478-481.

Clutton-Brock TH, Maccoll A, Chadwick P, Gaynor D, Kansky R, Skinner JD. 2003. Reproduction and survival of suricates (*Suricata suricatta*) in the southern Kalahari. African Journal of Ecology 37:69-80.

Cohen D. 1966. Optimizing reproduction in a randomly varying environment. Journal of Theoretical Biology 12(1):119-129.

Cohen D. 1968. A general model of optimal reproduction in a randomly varying environment. Journal of Ecology 56(1):219-228.

Connor RC. 1986. Pseudo-reciprocity: investing in mutualism. Animal Behaviour 34:1562-1566.

Connor RC. 1995a. The benefits of mutualism: a conceptual framework. Biological Reviews 70:427-457.

Connor RC. 1995b. Altruism among non-relatives: alternatives to the 'Prisoner's dilemma.' Trends in Ecology and Evolution 10:84-86.

Connor RC. 1995c. Impala grooming and the parcelling model of reciprocity. Animal Behaviour 49:528-530.

Crespi BJ. 1992. Eusociality in Australian gall thrips. Nature 359:724-726.

Crespi BJ, Yanega D. 1995. The definition of eusociality. Behavioral Ecology 6(1):109-115.

Dalton H. 1920. The measurement of the inequality of incomes. The Economic Journal 30:348-361.

Damgaard C, Weiner J. 2000. Describing inequality in plant size or fecundity. Ecology 81:1139-1142.

Darwin C. 1859. The Origin of Species. New York: Signet Classics.

Davis-Walton J, Sherman PW. 1994. Sleep arrhythmia in the eusocial naked mole-rat. Naturwissenschaften 81:272-275.

Dawkins R. 1976. The Selfish Gene. New York: Oxford University Press.

Dietl GP, Herbert GS, Vermeij GJ. 2004. Reduced competition and altered feeding behavior among marine snails after a mass extinction. Science 306: 2229-2231.

Dietl GP, Vermeij GJ. 2006. Comment on "Statistical Independence of Escalatory Ecological Trends in Phanerozoic Marine Invertebrates." Science 314: 925e (technical comments on the title article).

Dixon PM, Weiner J, Mitchell-Olds T, Woodley R. 1987. Bootstrapping the Gini coefficient of inequality. Ecology 68:1548-1551.

Dominguez-Rodrigo M, Pickering TR, Semaw S and Rogers MJ. 2005. Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. Journal of Human Evolution 48:109-121.

Dorfman R. 1979. A formula for the Gini coefficient. The Review of Economics and Statistics 61:146-149.

Drake A, Fraser D, Weary DM. 2008. Parent-offspring resource allocation in domestic pigs. Behavioral Ecology and Sociobiology 62:309-319.

Driver PM, Humphries DA. 1988. Protean Behaviour: the Biology of Unpredictability. New York: Oxford University Press.

Duffy JE. 2003. The ecology and evolution of eusociality in sponge-dwelling shrimp. In: Kikuchi T, Higashi S, Azuma N, editors. Genes, Behaviors and Evolution of Social Insects. Sapporo: Hokkaido University Press. p. 217-254.

Duffy JE, Morrison CL, Rios R. 2000. Multiple origins of eusociality among sponge-dwelling shrimps (*Synalpheus*). Evolution 54(2):503-516.

Fernandez-Llario P, Mateos-Quesada P. 2005. Udder preference in wild boar piglets. Acta Ethologica 8:51-55.

Field AJ. 2008. Why multilevel selection matters. Journal of Bioeconomics 10:203-238.

Field AJ, Shreeves G, Sumner S, Casiraghl M. 2000. Insurance-based advantage to helpers in a tropical hover wasp. Nature 404:869-871.

Fisher RA. 1930. The Genetical Theory of Natural Selection. Oxford: Oxford University Press.

Forbes S. 2005. A Natural History of Families. Princeton: Princeton University Press.

Foster KR, Ratnieks FLW. 2005. A new eusocial vertebrate? Trends in Ecology and Evolution 20(7):363-364.

Foster KR, Wenseleers T, Ratnieks FLW. 2006. Kin selection is the key to altruism. Trends in Ecology and Evolution 21:57-60.

Frison GC. 1989. Experimental use of Clovis weaponry and tools on African elephants. American Antiquity 54(4):766-784.

Gause GF. 1934. The Struggle for Existence. New York: Hafner.

Gavrilets S, Vose A. 2006. The dynamics of Machiavellian intelligence. Proceedings of the National Academy of Sciences USA 103(45):16823-16828.

Ghiselin MT. 1974. The Economy of Nature and the Evolution of Sex. Berkeley: University of California Press.

Gifford A Jr. 2000. The bioeconomics of cooperation. Journal of Bioeconomics 2:153-168.

Gillespie JH. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. The American Naturalist 111(981):1010-1014.

Goebel T, Waters MR, O'Rourke DH. 2008. The late Pleistocene dispersal of modern humans in the Americas. Science 319:1497-1502.

Grafen A. 1999. Formal Darwinism, the individual-as-maximizing-agent analogy and bet-hedging. Proceedings of the Royal Society of London B 266:799-803.

Graves HB. 1984. Behavior and ecology of wild and feral swine (*Sus scrofa*). Journal of Animal Science 58:482-492.

Grey M, Boulding EG, Brookfield ME. 2005. Shape differences among boreholes drilled by three species of Naticid gastropods. Journal of Molluscan Studies 71: 253-256.

Griffin AS, West SA. 2002. Kin selection: fact and fiction. Trends in Ecology and Evolution 17:15-21.

Hagen EH, Barrett HC. Cooperative breeding and adolescent siblings: evidence for the ecological constraints model? Current Anthropology 50(5):727-737.

Hamilton WD. 1964. The genetical evolution of social behaviour. I, II. Journal of Theoretical Biology 7:1-52.

Hamilton WD. 1967. Extraordinary sex ratios. Science 156:477-488.

Hamilton WD. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295-311.

Han L, Todd PA, Chou LM, Bong YV, Sivaloganathan B. 2008. The defensive role of scutes in juvenile fluted giant clams (*Tridacna squamosa*). Journal of Experimental Marine Biology and Ecology 359: 77-83.

Hardisty BE and Cassill DL. 2010a. Extending eusociality to include vertebrate family units. Biology & Philosophy 25(3):437-440.

Hardisty BE and Cassill DL. 2010b. Quantifying memes by studying tool-use in non-human animals. Biological Theory (in review).

Hardisty BE and Cassill DL. 2010c. Memes and the ecological niche. Journal of Cognition and Culture (in review).

Hardisty BE and Cassill DL. 2010d. De-escalating the predator-prey arms race. Paleobiology (in review).

Hardisty BE and Cassill DL. 2010e. De-animalization: an extension of Singer's speciesism concept. British Journal for the Philosophy of Science (in review).

Harper EM. 2006. Dissecting post-Paleozoic arms races. Palaeogeography, Palaeoclimatology, Palaeoecology 232: 322-343.

Hawkes K. 2003. Grandmothers and the evolution of human longevity. American Journal of Human Biology 15:380-400.

Hawkes K. 2004. Human longevity: the grandmother effect. Nature 428:128-129.

Hawkes K, O'Connell JF, Blurton Jones NG. 1997. Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal lifespans. Current Anthropology 38(4):551-577.

Hawkes K, O'Connell JF, Jones NGB, Alvarez H, Charnov EL. 1998. Grandmothering, menopause, and the evolution of human life histories. Proceedings of the National Academy of Sciences of the USA 95:1336-1339.

Hayashi M, Mizuno Y, Matsuzawa T. 2005. How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity. Primates 46:91-102.

Heikki H, Bargum K. 2007. Pedigree relatedness, not greenbeard genes, explains eusociality. Oikos 116:217-220.

Hill K, Hurtado AM. 1991. The evolution of premature reproductive senescence and menopause in human females: an evaluation of the "Grandmother Hypothesis". Human Nature 2(4):313-350.

Hill K, Hurtado AM. 1996. Ache Life History: The Ecology and Demography of a Foraging People. New York: Aldine de Gruyter.

Holland SM. 2007. Coupling of predation intensity and global diversity over geologic time. Proceedings of the National Academy of Sciences of the USA 104: 14885-14886.

Hölldobler B, Wilson EO. 1990. The Ants. Cambridge (MA): Harvard University Press.

Holldobler B, Wilson EO. 1995. Journey to the Ants. Cambridge (MA): Harvard Belknap Press (3d edition).

Holmes MM, Rosen GJ, Jordan CL, de Vries GJ, Goldman BD, Forger NG. 2007. Social control of brain morphology in a eusocial mammal. Proceedings of the National Academy of Sciences of the USA 104:10548-10552.

Hopper KR. 1999. Risk-spreading and bet-hedging in insect population biology. Annual Review of Entomology 44:535-60.

Hopper LM, Spiteri A, Lambeth SP, Schapiro SJ, Horner V, Whiten A. 2007. Experimental studies of traditions and underlying transmission processes in chimpanzees. Animal Behaviour 73:1021-1032.

Hrdy SB. 1999. Mother Nature: Maternal Instincts and How They Shape the Human Species. New York: Ballantine Books.

Huntley JW, Kowalewski M. 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. Proceedings of the National Academy of Sciences of the USA 104: 15006-150010.

Hutchinson GE. 1958. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415-427.

Jansen VAA, van Baalen M. 2006. Altruism through beard chromodynamics. Nature 440:663-666.

Jarvis JUM. 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. Science 212(4494):571-573.

Jarvis JUM, Sherman PW. 2002. *Heterocephalus glaber*. Mammalian Species 706:1-9.

Kaplan H, Hill K. 1985. Hunting ability and reproductive success among male Ache foragers: preliminary results. Current Anthropology 26(1):131-133.

Kelley PH, Hansen TA. 2006. Comparisons of class-and lower taxon-level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the U.S. Coastal Plain. Palaeogeography, Palaeoclimatology, Palaeoecology 236: 302-320.

Kingsbury J. 2008. Learning and selection. Biology & Philosophy 23:493-507.

Klobuchar EA, Deslippe RJ. 2002. A queen pheromone induces workers to kill sexual larvae in colonies of the red imported fire ant (*Solenopsis invicta*). Naturwissenschaften 89:302-304.

Kowalewski M, Hoffmeister AP, Baumiller TK, Bambach RK. 2005. Secondary evolutionary escalation between brachiopods and enemies of other prey. Science 308: 1774-1777.

Kowalewski M, Kiessling W, Aberhan M, Fursich FT, Scarponi D, Wood SLB, Hoffmeister AP. 2006. Ecological, taxonomic and taphonomic components of the post-Paleozoic increase in sample-level species diversity of marine benthos. Paleobiology 32: 533-561.

Kranendonk G, Van der Mheen H, Fillerup M, Hopster H. 2007. Social rank of pregnant sows affects their body weight gain and behavior and performance of the offspring. Journal of Animal Science 85:420-429.

Krutzen M, Mann J, Heithaus MR, Connor RC, Bejder L, Sherwin WB. 2005. Cultural transmission of tool use in bottlenose dolphins. Proceedings of the National Academy of Sciences of the USA 102:8939-8943.

Lahdenpera M, Lummaa V, Helle S, Tremblay M, Russell AF. 2004. Fitness benefits of prolonged post-reproductive lifespan in women. Nature 428:178-181.

Laland KN, Kendal JR, Brown GR. 2007. The niche construction perspective: implications for evolution and human behaviour. Journal of Evolutionary Psychology 5:51-66.

Laland KN, Sterelny K. 2006. Seven reasons (not) to neglect niche construction. Evolution 60(9):1751-1762.

Landa JT. 1998. Bioeconomics of schooling fishes: selfish fish, quasi-free riders, and other fishy tales. Environmental Biology of Fishes 53:353-364.

Landa JT. 2008. The bioeconomics of homogeneous middleman groups as adaptive units: theory and empirical evidence viewed from a group selection framework. Journal of Bioeconomics 10:259-278.

Lewin R. 1983. Santa Rosalia was a goat: Ecologists have for two decades made assumptions about the importance of competition in community organization; that idea is now under vigorous attack. Science 221:638-639.

Lewin R, Lewin R. 1983. Predators and hurricanes change ecology: Results from direct experimentation in natural communities has reemphasized the importance of predators and climate in community organization. Science 221:737-740.

Li J-L. 1995. China Snake Island. Dalian (China): Liaoning Science and Technology Press.

Lomborg B. 2001. The Skeptical Environmentalist: Measuring the Real State of the World. New York: Cambridge University Press.

Lonsdorf EV, Eberly LE, Pusey AE. 2004. Sex differences in learning in chimpanzees. Nature 428:715-716.

Lycett SJ, Collard M, McGrew WC. 2007. Phylogenetic analyses of behavior support existence of culture among wild chimpanzees. Proceedings of the National Academy of Sciences of the USA 104:17588-17592.

Madden JR. 2008. Do bowerbirds exhibit cultures? Animal Cognition 11:1-12.

Madin JS, Alroy J, Aberhan M, Fursich FT, Kiessling W, Kosnik MA, Wagner PJ. 2006. Statistical independence of escalatory ecological trends in Phanerozoic marine invertebrates. Science 312: 897-899.

Malthus TR. 1798. An Essay on the Principle of Population; or, a View of its Past and Present Effects on Human Happiness; With an Enquiry into our Prospects Respecting the Future Removal or Mitigation of the Evils which it Occasions. New York: Oxford University Press (2004 edition).

Marchant JN, Rudd AR, Mendl MT, Broom DM, Meredith MJ, Corning S, Simmins PH. 2000. Timing and causes of piglet mortality in alternative and conventional farrowing systems. The Veterinary Record 147:209-214.

McAuliffe K, Whitehead H. 2005. Eusociality, menopause and information in matrilineal whales. Trends in Ecology and Evolution 20(12):650-650.

McClintock B. 1950. The origin and behavior of mutable loci in maize. Proceedings of the National Academy of Sciences of the USA 36:344–55.

McClintock B. 1953. Induction of instability at selected loci in maize. Genetics 38:579-599.

McClintock JB, Baker BJ, Baumiller TK, Messing CG. 1999. Lack of chemical defense in two species of stalked crinoids: support for the predation hypothesis for Mesozoic bathymetric restriction. Journal of Experimental Marine Biology and Ecology 232: 1-7.

McGrew WC. 2010. Chimpanzee technology. Science 328:579-580.

Meyburg B-U. 1974. Sibling aggression and mortality among nestling eagles. Ibis 116:224-228.

Meyer DL, Macurda DB. 1977. Adaptive radiation of the comatulid crinoids. Paleobiology 3: 74-82.

Michener CD. 1974. The Social Behavior of Bees. Cambridge (MA): Harvard University Press.

Newberry RC, Wood-Gush DGM. 1985. The suckling behaviour of domestic pigs in a semi-natural environment. Behaviour 95:11-25.

O'Brien MJ, Holland TD, Hoard RJ, Fox GL. 1994. Evolutionary implications of design and performance characteristics of prehistoric pottery. Journal of Archaeological Method and Theory 1(3):259-304.

Odling-Smee FJ, Laland KN, Feldman MW. 2003. Niche Construction: the Neglected Process in Evolution. Princeton: Princeton University Press.

Odum EP. 1953. Fundamentals of Ecology. Philadelphia: Saunders.

Oji T. 1996. Is predation intensity reduced with increasing depth? Evidence from the West Atlantic stalked crinoid *Endoxocrinus parrae* (Gervais) and implications for the Mesozoic marine revolution. Paleobiology 22: 339-351.

Oster GF, Wilson EO. 1979. Caste and ecology in the social insects. Princeton: Princeton University Press.

Philippi T and Seger J. 1989. Hedging one's evolutionary bets, revisited. Trends in Ecology and Evolution 4(2):41-44.

Plotkin HC. 1988. Learning and evolution. In: Plotkin HC, editor. The Role of Behavior in Evolution. Cambridge (MA): MIT Press.

Plotkin HC, Odling-Smee FJ. 1979. Learning, change and evolution. Adv Study Behav 10: 1-41.

Plummer T. 2004. Flaked stones and old bones: biological and cultural evolution at the dawn of technology. Yearbook of Physical Anthropology 47:118-164.

Pruetz JD, Bertolani P. 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. Current Biology 17:412-417.

Puppe B, Tuchscherer A. 2000. The development of suckling frequency in pigs from birth to weaning of their piglets: a sociobiological approach. Animal Science 71:273-279.

Queller DC, Zacchi F, Cervo R, Turillazzi S, Henshaw MT, Santorelli LA, Strassmann JE. 2000. Unrelated helpers in a social insect. Nature 405:784-787.

Reader SM, Laland KN. 2001. Primate innovation: sex, age and social rank differences. International Journal of Primatology 22(5):787-805.

Rees CM, Metcalf JE, Childs DZ. 2010. Bet-hedging as an evolutionary game: the trade-off between egg size and number. Proceedings of the Royal Society of London B 277:1149-1151.

Reinhold ME, Kelley PH. 2005. The influence of anti-predatory morphology on survivorship of the Owl Creek Formation molluscan fauna through the end-Cretaceous extinction. Palaeogeography, Palaeoclimatology, Palaeoecology 217: 143-153.

Richerson PJ, Boyd R. 2005. Not By Genes Alone: How Culture Transformed Human Evolution. Chicago: University of Chicago Press.

Ridley M. 2003. Nature via Nurture: Genes, Experience, and What Makes us Human. New York: Harper Collins.

Ripa J, Olofsson H, Jonzen N. 2010. What is bet-hedging, really? Proceedings of the Royal Society of London B 277:1153-1154.

Roehe R, Shrestha NP, Mekkawy W, Baxter EM, Knap PW, Smurthwaite KM, Jarvis S, Lawrence AB, Edwards SA. 2009. Genetic analyses of piglet survival and individual birth weight on first generation data of a selection experiment for piglet survival under outdoor conditions. Livestock Science 121:173-181.

Roopnarine PD, Angielczyk KD, Hertog R. 2006. Comment on "Statistical Independence of Escalatory Ecological Trends in Phanerozoic Marine Invertebrates. Science 314: 925d (technical comments on the methodology of title study).

Sall J, Lehman A, Creighton L. 2001. JMP Start Statistics: A Guide to Statistics and Data Analysis Using JMP and JMP IN Software. Albany (NY): Duxbury Press.

Sanz CM, Morgan DB. 2009. Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. International Journal of Primatology 30:411-427.

Savage JM. 2002. The Amphibians and Reptiles of Costa Rica. Chicago: University of Chicago Press.

Seger J, Brockmann HJ. 1987. What is bet-hedging? Oxford Surveys in Evolutionary Biology 4:182-211.

Sear R, Mace R. 2008. Who keeps children alive? a review of the effects of kin on child survival. Human Evolution and Behavior 29(1):1-18.

Sergeant BL, Mann J. 2009. Developmental evidence for foraging traditions in wild bottlenose dolphins. Animal Behaviour 78:715-721.

Seyfarth RM, Cheney DL. 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. Nature 308:541-543.

Shanley DP, Sear R, Mace R, Kirkwood TBL. 2007. Testing evolutionary theories of menopause. Proceedings of the Royal Society of London, B 274:2943-2949.

Sherman PW, Lacey EA, Reeve HK. 1995. The eusociality continuum. Behavioral Ecology 6(1):102-108.

Shine R. 1983. Arboreality in snakes: ecology of the Australian elapid genus *Hoplocephalus*. Copeia 1:198-205.

Shine R, Sun L-X, Fitzgerald M, Kearney M. 2002a. Accidental altruism in insular pit vipers (*Gloydius shedaoensis*, Viperidae). Evolutionary Ecology 16:541-548.

Shine R, Sun L-X, Kearney M, Fitzgerald M. 2002b. Why do juvenile Chinese pit vipers (*Gloydius shedaoensis*) select arboreal sites? Ethology 108:897-910.

Signor III PW, Brett CE. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. Paleobiology 10: 229-245.

Silva HR, Britto-Pereira MC, Caramaschi U. 1989. Frugivory and seed dispersal by *Hyla truncata*, a neotropical treefrog. Copeia 3:781–783.

Simberloff D. 1982. The status of competition theory in ecology. Annals of the Zoologici Fennici 19:241-253.

Smith CS, Fretwell SD. 1974. The optimal balance between size and number of offspring. The American Naturalist 108:499-506.

Smolker R, Richards A, Connor RC, Mann J, Berggren P. 1997. Sponge carrying by dolphins (Delphinidae, *Tursiops* sp.): a foraging specialization involving tool use? Ethology 103:454-465.

Snider AT, Bowler JK. 1992. Longevity of reptiles and amphibians in North American collections, 2nd ed. Herpetological Circular No. 21.

Sober E, Wilson DS. 1998. Unto Others: the Evolution and Psychology of Unselfish Behavior. Cambridge (MA): Harvard University Press.

Stanford CB. 1996. The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids. American Anthropologist 98(1):96-113.

Stanford CB, Wallis J, Mpongo E, Goodall J. 1994. Hunting decisions in wild chimpanzees. Behaviour 131:1-18.

Stanley SM. 1977. Trends, rates and patterns of evolution in the *Bivalvia*. In: Hallam A, editor. Patterns of Evolution, as illustrated by the fossil record. Amsterdam: Elsevier. p. 209-250.

Stanley SM. 2008. Predation defeats competition on the seafloor. Paleobiology 34: 1-21.

Stearns SC. 1992. The Evolution of Life Histories. New York: Oxford University Press.

Sterelny K. 2006. Memes revisited. British Journal for the Philosophy of Science 57:145-165.

Stern DL, Foster WA. 1996. The evolution of soldiers in aphids. Biological Reviews 71(1):27-79.

Sun L. 1990. Observation on the pattern of activities of Agkistrodon shedaoensis Zhao In: Zhao E, editor. From Water Onto Land. Beijing: China Forestry Press. p. 277-280.

Sun L-X, Shine R, Debi Z, Zhengren T. 2002. Low costs, high output: reproduction in an insular pit-viper (*Gloydius shedaoensis*, Viperidae) from north-eastern China. Journal of Zoology, London 256:511-521.

Surbeck M, Fowler A, Deimel C, Hohmann G. 2009. Evidence for the consumption of arboreal, diurnal primates by Bonobos (*Pan paniscus*). American Journal of Primatology 71:171-174.

Surbeck M, Hohmann G. 2008. Primate hunting by bonobos at Lui Kotale, Salonga National Park. Current Biology 18(19):R906-R907.

Susman RL. 1991. Who made the Oldowan tools? Fossil evidence for tool behavior in Plio-Pleistocene hominids. Journal of Anthropological Research 47(2):129-151.

Teyssedre A, Couvet D, Nunney L. 2006. Lower group productivity under kin-selected reproductive altruism. Evolution 60:2023-2031.

Toth N, Schick K. 2009. The Oldowan: the tool making of early hominins and chimpanzees compared. Annual Review of Anthropology 38:289-305.

Trivers RL. 1971. The evolution of reciprocal altruism. Quarterly Review of Biology 46:35-57.

Trivers RL. 1974. Parent-offspring conflict. American Zoologist 14:249-264.

Tschinkel WR. 2006. The Fire Ants. Cambridge (MA): Harvard University Press.

Tuomi J, Agrell J, Mappes T. 1997. On the evolutionary stability of female infanticide. Behavioral Ecology and Sociobiology 40:227-233.

Vermeij GJ. 1973. Adaptation, versatility, and evolution. Systematic Zoology 22: 466-477.

Vermeij GJ. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. Paleobiology 3: 245-258.

Vermeij GJ. 1978. Biogeography and Adaptation: Patterns of Marine Life. Cambridge (MA): Harvard University Press.

Vermeij GJ. 1987. Evolution and Escalation: an Ecological History of Life. Princeton: Princeton University Press.

Vermeij GJ. 1999. Inequality and the directionality of history. The American Naturalist 153(3):243-253.

Vermeij GJ. 2004. Nature: an Economic History. Princeton: Princeton University Press.

Vermeij GJ. 2005. One-way traffic in the western Atlantic: causes and consequences of Miocene to early Pleistocene molluscan invasions in Florida and the Caribbean. Paleobiology 31: 624-642.

Vermeij GJ. 2006a. Historical contingency and the purported uniqueness of evolutionary innovations. Proceedings of the National Academy of Sciences of the USA 103: 1804-1809.

Vermeij GJ. 2006b. Majority rule: adaptation and the long-term dynamics of species. Paleobiology 32(2):173-178.

Vermeij GJ. 2007. The ecology of invasion: acquisition and loss of the siphonal canal in gastropods. Paleobiology 33: 469-493.

Vermeij GJ. 2008. Escalation and its role in Jurassic biotic history. Palaeogeography, Palaeoclimatology, Palaeoecology 263: 3-8.

Vermeij GJ, Dietl GP. 2006. Majority rule: adaptation and the long-term dynamics of species. Paleobiology 32: 173-178.

Vermeij GJ, Dietl GP, Reid DG. 2008. The trans-Atlantic history of diversity and body size in ecological guilds. Ecology 89(11): supplement, pp. S39-S52.

Vermeij GJ, Williams SJ. 2007. Predation and the geography of opercular thickness in Turbinid gastropods. Journal of Molluscan Studies 73: 67-73.

Voland E and Beise J. 2002. Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhorn. Behavioral Ecology and Sociobiology 52:435-443.

Waguespack NM, Surovell TA. 2003. Clovis hunting strategies, or how to make out on plentiful resources. American Antiquity 68(2):333-352.

Walker R, Hill K, Kaplan H, McMillan G. 2002. Age-dependency in hunting ability among the Ache of Eastern Paraguay. Journal of Human Evolution 42:1-20.

Weiner J. 1985. Size hierarchies in experimental populations of annual plants. Ecology 66:743-752.

Weiner J. 1986. How competition for light and nutrients affects size variability in Ipomoea Tricolor populations. Ecology 67:1425-1427.

Weiner J, Solbrig OT. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia 61:334-336.

West-Eberhard MJ. 1989. Phenotypic plasticity and origins of diversity. Annual Review of Ecology and Systematics 20:249-278.

West-Eberhard MJ. 2003. Developmental Plasticity and Evolution. New York: Oxford University Press.

Wheeler DE, Buck NA. 1995. Storage proteins in ants during development and colony founding. Journal of Insect Physiology 41:885-894.

Wheeler DE, Tuchinskaya I, Buck NA, Tabashnik BE. 2000. Hexameric storage proteins during metamorphosis and egg production in the diamondback moth, *Plutella xylostella* (Lepidoptera). Journal of Insect Physiology 46:951-958.

Whiten A. 2005. The second inheritance system of chimpanzees and humans. Nature 437:52-55.

Whiten A, Horner V, de Waal FBM. 2005. Conformity to cultural norms of tool use in chimpanzees. Nature 437:737-740.

Whiten A, Spiteri A, Horner V, Bonnie KE, Lambeth SP, Schapiro SJ, de Waal FBM. 2007. Transmission of multiple traditions within and between chimpanzee groups. Current Biology 17:1038-1043.

Whittaker RH, Levin SA, Root RB. 1973. Niche, habitat and ecotope. American Naturalist 107(955):321-338.

Williams GC. 1966. Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought. Princeton: Princeton University Press.

Wilson DS. 1997. Human groups as units of selection. Science 276:1816-1817.

Wilson DS, Dugatkin LA. 1997. Group selection and assortative interactions. American Naturalist 149:336-351.

Wilson DS, Sober E. 1989. Reviving the superorganism. Journal of Theoretical Biology 136:337-356.

Wilson DS, Wilson EO. 2007. Rethinking the theoretical foundation of sociobiology. The Quarterly Review of Biology 82:327-348.

Wilson EO. 1971. The Insect Societies. Cambridge (MA): Harvard Belknap Press.

Wilson EO. 1975. Sociobiology: the New Synthesis. Cambridge (MA): Harvard Belknap Press.

Wilson EO. 2005. Kin selection as the key to altruism: its rise and fall. Social Research 72:1-8.

Wilson MA, Taylor PD. 2006. Predatory drill holes and partial mortality in Devonian colonial metazoans. Geology 34: 565-568.

Wourms JP. 1973. The developmental biology of annual fishes III: Pre-embryonic and embryonic diapause of variable duration in the eggs of annual fishes. Journal of Experimental Zoology 182:389-414.

Wüster W, Duarte MR, Salomão MG. 2005. Morphological correlates of incipient arboreality and ornithophagy in island pitvipers, and the phylogenetic position of *Bothrops insularis*. Journal of Zoology, London 266:1-10.

Wynne-Edwards VC. 1963. Intergroup selection in the evolution of social systems. Nature 200:623-626.

Wynne-Edwards VC. 1965. Self-regulating systems in populations of animals. Science 147:1543-1548.

Young BA, Lee CE, Kylle MD. 2002. Do snakes meter venom? BioScience 52:1121 -1126.

Zhao E, Wu G, Yang W. 1979. Comparisons of toxicity and neutralization test among Pallas' pit viper, Snake-Island pit viper and black eye-brow pit viper (English summary). Acta Herpetology Sinica Service 3:1-6.

ABOUT THE AUTHOR

Benjamin Hardisty was born and raised in the state of Rhode Island and received his B.A. in Politics from the University of South Florida, with a minor in Political Theory. He plans to continue his higher education by pursuing a PhD in the graduate program in Ecology, Evolution and Organismal Biology at the University of Utah. He has published one paper, written while still an undergraduate, in the *Journal of Bioeconomics* and another, written for his Master's thesis, in *Biology & Philosophy*, and hopes to publish more in the coming years. In his spare time he enjoys listening to opera and classical music, playing chess, drinking coffee, writing poetry and reading Postmodern novels.