ABSTRACT

Title of Dissertation:	EXPLAINING THE EMERGENCE OF COOPERATIVE TRAITS:
	AN AXIOMATIC THEORY OF ACCUMULATION

Michael Perlitz, Doctor of Philosophy, 2003

Dissertation directed by:	Professor Dr. Piotr Swistak
	Department of Political Sciences

In this dissertation I construct an axiomatic theory of action that explains how originally selfish individuals form aggregations and develop cooperative abilities. This theory is more general than the two most widespread biological explanations of the emergence of cooperation: kinship theory and game theoretic models. In particular, it introduces the notions of space and time that are more general (individual specific) than standard physical notions on which biological theories mostly rely. While predictions of my theory agree, in principle, with predictions of other main theories of aggregation, its scope goes well beyond that of any other theory of aggregation. For instance, I am able to show that two different arguments about properties of optimal size aggregations do in fact follow from a single set of assumptions, namely those of my theory of accumulations. I am also able to explain a paradoxical empirical finding on genetic variation.

More specifically, Sibly (1983) has shown that under a certain type of a fitness function individuals will form aggregations with fitness optimizing group size being larger than the eventually emerging in equilibrium group size. In a response to Sibly, Giraldeau and Gillis (1984) presented a type of fitness function where the optimal group

size is equal to the equilibrium group size. Both arguments rely, however, on fitness functions that are postulated ad hoc. In my theory I show how both of these functions can be derived analytically from a set of more fundamental assumptions. This shows that claims of Sibly and Giraldeau's and Gillis' while seemingly contradictory, were in fact consistent. Another example of an application of my theory concerns a genetic puzzle posed by Hedrick and Parker (1997). Hedric and Parker have observed that genetic variation in eusocials is not only a higher than predicted by kinship but even higher than in solitaries. This empirical observation, paradoxical in the light of standard biological explanations, can in fact be explained by my theory.

EXPLAINING THE EMERGENCE OF COOPERATIVE TRAITS:

AN AXIOMATIC THEORY OF ACCUMULATION

by

Michael Perlitz

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2003

Advisory Committee:

Professor Piotr T. Swistak, Chair/Advisor
Professor Mike M. Boyle
Professor Charles D. Levermore
Professor William R. Stricklin
Professor Daniel Sweet

ACKNOWLEDGMENTS

Finally I am grateful to Dr. Michael Boyle for reading over my thesis, and pointing out some inconsistencies.

Any mistakes and remaining inconsistencies are, of course, due to my negligence.

TABLE OF CONTENTS

Introduction

The common feature of all previous research on cooperation is the assumption that individuals have a fully developed ability to cooperate. I find this assumption fundamentally unsettling. It is not at all obvious that this assumption is in general satisfied in real life systems and it is very troubling not to know what would happen to the emergence of cooperative abilities if this assumption does not hold. Hence, there is an important need for a theory that would be able to explain how cooperative abilities have originally come into existence. Constructing such a theory is the purpose of my thesis.

Within a world of individuals competing for limited resources it is difficult to explain the emergence of tolerating, cooperative or altruistic behavior. After all members of the same biological species are predominantly competitors for metabolic resources. Yet in nature we observe many examples of individuals forming aggregations that vary from simple groups to complex societies. Indeed, the most complex aggregations are composed within the same species, among individuals who are each other most direct competitors. How can this seemingly paradoxical phenomenon be explained?

Biology offers two types of explanations for the emergence of cooperation: kinship theory and game theoretic models. I will shortly describe the major ideas behind both types of explanations, comment on why I find neither of them satisfactory, and indicate how my theory solves the problems that are inherent in these two modes of explanation.

Kinship Theory.   The most extreme form of helping, altruism, does not appear in

arbitrary conspecifics. With the exception of humans it is mostly observed between closely related individuals (See e.g., Axelrod, 1984, Chapter 5: The Evolution of Cooperation in Biological Systems, with William D. Hamilton). Hence explaining the emergence of altruism seems to require a kinship argument. The mathematical foundation for the development of kinship theory was established by Hamilton (1964) in what is now called "Hamilton's rule." Hamilton's rule states that there is a selection for a behavior whose overall benefit to the individual exhibiting this behavior and its relatives supersedes the cost to the individual. Symbolically the rule is stated by $rb > c$, where r is Wright's coefficient of relatedness, b the reproductive benefit to the relative with relatedness r, and c the cost of the behavior to the individual. Wright's coefficient measures the proportion of genetic relatedness between individuals, e.g., $r = \dfrac{1}{2}$ for two brothers, and $r = \dfrac{1}{4}$ between first degree cousins. Hamilton (1972) and Trivers and Hare (1976) applied Hamilton's rule to eusocial insects to explain why their states mainly consist of sisters. The argument is based on the assumption that Hamiltons rule holds for those eusocial insects and the fact that hymenoptera are haplodiploid (males have one set of chromosomes, females two). However, all hymenoptera are haplodiploid, but not all are eusocial. Furthermore, termites and naked mole-rats are eusocial, but not haplodiploid. Sherman *et al.* (1991) conclude on page 7 that "haplodiploidy, then, is neither necessary nor sufficient to account for the appearance and maintenance of eusociality". Even if the eventual ratio of females to males in eusocial states can be explained by the kinship theory, the very emergence of the helping traits cannot.

But even if we were able to explain the emergence of cooperation between related individuals using kinship theory (assuming this theory were able to explain the emergence of cooperative traits), then how can we explain the emergence of cooperation between unrelated individuals? Indeed, from what we know about helping

behavior relatedness is not necessary for cooperatives traits to evolve. This inadequate descriptive validity of kinship theory is perhaps its most troubling aspect. Kinship theory predicts the emergence of cooperation among related individuals but fails to explain the emergence of cooperation among unrelated individuals. Thus the need for the generalization of kinship theory has been obvious for a long time.[1] In one early influential attempt Trivers (1971) has shown, for instance, how cooperation can emerge between individuals of different species. A general solution to the problem would require theories of cooperation that do not rely in a critical way on any kinship assumptions. The need for such theories explains in part an explosive popularity of game theoretic models.

Game Theoretic Models. Without using any kinship arguments, Axelrod (1984) showed that cooperation can emerge even in a world of unconditional defection, if there is a small cluster of individuals who base their cooperation on reciprocity and who interact with each other frequently. Axelrod based his investigation on prisoners dilemma (PD) kinds of situations. The PD (see figure A) is a regime which is defined by a 2×2 payoff matrix which declares the highest payoff T for cheating (defecting, D) when it is successful, intermediate payoff R for not cheating (cooperating, C), low payoff for unsuccessful cheating P, and the lowest one, S, for being cheated on successfully. The concepts of cooperation and defection are defined by their relation to each other given by the PD payoff matrix. Formally the inequalities $R > \dfrac{S+T}{2}$ (the reward for mutual cooperation has to be greater than the average of temptation to defect

[1]Dawkins 'selfish gene hypothesis', presented in his widely popular book (1976), is Hamiltons' idea developed from the perspective of a single allele. An allele is a version of a gene. For instance, the gene of eye color in humans has alleles for different colors. Dawkins' idea is to consider an allele to be a player in the game theoretic sense whose payoff is the relative frequency of its copies in the next generation.

and the payoff of being cheated. This means that two times cooperating will compensate for one successful cheating and for one successful being cheated), and $T > R > P > S$. In the PD games defection should also yield a higher payoff than cooperation, no matter what the move of the opponent. Thus $T > R$ and $T > P$. Also, mutual cooperation should have a higher payoff than the payoff for mutual defection, i.e., $R > P$. A PD game is, therefore, an adequate model of a regime under which mutual cooperation benefits both players, yet each is always tempted by the possibility of reaping higher benefits through defection. If the PD game is played only once, then a payoff maximizing player should defect, since regardless of the move of the opponent defection gives him a higher payoff. The result will be that two such players will end up with payoff P. The dilemma is, that they both could have received the higher payoff R by cooperating.

Usually, however, players in the real world do not meet just once. To study a repeated PD context Axelrod initiated two round robin tournaments inviting scientists from different areas of research to submit strategies for the iterated PD (IPD) that would be played against each other. Both tournaments were won by tit-for-tat (TFT), both times submitted by Anatol Rappaport. TFT will start by cooperating, and will reciprocate his opponent's cooperation from the previous move by cooperation and punish his defection by defection. Note that TFT is a "nice" strategy in that it is never the first one to defect. Axelrod has argued that a strategy based on reciprocity can be successful when played against other strategies. Furthermore, cooperation, once established on the basis of reciprocity, can be maintained if the strategy played retaliates swiftly against defection.

Column Player

		Cooperate	Defect
Row Player	Cooperate	R=3, R=3 Reward for mutual cooperation	S=0, T=5 Sucker's payoff and temptation to defect
	Defect	T=5, S=0 Temptation to defect and sucker's payoff	P=1, P=1 Punishment for mutual defection

Figure A : The Prisoner's Dilemma. [Adopted from Axelrod (1984), p. 8]
The inequalities $2R > S + T$ and $T > R > P > S$ for the payoffs
define the concepts of cooperation and defection.

One problem with Axelrod's conclusions was that they were mostly based on

simulations and lacked robust deductive results.[2] However the general problem of the

evolutionary stability of cooperative behaviors has turned out to have a workable

deductive solution. Bendor and Swistak (1997) have shown that under assumptions of

the general evolutionary model nice and retaliatory strategies (like tit-for tat) are more

stable than others lies in their lower minimal stabilizing frequencies. A nice and

retaliatory strategy is, therefore, more likely to become stable than a strategy without

these properties, other factors equal.[3]

But prisoners dilemma is not the only form of interaction among individuals that is

---

[2]For instance, his concept of 'collectively stable' turned out to be not a stability
concept at all (Bendor and Swistak, 1997).

[3]Whether a certain nice and retaliatory strategy becomes stable or not is
irrelevant for explaining the emergence of cooperation. It is only relevant for the
problem of stability: it explains why once there is enough nice and retaliatory strategies
cooperation in a group will remain stable. Focusing on the problem of stability is, in
general, unlikely to help us explain the emergence of cooperation.

important to investigate. Indeed, 'helping behavior' among animals has been called 'cooperative,' 'altruistic,' 'symbiotic,' etc., and all these concepts were meant to have different connotations. Cooperation, as defined in the PD game, is a specific form of a helping behavior that may also have many forms other than cooperation.

For instance, Trivers (1971) has showed how a helping behavior can emerge between a grouper and cleaner fishes. Trivers calls this behavior 'altruistic.' More specifically, Trivers calls the grouper 'altruistic' because it "desists from eating the cleaner even when it easily could do so and when it must go to special pains (sometimes at danger to itself) to avoid doing so." (Trivers (1971), p. 41). The relationship between grouper and cleaner is of a PD type, but only from the grouper's perspective. If the game between grouper and cleaner is played only once, the grouper should eat the cooperating cleaner (i.e., defect) to obtain the highest payoff. If the grouper cooperates (does not eat the cleaner) it receives an intermediate payoff, and it receives the lowest payoff when the cleaner defects (does not show up for cleaning). In contrast to the PD not both players can defect in this setup: The grouper cannot eat the cleaner when the cleaner doesn't show up for cleaning in the first place. If we want to extend the concept of cooperation beyond the PD game, relations like that between grouper and cleaner would have to be considered.

One may also argue that Trivers' use of the concept 'altruism' was not really appropriate. The American Heritage Dictionary defines altruism as "unselfish concern for the welfare of others; selflessness", and so the concept of 'altruism' should be reserved for cases of true self sacrifice with no compensation whatsoever. To call the behavior of the grouper towards the cleaner 'altruism' is therefore inappropriate—the grouper receives a tremendous health benefit from maintaining a trusting relationship with its cleaners. Yet altruistic behaviors abound in other interactions. For instance, metabolic altruism can always be observed in child caring species: giving birth to and

rearing an offspring is a metabolically altruistic act. An extreme example of metabolic altruism appears in the honey pot ants (*myrmecocystus*).   Some members of each ant state become living food containers, attaching themselves to the ceilings of chambers deep underground. They are filled up with food by other worker ants until they are greatly swollen. In times of low food supply the contents of their abdomen serves as food source for the colony. Once emptied they die.   This pure altruism is yet another type of a helping behavior that needs to be explained.

Other forms of helping behavior have been investigated by Mesterton-Gibbons and Dugatkin (1992).   One behavior that will be of special interest to us is what they refer to as a 'by-product mutualism.' By-product mutualism is an interesting form of helping, since the helping is a by-product of pure self-interest. Brown (1983) explains by-product mutualism as follows:

> In *by-product mutualism*, each animal must perform a necessary minimum for itself that may benefit another individual as a by-product. These are typically behaviors a solitary individual must do regardless of the presence or behavior of others, such as hunting for food.

And in their review of Dugatkin (1983) Newak and Sigmund (1998) wrote:

> By-product mutualism holds when the best one can do for oneself also happens to be best for the other. Most theoreticians fail to be excited by this type of cooperation which can obviously not be threatened by cheating, and by-product mutualism has been branded as a solution without a problem. But the concept may account for

most instances of cooperation, as emerges from Dugatkin's empirical

chapters.

Note that the by-product mutualism is not an act of cooperation in the sense of PD

game.   In fact the structure of the game is very different from that of the PD. Here

'defection' (better: not-helping) would always hurt the defector.   Mesterton-Gibbons

and Dugatkin (1992) give an example of communal breeding in unrelated cofoundresses

in ants (Mesterton-Gibbons and Dugatkin (1992), p. 274). Multiple insect foundresses

might join in order to build a nest and raise workers. In particular an example of the

seed harvester ant is discussed. Adult colonies of that ant engage in brood raiding of

colonies of their own species. The more workers are raised in short time the more likely

a colony can withstand a brood raiding by another colony and the more likely it wins a

brood raiding it initiated. Once there is only one nest in a territory that has survived the

brood raiding, the mutual helping between the cofoundresses ceases and they fight each

other until only one cofoundress survives. The surviving one becomes the queen of the

state. The mutual helping between cofoundresses is again not an act of 'cooperation' in

the prisoners dilemma sense. In forming the initial state the cofoundresses actually

engage in by-product mutualism, which means they are subjected to a selective regime

where 'cooperation' (helping behavior) dominates (yields a higher payoff) than

defection.

We have now seen different games including one-shot PD, repeated PD, game of

'altruism' in the sense of Trivers, game of pure altruism and game of by-product

mutualism.   In this variety of games that can be used to define different forms of

helping behavior, cooperation does not seem to be equally easy to attain. For instance,

overcoming defection in a one-shot PD is not at all possible—defection is the only

equilibrium behavior. Cooperative equilibrium is, however, possible in a repeated PD.

Yet in a repeated PD overcoming defection seems much more difficult than overcoming defection in a game of by-product mutualism. A game theoretic reason behind this intuition is straightforward: cooperation is the only equilibrium strategy in the game of by-product mutualism, yet it is one of infinitely many equilibrium strategies in the repeated PD (including strategies that are purely defective). Hence an evolution towards a cooperative state seems much more straightforward and much more likely in a game of by-product mutualism than in the repeated PD game.[4]

Game Theory versus My Approach. With these game theoretic intuitions in mind it will be easier to see how my theory differs from the game theoretic explanations. There are two fundamental points of difference. The first point concerns the subject of evolution. In evolutionary game theory we first specify a game (players, strategies and payoffs). Next, we assume that higher scoring strategies, or, equivalently, their carriers, evolve at higher rates. Finally we analyze the flow of the dynamic process and identify its equilibria. Thus, for instance, in the evolutionary analyses of the repeated PD it is a priori assumed that interactions have a form of the repeated PD. Once the form of the game is fixed, the analysis is then reduced to studying the evolution of strategies in this specific game. In contrast, in my theory it is the entire games, and not only strategies in a fixed game, that are allowed to evolve. I see an evolutionary process as a sequence of games evolving into one another, rather than a sequence of states in a given game. Thus I am not only interested in solving a specific game of cooperation, e.g., an evolutionary repeated PD, but I am primarily interested in explaining how all such game could have evolved from some other, more basic, form of an interaction. This brings me to the

[4]We may also say that mutations in equilibrium strategies are more likely to appear than mutations in non-equilibrium strategies. Some researchers would even make a more extreme claim and assume that the only possible mutations are those of equilibrium strategies.

second difference between my approach and game theoretic models. The difference
stems from my belief that all assumptions about the initial state of nature are equally
valid.   For instance, I do not believe that a PD game, both one-shot and repeated,
constitutes a valid staring point to explain the emergence of cooperation. By assuming
the existence of both cooperative and defective actions in a PD game, a game theoretic
analysis tacitly assumes that individuals already have an ability to cooperate. In a
one-shot PD game, for instance, this means that individuals have an ability to play an
off-equilibrium strategy. But this is a very strong assumption and it may not be valid at
all. The only assumption I would find justified to make is that initially individuals' sole
ability is to act in their self-interest. This limits, in consequence, the class of games
from which my analysis can start. More specifically, given some other assumptions of
my theory, it limits my starting point to a game of by-product mutualism.

The Nature of the Assumptions.   A form of by-product mutualism that is essential
for my discussion is the aggregation of individuals for the sake of seeking cover from
threats. This idea is extensively discussed in Hamilton (1971). Hamilton argues that
individuals should aggregate for purely selfish reasons if they can use other individuals
as cover from predators or parasites. He points out that schooling fish, herding
mammals and flocking birds show the tendency of closing-in once a respective predator
appears. Furthermore, fish living in open waters, ungulates living in open grassy areas,
and birds breeding in easily accessible terrain show a strong tendency to aggregate
contrary to their equivalents dwelling in more cover providing environments.

This aggregating under a common threat is clearly due to by-product mutualism.
An individual who for selfish reasons seeks the presence of another is automatically
benefiting the other individual as well. If such an individual would decide not to
aggregate with others it will damage itself as well as the others. These are the

conditions of by-product mutualism.

The starting point of my thesis is that it is necessary to justify how cooperative traits can emerge in the first place if the originally given population consists of purely competitive solitary metabolic individuals who do not possess those traits. I assume that competition is over metabolic resources which mean essentially food (this implies competition over the space within which the food is distributed). I do not involve any genetic arguments in order to keep the approach as widely applicable as possible. Individuals are assumed to be purely metabolic and no assumptions are made about their mode of reproduction, their degree of relatedness or even whether they belong to the same species. Per se, there is no reason that under those conditions an individual will have abilities which will be cooperative once the selective regime changes to a PD type for instance. Such abilities cannot be taken for granted even when the potential to cooperate is present. The ability to cooperate, initially not present, has to evolve as games are being played. How this evolution happens – be it in biological, sociological or individual learning systems - is a problem of fundamental importance. In the first sentence of his book Axelrod (1984) asks:

> Under what conditions will cooperation emerge in a world of egoists without central authority?

To paraphrase Axelrod's sentence, the central question of my thesis is:

> Under what conditions will the *ability to cooperate* emerge in a world of egoists without central authority?

The starting point of our analysis is an original state where in the absence of threats

individuals are solitary. The emergence of a threat changes this situation and makes the emergence of accumulations viable. Two facts make accumulations feasible: First, accumulation can happen for purely selfish metabolic reasons, so to assume an intrinsic tendency of an individual to benefit kin, group, or species is not necessary. The original competitive solitary selfish setup suffices. Second, in order to accumulate no new abilities have to be evolved, only old ones - namely those of high competitiveness - have to be degraded. Once selection pressure declines degradation can easily happen in evolutionary systems with random mutation. The reason why accumulations will form once degradation of combativeness occurs is simply due to the fact that individuals who are solitary will be more likely to succumb to a threat than individuals who are not. Thus in a group where some individuals avoid others (remain solitary) while other individuals move randomly with respect to each other, selection will favor individuals who move randomly; all of those who are solitary would be eradicated. Similarly, in a group where some individuals move towards each other while others move randomly, the ones who move towards each other will be selected for. And so, the process will give rise to accumulations.

In short, then, the topic of my dissertation is the emergence of accumulations due to degradation of competitiveness under a common threat. This is the fundamental first step in explaining the emergence of cooperation in general. I see accumulations are the prerequisite for the emergence of cooperative traits once the selective regime changes to one of the PD type, for example. What type of traits those are is a subject for further research.

The Content of the Dissertation. My analysis begins with an assumption that for individuals to effectively compete over resources two types of abilities had to evolve: (1) perceptive and locomotive abilities (being aware of each others presence, distance

estimation, estimation of the opponents physical condition, food discovery, manipulation of speed, etc.), and (2) defense and attack abilities (defending acquired food items, attacking other individuals to acquire their food items). The first type of abilities concerns the manipulation of physical space and time within which the individual has to operate and will serve emergent cooperative abilities as well as they do competitive ones. The second type is the truly competitive one and will counteract the emergence of cooperative traits.

I assume that competitive traits are originally highly evolved due to the selection pressure towards competitiveness over metabolic resources. In consequence individuals will try to avoid each other. According to Hamilton (1971) metabolic threats can have the opposite effect—individuals will seek out each other companionship. Individuals who do not want to share benefits, might nevertheless benefit from sharing threats. In order to signify the dualism between metabolic resources and metabolic threats I call them *metabolic sources* and *metabolic sinks*, respectively. Examples of metabolic sources are food and oxygen (for vertebrates at least) while examples of metabolic sinks are predators and earthquakes (for mammals at least). I chose these examples to distinguish between two types of metabolic sources and sinks: distributable and non-distributable. This distinction is necessary since individuals do not have to compete over all metabolic sources. Zebras, for instance, do not compete over oxygen. They will, however, compete over grass once grass becomes sparse. The difference here is that between *distributable* and *non-distributable* metabolic sources. Under a distributable metabolic source individuals will compete with each other since the metabolic benefit of the source can be distributed among the individuals. This is usually the case with food. If a source can be distributed then individuals can receive more or less of that benefit and this forms the basis for competitiveness. Non-distributable metabolic sources are those where there is no distribution problem.

Oxygen is readily available in the air, so no competition for breathing will evolve among Zebras. Analogously we can distinguish between distributable and non-distributable metabolic sinks. Individuals will not benefit from the presence of others when an earthquake occurs. An earthquake thus is a not distributable metabolic sink. I have already discussed how individuals can benefit from accumulating under predators or parasites. Those are examples of distributable metabolic sinks.

It may not be immediately clear that the assumption of competitiveness over distributable sources is valid. In fact, a widespread phenomenon of 'cooperative hunting' seems to contradict the assumption that individuals will always compete under distributable metabolic sources. It will, hence, be instructive to revisit the meaning of our assumptions in the light of the phenomenon of 'cooperative hunting' which is considered to be probably the most widely distributed form of cooperative behavior in animals (Packer and Ruttan, 1987). First we have to note that joining a hunt should only be considered an act of cooperation when there is also a possibility to cheat, i.e., to let others hunt and then benefit from the outcome. Thus, not every collective hunting is cooperative hunting. Second, in the light of my assumptions cooperative hunting cannot be considered as an initial foraging strategy since it has to emerge *after* competitiveness in the hunting species is to some extend degraded. Piranhas practice probably the most basic form of collective hunting which is not cooperative hunting. All piranhas of a school will approach a prey individual simultaneously without interacting with any other piranha. The prey individual is then simply overwhelmed by the approaching number of predators. Since a single piranha cannot benefit form cheating, this type of hunting cannot be called cooperative, but only collective. The very emergence of schools is not, however, rooted in the benefit of collective hunting, but rather in the fact that the piranha itself is subject to predation by crocodiles and caymans and therefore benefits from the protection of the school. Similarly killer

whales (Baird and Dill, 1996, Giraldeau and Caraco, 2000) form hunting groups were a group of size three maximizes the energy intake of each whale. However, the emergence of group formation goes back to a time when the ancestors of the killer whales where themselves prey to sharks. I would conjecture that the evolutionary process of group formation in whales looked as follows. First, predation combativeness for food degraded. Second, the foraging groups emerged as a result of predator avoidance. Finally, since simultaneous encounter of food items by a group became more likely and a group could capture a bigger and/or a more skillful prey, a selection pressures kept the group together.

This discussion suggests, therefore, the following general approach: Individuals are assumed to be initially highly evolved in competing for distributable metabolic sources. At this point they are solitary. Introducing metabolic sinks can change this original selective regime such that the solitary life-style is not the one with the highest metabolic benefit anymore. Competitive traits will then start to degenerate resulting in individuals becoming more tolerant towards the presence of others. Since solitary individuals are more likely to be removed by the distributable metabolic sinks, accumulations will emerge. At this point the stage is set for evolving traits like the ability to share food, first passively (communal feeding due protection from predation), then actively (e.g., evolution of discovery calls to draw attention of the group to a feeding location).

I derive the formation of accumulations of individuals under metabolic sources and sinks based from a set of general axioms. After a motivational first chapter a fundamental system of axioms is formulated and described in the second chapter (it is then extended in subsequent chapters.) In this fundamental system of axioms the existence of individuals, metabolic sources and metabolic sinks is postulated, and the relation of individuals to metabolic sources and sinks is described by set-theoretical relations. The relation between an individual and a metabolic source or sink concerns

the meeting between an individual and a metabolic source or sink and a potential change in individual's metabolic level due to such a meeting. The meeting itself is called *encounter between individual(s) and metabolic source or sink*, the change in metabolic level *reception of the metabolic source or sink by (an) individual(s).* When a predator encounters a group of individuals, then not every individual of that group is necessarily confronted by the predator. Yet, for a predator to encounter a group of individuals a confrontation with a single group member is sufficient. Thus the set-theoretical structure of an encounter event is such that an encounter event that happens to a certain set of individuals also happens to each super set of those individuals. In particular, if a single individual is encountered, then the set of all individuals is also encountered. A reception event has an opposite set-theoretical nature. If a certain group of individuals experiences metabolic change then each subset of that group has to experience metabolic change. Encounter and reception events are not, however, sufficient to paint the entire picture of the interaction between individuals and metabolic sources and sinks. Studying the relation between a predator and its prey, e.g., lions and zebras, it becomes apparent that a third type of event has to be included in the investigation. Once a predator has encountered a group of individuals he is usually confronted with more than one individual at once and may have to make a choice whether to capture one of them or keep searching. A single male lion (females in general hunt in groups), for instance, is on encounter with a herd of zebras confronted with perhaps 10 zebras at once. He will then choose one individual among those or travel along the herd to find another one. Finally he makes the decision to hunt one specific zebra down, which either ends in a successful kill for the lion (a reception of the lion by the zebra), or a failure (a *resignation* event). This type of event is important to consider. Before a predator makes his decision, there makes a significant difference for the prey whether it is a part of a small or large group, or whether it is solitary. I call

this type of event a *focus* event. After a focus event has happened all individuals focused on will interact with the metabolic source or sink independently from all other individuals. Once a focus event has occurred an individual within focus is with regard to the metabolic source or sink in a solitary state. Encounter and focus will occur simultaneously in case of solitary individuals. However the expected time between encounter and focus will increase if individuals are living in groups. During the time between encounter and focus the metabolic source or sink interacts with the group. The set-theoretical structure of a focus event is identical to that of a reception event, since focus between a set of individuals and a metabolic source or sink is also a focus for any subsets of that set.

Once the concepts of *individual, metabolic source, metabolic sink, encounter, focus, reception and resignation* are axiomatically established the concept of *accumulation* can be derived (the concepts of focus, reception and resignation are not used in the derivation). That is done in chapter 3. The concept of accumulation is a spatial concept which signifies closeness of individuals to each other under a metabolic source or sink. Yet, no metric space has to be introduced in order to define this concept. The only relational concept necessary is that of encounter which is of a set-theoretical nature. This opens the possibility to investigate spatial relations without having to introduce a space within which interactions occur. In particular, spatial models developed with this approach are not limited to Euclidean spaces. This property becomes essential with the emergence of information exchange which is independent of Euclidean distances, e.g., newspapers, telephones, internet. For instance, the institution of an insurance company is designed to form accumulations of individuals under non-distributable threats, e.g., flooding. By becoming a member of such accumulation an individual enjoys the benefit of the accumulation without having to relocate in a physical/Euclidean space. The concept of space which is implied by my approach is, thus, more general than the

Euclidean one. In my theory, for instance, the same Euclidean distance can have different significance to different individuals. In models that use Euclidean distance this distinction is impossible to make. (Formally, interpretation of Euclidean models always requires a translation of Euclidean distance into significance for individuals.)

Once the concept of accumulation has been developed, in chapter 4 I investigate conditions under which individuals form accumulations. An incentive for individuals to accumulate is given by the presence of a distributable metabolic sink. This incentive, however, is offset by the benefit individuals derive by competing over a distributable metabolic source. Using the axioms of my theory I derive specific fitness functions, dependent on the size of the accumulation, for individuals under a metabolic source and a metabolic sink. The general shape of such functions has been postulated in the literature before. Luc-Alain Giraldeau and Thomas Caraco (2000 p.88) postulate the shape of a fitness function for an individual under an aggregation economy (deriving benefits from the presence of others while competing with them over resources) which depends on group size. They do not, however, provide a mathematical derivation of how such fitness function can be obtained. Their family of fitness functions can be shown to follow from my set of axioms. Their argument for the shape of those fitness functions is, however, similar to mine and goes roughly as follows. Within an environment which supports the formation of groups (accumulations) fitness will first increase with group size. As group size increases so does the competition within the accumulation. Once the detrimental effect of competition outweighs the benefit of grouping, fitness will start to decline towards 0. This general argument suggests that there is a unique fitness optimizing group size. But would it also be an equilibrium size? I show that in general the optimal group size is not the size that would emerge in equilibrium. This fact has already been recognized by Sibly (1983). However, in a response to Sibly, Giraldeau and Gillis (1984) present a type of fitness function that

generates stable and optimal group size. Both arguments rely on types of fitness functions that are adopted ad hoc. In my approach both types of fitness functions can be derived analytically. The remainder of chapter 4 is devoted to deriving some equilibrium statements for fitness functions. The overall conclusion is that individuals in general should accumulate beyond the fitness maximizing accumulation size.

In chapter 5 I discuss an essential population genetic consequence arising from the formation of accumulations under a distributable metabolic sink, namely an increase in genetic variation. Accumulating under a distributable metabolic sink decreases not only the selection pressure on individuals, but also lowers their differences in fitness. Accumulating raises and flattens the fitness function: The lower the fitness of an individual, the higher the benefit obtained from accumulating. This implies that some mutations which are deleterious under the solitary regime might not be deleterious anymore under accumulations. This will lead to an increase of genetic variation in the population and, at least initially, to a decrease in solitary fitness.

It is known that in eusocial insects the genetic variation within colonies is often higher than suggested by kinship theory (Shykoff and Schmid-Hempel,1991, and Schmid-Hempel,1994). One hypothesis is that mating systems which support outbreeding are selected for because increased genetic variability increases resistance against parasites and infections. Statistics presented in Hedrick and Parker (1997) do, however, suggest that genetic variation in eusocials is not only a higher than predicted by kinship but even higher than in solitaries. The mean expected allozyme heterozygosity in 4 species of advanced eusocial bees is .069, while it is .035 in 10 species of solitary bees. In 38 species of primitive eusocial bees this heterozygosity is .027, thus lower than in solitary bees. Overall advanced eusocial species (31 species of ants, bees and wasps) show an allozyme heterozygosity of .045, primitive euscial species (42 bees and wasps species) have .031, and solitary species (37 species of bees,

wasps and sawflies) have a heterozygosity of .069. A similar tendency can be observed in the mean expected microsatellite heterozygosity, also presented in Hedrick and Parker (1997). That heterozygosity in advanced eusocial insects is higher than predicted by kinship theory alone can be explained by introducing certain mating systems promoting outbreeding. How can those mating systems, however, produce heterozygosity which is larger in eusocials than in solitary species? We would expect a heterozygosity in eusocials to be between that of the solitary species and the one predicted by kinship theory. To explain this phenomenon I propose to take into account the change of the selective regime which happens when going from solitary to eusocial species. In primitive eusocials the effect of kinship might still outweigh the increase of genetic variation due to accumulation. This is then reversed in the advanced eusocial species.

The increase of genetic variation under accumulation might also shed some light on another fundamental problem in evolution. An essential problem in the theory of evolutionary biology is the question whether evolution under directional selection is a globally or a merely locally optimizing mechanism. A discussion of this problem can be found in Elster (1979). If the principle of 'survival of the fittest' strictly applies, then it is very unlikely that the globally optimal solution can be found by selection and mutation alone. It is rather expected that the species will get trapped in a local optimum which will in general support a smaller fitness than the global one. This makes it difficult to explain many highly evolved - and furthermore highly adaptable - traits as, e.g., the bird wing. An increase in genetic variation makes it more likely that a part of the population will cross genetically valleys of lower fitness and reach another fitness optimizing genetics. Accumulation under a distributable metabolic sink is, therefore, a mechanism which might turn a selection-mutation process from a locally optimizing mechanism to a not-merely locally optimizing one. Whether this not-merely locally

optimizing mechanism can become a globally optimizing one depends on how much individuals support each other under the selection pressure. If the support is effective, then significant genetic variation will increase the probability to reach the globally optimizing genetics. Many species of birds, for example, form breeding colonies. Furthermore, migratory birds often travel in large flocks which offer protection from predators and mutual aerodynamic support. Those flocks are therefore accumulations under at least two distributable metabolic sinks, namely predators, and the physical labor cost of migration itself.

One final essential consequence of the ideas described in this thesis is, that in order to understand the behavior of biological individuals one has to have a valid model of their interpretation of space and time. The idea to move beyond Euclidean space has been pursued by others. For instance, Stadler *et al*. (2001) propose the notion of a formal space which captures the phenomena associated with the phenotype of an RNA molecule (its shape, and therefore its chemical properties) more accurately than the space based on the sequence of bases within this molecule. In my theory space and time have a meaning for a metabolic individual insofar as they have metabolic significance. All that happens within space and time is the interaction of individuals with threats and benefits. The probability that such interaction events happen constitute a formal representation of a subjective notion of space and time. Individuals have incentives to use strategies that decrease the probability of being exposed to a threat and increase the probability of being exposed to a benefit. If an individual reaches a state in which the probability of being exposed to a threat is 0, and the probability of being exposed to all necessary benefits is 1, then the notion of space and time becomes meaningless. Since this is, however, the state which is the most beneficial one, we can conclude that ultimate goal in the evolution of a biological species (which might be attainable or not) is the elimination of space and time as relevant factors of fitness.

Chapter 1.   Motivation

Finding an answer to the question why individuals of certain biological species form accumulations like, e.g., herds, social groups, or collectives, is of fundamental importance. Life can reach levels of higher complexity through the emergence of systems in which many individuals interact and cooperate. Within those systems individuals often behave contrary to their immediate metabolic interest by exhibiting behavior of altruism and even self-sacrifice. This contradicts the intuition that individuals of one biological species, being dependent on the same metabolic support from their environment, should be in competition over resources all the time. Selection of individuals for their ability to survive as independently of each other as possible is much easier to understand than cooperation. A theory of accumulations has to answer the question what motivates individuals to seek out each others company, before such phenomena like cooperation or altruism can be tackled.

One of the most fundamental types of accumulations are herds. Hamilton (1971) pointed out that accumulation of individuals are caused by an individuals selfishness as an attempt to increase its own survival probability when under threat of predation. Hamilton (1971) and also Barta *et al.* (1997) claim that living in a herd is advantageous, because of lower predation hazard and higher efficiency of foraging.

In this dissertation I develop an axiomatic theory, which I use to explain the emergence of the ability to accumulate in populations of originally solitary individuals. My approach is based on the assumption that those individuals are players in a game in which payoff is interpreted as metabolic energy. This is different from the approach of traditional evolutionary game theory where the genes are the players. Indeed genes, or any concept of relatedness, will not factor into my considerations at all. I am interested in discovering the roots of cooperative and altruistic behavior between conspecifics

without assuming any kinship theory.

The main objective of this chapter is to motivate the axioms which will be introduced in chapter 2. Since I am interested in the emergence of accumulations, I chose to base my considerations on a description of two biological species which exhibit accumulating behavior. The two species are the Plains Zebra, and the Red-Bellied Piranha. Given that piranhas are cannibalistic predators they differ significantly from the zebra. The accumulating behavior of piranhas is more complex. After discussing those two species I generalize my observations.

The fundamental concepts introduced in this chapter are the concepts of *(distributable or magnifyable) metabolic source, (distributable or magnifyable) metabolic sink, encounter between a set of individuals and a metabolic source or sink, focus between a set of individuals and a metabolic source or sink, reception of a metabolic source or sink by an individual.*

1.1. Two Examples

In this section I discuss two examples of biological species exhibiting herding behavior: the Plains Zebra and the Red-Bellied Piranha. The two examples will help us to understand which conditions contribute to accumulating behavior. First I will give descriptions of the species. Later I will extract from these descriptions the main conceptual points.

1.1.1. The Plains Zebra (Equus burchelli)

Description. The Plains Zebra can be found from southeastern Sudan to South Africa, in the Somali-Masai Arid Zone, Southern Savanna, and the South West Arid Zone.

The zebra is a nomadic herbivore, it is an exclusive grazer, grazing most of the time. A male weighs about 550 lb (250 kg), and is 51-56 in (127-140 cm) in height. A female weighs about 484 lb (220 kg), and is slightly shorter than the male. There is no sexual dimorphism. The life-span of a zebra can be 20 years.

Females reach maturity at about 3 years of age, remain with their families, and give birth to a 70 lb (31-33 kg) foal in intervals of 2 years. The gestation period lasts about one year. After birth the foal is able to stand within 15 minutes, and to suckle within an hour. The mother keeps other zebras (including her last offspring) away from the newborn until a stable maternal bond is established.

Colts leave their families voluntarily at 2-3 years of age to join a bachelor herd. They remain with the bachelor herd until they are mature, and ready to start a family on their own at about an age of 5.

If a filly is ovulating the first time, she starts to advertise her estrus very publicly. Up to 18 stallions will then gather around her family, fighting for her with each other and with her father. Once the filly is separated from her father's family by another stallion, she will stay after insemination with him, and will - not attracting her stallions rivals anymore - advertise subsequent estrus periods much more discreetly.

Zebras live in stable family groups, consisting of a stallion, 2-6 mares, and their foals. A family is guided by its oldest and most experienced mares, and it is watched from the rear by its stallion who monitors for predators and other disturbances. The stallions of different families can form close social ties with each other, exhibiting elaborate greeting and bonding behavior. The mares within a family can form alliances among each other as well. These alliances will last even if their stallion dies or is replaced by another. In their continued search for green pastures and water many families can merge forming herds of hundred thousand or more individuals, migrating peacefully together. Even in such large herds the original family groups remain intact.

Competition between the stallions however increases with the herd's, as they attempt to keep each other away from their respective mares. A herd might travel over 10 miles a day before settling for the night.

The zebra is active during daylight and spends nights resting. When zebras go to sleep, then at least one close to the group remains standing and alert. All zebras will therefore obtain sufficient sleep during the night.

The main predator of the Plains Zebra is the lion. The zebra is also often hunted by packs of spotted hyenas.

Discussion. Why do Plains Zebras form those incredibly large herds? When searching for food and water zebras are continuously in competition with each other over those resources. There is, however, some benefit to forming accumulations.

First, a lion close by can be discovered more likely if the number of individuals is larger. Second, even if a predator is not discovered before his attack, the probability of a given individual being attacked decreases as the size of the herd increases.

Third, the herd itself serves as a protection against a lion attack, even if that attack is already launched, and the lion was not discovered by then: Once the attack is launched the zebras can move around very quickly, and by taking advantage of their very similar appearance make the lion loose focus of the individual it was about to attack.

There is a certain sequence of events which result in a lion killing a zebra. First the lion needs to *encounter* (i.e., to discover) the zebra herd. Second, the lion has to *focus* on a single zebra (i.e., overcome the confusion effect of the herd and choose the zebra to be attacked). Third the lion has to *kill* the zebra (i.e., the lion has to match his performance to hunt down the zebra with the zebras' performance to escape. This match happens without the rest of the herd being involved). A solitary zebra does neither

benefit from the confusion effect of a herd nor does it provide any choice to the lion on whom to focus. A solitary zebra is therefore more likely to be killed on encounter with a lion than a herd-dwelling one.

Three concepts can therefore be introduced. The *encounter* between the lion and individuals, the *focus* between the lion and one or more individuals, and eventually the *reception* of the lion by one or more individuals.

The lack of sexual dimorphism in zebras can be interpreted as an adaptation to a herding life which supports confusion of predator attacks. The stallions and the mares have very different roles to play. A larger stallion would have an advantage over other males when competing with them over females. However, males and females are in about the same weight class and height range. That this does not necessarily has to be the case in all species can be seen in the lion species, which exhibits extreme sexual dimorphism. The zebra shares with the lion not only the same environment, but also has a very similar life history (the males in both species leave their birth families as adolescents, and forming their own families by intruding already established ones; the females stay with their birth families). Male lions significantly outweigh females, and they feature a thick layer of protective hair around their heads and throats. If a male zebra were significantly larger than its peers then his protection by the group would decrease. Lions would single him out immediately and the confusion effect of the herd would not apply to him. The absence of sexual dimorphism among zebras is an indication that the protective function of the herd agains predators has high significance.

The lack of sexual dimorphism is only one trait of the zebra which can be interpreted as an adaptation to a life as herd animal. Newborn zebras are very soon able to walk and run. Although they are smaller than adult zebras, their legs are comparably very long, lifting the rest of their body nearly as far away from the ground as in adult zebras. This makes it difficult for a predator to gain and keep focus on a zebra child.

Again, compare the length of the legs of a lion cup with the length of the legs of a zebra foal.

The zebra is therefore highly adapted for living in a herd. It is able to take advantage of the spatial proximity to conspecifics to increase the probability of surviving a predator attack by (1) *distributing* the risk and, (2) *diluting* the predators focus. Confusion is an ability of the herd which can be improved by selection and mutation. That will happen once individuals are subjected to a selective regime which supports distributing risks by spatial proximity.

Risk means that an individual might loose part or all of its accumulated metabolic payoff during a predator attack. This possible loss of accumulated metabolic payoff associated with, e.g., a lion motivates to call the lion a *metabolic sink* with regard to the zebra. In general it is expected that individuals will form accumulations, i.e., they will show a degradation in spatial competitiveness, once they are subjected to a metabolic sink, whose effect can be distributed among individuals who are spatially close. I call those metabolic sinks *distributable*. A metabolic sink which is not distributable is an earth quake. Whether a certain zebra suffers damage during an earth quake or not is not affected by the number of zebras in the herd.

The concept of metabolic sinks implies the concept of *metabolic sources*. Instead of decreasing the metabolic level of an individual metabolic sources increase that level. A metabolic source for zebras is the grass they are feeding on. Grass is distributed evenly over the ground. Once a zebra takes a bite, i.e., claims some grass for itself, no other zebra can acquire that bite. Some slight competition for grass is expected, especially when grass is sparse. Competition would, however, be more intense if the grass was distributed in chunks that cannot be swallowed at once. When grass is sparse then it is a *distributable metabolic source*. If grass is abundant then it is a *not distributable metabolic source*. Migration of the zebra herd can be interpreted as a

strategy to keep the metabolic source 'grass' not distributable. This keeps competition low and stabilizes the herd. Another metabolic source is the oxygen the zebras are breathing. This is an example for a *not distributable metabolic source*,

Already at this stage I can therefore state a serious conjecture:

The formation of accumulations of individuals is promoted under a selective regime which features distributable metabolic sinks, and not-distributable metabolic sources.

In the next section I will talk about the Red-Bellied Piranha, a predatory fish, in order to elaborate somewhat more on the ideas of metabolic sources and sinks, and the concepts of distributibility, encounter and reception.

1.1.2.   The Red-Bellied Piranha (Pygocentrus nattereri)

Description. The Red-Bellied Piranha is an exclusive freshwater fish (23 - 27^{0}C), which can be found in the rivers of Central and South America, east of the Andes, from Venezuela south to Rio de La Plata, and the coastal rivers of Guianas and Brazil.

The Red-Bellied Piranha has a stocky silver-green body with a reddish belly. Piranhas have a great sense of smell. The deep head has short and powerful jaws bearing razor sharp teeth. The teeth of the upper and lower jaw interlock with each other just like those of a bear trap. The Red-Bellied Piranha is an opportunistic carnivore, which is itself subject to predation mainly by crocodiles and caimans. The bite of a piranha will inflict gaping wounds, and its bite is specialized in taking mouth sized chunks out of its prey instantaneously, letting the piranha escape as fast as it

attacked. Its main diet consists of insects, worms and fish, and the primary times of activity are at dusk and dawn. Individuals are relatively small, usually weighing below 3 pounds, and the average adult length is between 6 - 9 in (15 - 23 cm).

The Red-Bellied Piranha is an ambush predator. It is classified as dangerous to humans, and accumulates to hierarchical schools, which are characterized by piranhas of similar size swimming besides each other, and larger specimens following in at least one body length distance the smaller ones. Piranhas swim besides each other all facing in the same direction, avoiding all unnecessary movement, which could lead to mutual attacks.

The piranha is extremely shy and very easy to agitate. Movement in the water - even rapid movements of a conspecific - will cause a school of piranhas to home in on the source of the movement and engage in a biting frenzy which can also seriously injure members of the school, and even get them killed and eaten. This way several hundred piranhas can be attracted to a single source of movement. It is also known that blood in the water will cause piranhas to engage in a biting frenzy.

Piranhas will cannibalize each other, either if provoked or if hungry. An adult piranha has usually been bitten by its conspecifics many times. I should note that piranhas have an astonishing ability to heal fast and recover quickly even from serious injuries. This fast-healing ability might be seen as an adaptation to living in groups of cannibalistic conspecifics.

Discussion. Why do Red-Bellied Piranhas form schools? They are not only in competition with each other over common food resources, but they are also cannibalistic and highly aggressive predators. Like the zebra, however, they are themselves under predation, by crocodiles and caimans. A crocodile or a caiman attacking a single piranha will have no problems doing so. However if the predator

attacks a school of piranhas it will very likely find itself under attack a moment later.

Hence the effect of piranha schools is not restricted to the distribution of danger and the confusion of a predator's focus. A school of piranhas can effectively attack a predator, something a single piranha cannot do. A predator encountering a large enough school of piranhas might choose not to attack. In zebras, the larger the herd the higher the exposure of the herd to predator. In piranhas formation of schools has the opposite effect. Piranhas, by forming schools, reduce the *exposure* (i.e., the probability of encounter) of their schools to predators. The larger the school, the more dangerous it is for an encountering predator to launch an attack, and the more likely the predator will pass on that "opportunity". Hence the exposure of larger schools is lower than that of smaller schools, and together with confusion and distribution a single piranha is very safe within a school of even moderate size.

Defense against predators is not the only benefit the piranha gets from forming schools. Assume that a large animal - a cow for example - gets into the water, and meets a single solitary piranha. Attracted by her movement the piranha will now attack the cow, and take a bite. The cow of course will immediately escape in panic and pain, and the piranha is left with only one bite out of a very big potential meal. The situation looks very different if the cow meets a group of, say, 100 piranhas. They will attack the cow from all sides, and each of them will very likely obtain many nutritional bites. Using my conceptual framework I can say that the exposure of the single piranha to certain sources of food (e.g. cows) will increase due to schooling. Again, this is a different picture than that presented by the zebra who is always in slight competition with its conspecifics over areas of grass.

In contrast to herds of zebras schools of piranhas accomplish therefore two things: they *decrease individual exposure to some metabolic sinks*, and they *increase individual exposure to some metabolic sources.*

The same mechanism that enable the piranha to lower exposure by forming schools (i.e.,their teeth and aggressive behavior in response to a movement) result, however, in complications in their relations towards each other within a school. In contrast to zebras a simple degradation of competitiveness is not sufficient to let piranha schools emerge. Piranhas behavior towards each other when moving through the water can be called "ritualized": The school travels in layers consisting of equally sized fish, swimming besides each other in a very stiff, nearly ritualistic, fashion. Every sudden movement can trigger a biting frenzy, so the piranha is always wary of its own movements, and of the movements of its neighbors. This is a very energy consuming behavior. Nevertheless the schools are very stable formations.

How did piranha schooling originally evolve? Originally a solitary ambush predator, the ancestor of the piranha, was probably escaping from sources of stronger movement in the water, while attacking sources of weaker movement interpreting them as possible prey. Under predation by crocodiles and caimans a selective regime was established supporting degradation of spatial competitiveness. At this stage the piranha-crocodile relationship looked very similar to the lion-zebra relationship today. The problem with the evolving group life was that the piranha was dependent on sensing weak movements of possible prey. Thus very early on there must have been selection for coordinated movement in schools, in order to not disturb the foraging of its members. Once a movement of a possible prey individual was sensed, the piranhas who sensed it approached it simultaneously trying to outcompete each other. In addition to that the threat associated with larger movements could now, at least partially, be ignored by a single piranha because of the confusion and distribution effect of its school. These two reasons could have led to the emergence of piranhas who would approach larger than the traditional prey. Given the power of the school such approaches would be very successful. Eventually any movement in the water triggered a homing in on the source

and a biting frenzy. In competing with each other to be the first one to bite, piranhas formed a united front even against their natural predators, who now became their prey.

1.1.3.   Conclusion

From the discussion of the Plains Zebra and the Red-Bellied Piranha I have derived the concepts of a *metabolic sink* and a *metabolic source* as two essential components in a metabolic game. Individuals are *exposed* to metabolic sources and sinks. That means that there is a certain probability of an *encounter*, where *encounter* means, that at least one - namely the individual or the metabolic source or sink - becomes aware of the other. We have also seen that the concepts of *exposure* and *encounter* do not apply only to single individuals but also to accumulations.

An encounter between e.g. a predator (lion/crocodile) and its prey (zebra/piranha) can happen in different ways. If the prey is solitary, then the predator will encounter this prey individual only. If the prey lives in accumulations, the predator will encounter (i.e., discover) the accumulation first, and then possibly focus on a single prey individual. Therefore, an encounter can happen to a single individual and it can happen to many individuals simultaneously. If the encounter happens to many individuals simultaneously, then some the encountered individuals might then be subject to an interaction with the predator that might change their metabolic level. It is essential to note, that a metabolic source or sink encountering a set of individuals does not imply that at least one of those individuals is being focussed on. When a predator encounters a single individual he might be satiated, so that he does not focus on the prey. Or a predator might have discovered an accumulation, however might not have focussed on a specific individual yet. Even if focus on a single individual has already occurred then confusion effects due to the movement of prey individuals and their similarity to each

other might cause the predator to loose focus, and he might be forced to abort the attack. Given an accumulation of prey individuals a predator does not only *encounter* the accumulation before being able to encounter an individual, it also *interacts* with the accumulation before *focussing* on an individual.

Once a focus between an individual and a metabolic source or sink took place, there is - after a period of interaction - a probability that a metabolic change will occur due to that metabolic source or sink. The event of such a change occurring was called *reception of the encounterer by the individual.*

In conclusion I have introduced six new concepts that will help us define games with metabolic individuals: *metabolic source*, *metabolic sink*, *exposure*, *encounter*, *focus* and *receptance*.

Causes of external metabolic loss to an individual are not only due to receptions of metabolic sinks. For example, a disease within a species which serves as food can reduce the population size of that species. That disease can therefore be considered a *reducer of metabolic payoff* for individuals of species living of that food species. Any metabolic sink is a reducer of metabolic payoff, however not vice versa. Another example for a reducer of metabolic payoff is a food competitor, especially a conspecific. Encounter with a competitor will not necessarily lead to a metabolic loss, but its presence will over time probably result in lowering the encounter probability with food. In my theory I will not explicitly introduce reducers of metabolic payoffs.

1.2. Theory behind the Examples

Metabolic individuals. The discussion of the accumulation behavior of the Plains Zebra and the Red-Bellied Piranha showed the importance of the presence of *metabolic sources* and *metabolic sinks*. They are important because the zebra as well as the

piranha are *metabolic individuals*, meaning that at any given time they possess a *metabolism.* A metabolism is given at any time by a *metabolic level*, a *basic metabolic decay rule* which strictly decreases the metabolic level over time, and possibly other metabolic decay rules associated with the strategies of the individual. Fast movement, for example, might cause an additional decrease of the metabolic level besides the one caused by the basic metabolic decay rule. A metabolic individual is a player in the game theoretical sense with *metabolic energy* as the currency of payoff. Its metabolic level at a certain time point is the payoff it accumulated from the time of entering the game until that time point.

Once its metabolic level falls below a certain level, an individual will "die", which means that it will be removed as a player from the game. It might still remain in the game in form of a metabolic sink or source. In order to keep a given population of individuals from extinction I assume that some mechanism of replacement of dead individuals by new individuals is in place. This mechanism will maintain the population above a certain minimum - and maybe below a certain maximum size.

Further the concept of *encounter* is relevant. An encounter between a set of individuals and a metabolic source or sink has happened if either some of the individuals or the metabolic source or sink or both became aware of the other. After the encounter follows a period of orientation during which either a *focus* is established or not between the individuals and the metabolic source or sink. Once a focus is established a period of interaction follows, after which some or all individuals in focus receive a change of metabolic energy associated with the metabolic source or sink. This final event of change of metabolic energy is called *reception.*

The probability of encounter is called *exposure.* The probability of a focus event happening between an individual and a metabolic source or sink given that an encounter already happend is called *acceptance.* The probability of reception given that the

encounter and focus has already happened is called *receptance*. This allows us to

calculate the probability of change of metabolic energy for a given individual.

From the previously stated ideas we can derive a sketch of the nature of the

relations between a set of individuals, and a metabolic source or sink. Figure 1.1

illustrates this. The figure includes notation that will formally be introduced in chapter

2.

Prospect of metabolic change in individual α
given metabolic source or sink Γ through set S

$$\pi_{\alpha,H,S}^{\Gamma} = \hat{\eta}_S^{\Gamma} \cdot \hat{\varphi}_H^{\Gamma} \cdot \rho_{\alpha}^{\Gamma}, \alpha \in H$$

Acceptance
(Probability of
focus between at least α
and Γ given encounter)

Receptance
(Probability of metabolic
change of α by Γ
given focus)

Reception
(Change in
metabolic
level)

$\hat{\varphi}_H^{\Gamma}$

$\hat{\eta}_S^{\Gamma}$

Encounter

Focus
$\alpha \in H$

ρ_{α}^{Γ}

$1 - \rho_{\alpha}^{\Gamma}$

Probability of
avoiding focus
between α and Γ
given encounter

$1 - \hat{\varphi}_H^{\Gamma}$

Escapability
(Probability of avoiding
metabolic change given
focus)

Escape
(No change in
metabolic level)

Figure 1.1.: Relation of a metabolic individual to a metabolic source or sink through a set.

Distributable metabolic sources and sinks. There is an incentive for a set of

individuals to accumulate under a given metabolic sink, if for each individual of that set

the prospect of a metabolic change due to reception of the metabolic sink decreases as

the accumulation size increases. I call a metabolic source or sink under which

individuals experience decreasing probability of metabolic change with increasing size of accumulation *distributable.* A distributable metabolic sink furthers accumulation, while a distributable metabolic source hinders it. For example, if attacked by a small school of piranha a cow will be able to escape after having received one or a few bites, while the expected number of bites a piranha can apply will decrease with increasing school size. Hence the cow will be a distributable metabolic source for a certain range of small school sizes of piranhas. However if the school size increases sufficiently, then the cow will be less likely to escape. At some size of the school the cow will not be able to escape at all. Beyond a certain school size the expected payoff for a piranha when attacking a cow will therefore increase up to a level when the cow is, with certainty, brought down by the school. Above that school size the expected payoff will remain constant for a certain range, and will afterwards keep on declining. Figure 1.2 illustrates this, and also introduces the concept of a *magnifyable metabolic sink or source.* A metabolic source or sink is called *magnifyable*, if individuals of an accumulation under that metabolic source or sink experience constant or increasing prospect of metabolic change with increasing size of accumulation. 'Magnifyable' and 'Distributable' are therefore opposite concepts. Individuals will have an incentive to accumulate under a magnifyable metabolic source and under a distributable metabolic sink. They will tend to disperse under a distributable metabolic source, and under a magnifyable metabolic sink. Figure 1.2 also illustrates that a solitary piranha should join a school of piranhas as long as the resulting accumulation will have a size resulting in an individual expected payoff above the solitary payoff. If that condition is satisfied a joining solitary piranha will always benefit by joining, however benefiting the individuals of the remainder of the accumulation only as long as the accumulation size is one short of reaching the exploitation limit. This also shows that small schools when they encounter each other can increase individual expected payoff by forming one

larger school.
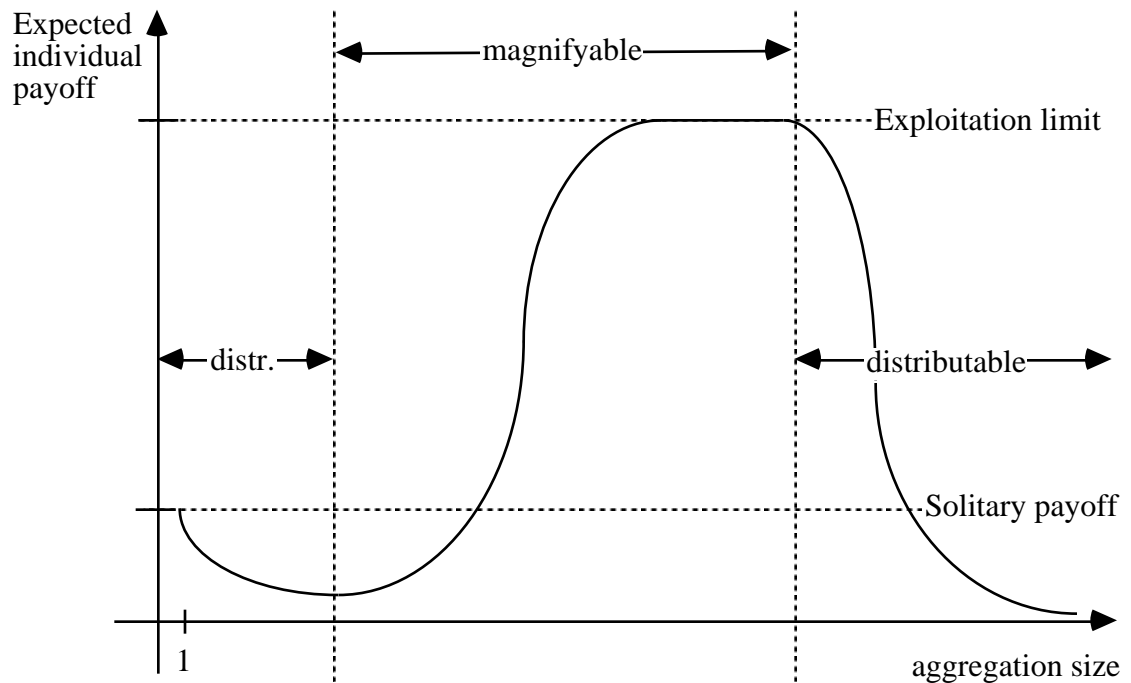
Figure 1.2.: A cow as metabolic source for piranhas.
        The cow is a distributable metabolic source for small and very large
        school sizes, and is a magnifyable metabolic source for intermediate
        ones.

     Since I assume individuals to be highly competitive towards each other with
regard to metabolic sources, metabolic sources are assumed to be not magnifyable under
at least small accumulations. We further assume metabolic sources and sinks to be
spatially distributed, locally limited in number (only a finite number of metabolic
sources or sinks can be encountered by a given individual at any time point), and
providing only a finite metabolic change over a finite time. We further assume that
fundamental metabolic sources that are essential for the individuals make their
metabolic support immediately available to the individual on encounter. Then the
competition for encountering metabolic sources will result in competition for space.

Conspecifics can then be interpreted as metabolic sinks and hence the individuals will all be solitary. Given this setup we attempt to find reasons for populations of those individuals to acquire the ability to form spatial accumulations, that means to degrade their original spatial competitiveness. We can see from our previous discussion, that this may happen, if they are exposed to an environment featuring the presence of distributable metabolic sinks.

Accumulation is initiated by enabling the degradation of spatial competitiveness. We assume that individuals are originally highly competitive with regard to metabolic sources. The competitive traits of the individuals are also assumed to be highly evolved, i.e. optimized. Those traits are mainly the abilities to find metabolic sources fast, to acquire access to metabolic sources fast on encounter, and to defend that access effectively once acquired. Oxygen is a metabolic source for zebras, as is the grass. There is, however, no competition among zebras for oxygen. Oxygen is available to everyone at any time everywhere in sufficient quantities. There can be, however, some competition for grass, if grass patches are sparse. The oxygen in the air is a non-distributable, magnifyable metabolic source, grass is a distributable, non-magnifyable metabolic source. Here we are only concerned with distributable metabolic sources. If an individual experiences an encounter with such a metabolic source, then this encounter has to be with sufficiently high probability only with that individual, in order for that individual to acquire access to the metabolic source effectively. This means however, that in terms of the space the individuals share with each other, the distance between individuals has to be large enough to make such encounter possible. Assuming high competitiveness with regard to metabolic sources implies therefore, that the selective regime is *solitary.* In other words, that solitary individuals have the highest fitness. Those individuals will, by competing over access to distributable metabolic

sources, be competitive with regard to the space they share: There will be minimum distance those individuals will attempt to keep from each other. For an individual the presence of a conspecific will be therefore regarded as a non-distributable, magnifyable metabolic sink, comparable to an earth-quake, a fire or a flood. A formation of accumulations can only be initiated, if the selective regime changes such that spatial and metabolic competitiveness can degrade. This is, however, only possible if closeness between individuals bears some metabolic benefit for those individuals. Introducing distributable metabolic sinks can get this accomplished. Degradation of competitiveness can then happen as a result of a learning process within a single individual, or as a result of an evolutionary process featuring mutation and heritability - assuming the presence of some kind of genetics. Both approaches will eventually lead to the same results. We will focus on the population genetical approach. While there are many models of learning, there is only one model of population genetics, based on the concepts of mutation, selection, and heritability. We need to point out here again, that kinship theory - which claims that individuals support each other according to their relatedness - will not enter the picture at all. Mother-child relationships are, for example, ignored. The only purpose of the reproductive process is to keep the population from going extinct, reproducing with higher probability those individuals which were more successful. We assume, that reproduction - the mechanism which replaces dead individuals -, is, as in real life, used to introduce quantitative variation into the individuals' traits: a given trait can be more or less expressed, but new traits will not emerge. Whether we assume learning or evolution will have no consequences on the results. The only assumption is that ambivalence towards closeness of conspecifics, followed by accumulation and eventually cooperation, has its roots in the degradation of spatially competitive behavior, which is assumed to be the only original force.

Accumulation can remove an individual from the original solitary selective regime.
The distinction between encounter and reception results in two possibilities to change
the overall probability of metabolic change of an individual via a metabolic source or
sink: To change the probability of encounter, or to change the probability of reception.
The later option means a change in the very ability of the individual to interact with the
metabolic source or sink. It means in case of a metabolic sink given by a predator e.g.
the evolution of defense and/or escape features in a prey species in response to the
predatory selective regime it is subjected to. The species will respond to selection
pressure by adaptation to the selective regime. In case of change of encounter
probability this is not the case. Prey species might evolve ways such that its individuals
avoid their predators altogether. This will not require a change in its ability to interact
with the predator. By avoiding reception completely or at least reducing the probability
of its occurrence, the prey species is completely or partially removed from its original
selective regime. We saw already that the formation of accumulations can get this
accomplished. In summary, we can say that a change in exposure towards a metabolic
source or sink changes the extend to which the individual is subjected to the selective
regime, and a change in receptance of a metabolic source or sink indicates that the
adaptation of the individual to the selective regime has changed.

**Elimination of space and time as the ideal state for the individuals of any biological
species.** Interactions between individuals and metabolic sources and sinks are assumed
to happen within a given space, within which the individual and the metabolic sources
and sinks can change their relations towards each other. A process by which the
individual uses exclusively spatial properties in order to change its relation towards
other individuals and/or metabolic sources or sinks is called *movement.* A metabolic
individuals ability to die, its ability to move and its subjection to an existential

metabolic decay rule can impose a selection regime favoring the presence of individuals who apply strategies which increase their probability of metabolic change due to metabolic sources, and lower their probability of metabolic change due to metabolic sinks. Those strategies are sequences of movements, and changing the probability of metabolic change due to a metabolic source or sink means that the individual will change its distance to that metabolic source or sink in terms of the given space. We can, therefore, interpret the prospect of metabolic change of an individual with regard to a metabolic source or sink as a *distance* between the individual and the metabolic source or sink. Indeed, in our approach the concept of space makes only sense in terms of exposure and receptance. The space with the distance function 'prospect of metabolic change' is certainly not metric in the mathematical sense. This however, is not necessary. If the prospect of metabolic change of an individual with regard to a given metabolic source or sink is either 0 or 1, then space between the individual and that metabolic source or sink can be regarded as eliminated: When the prospect is 0, the metabolic source or sink is "infinitely far away", when the prospect is 1, the metabolic source or sink is immediately accessible to the individual. An individual has reached an ideal state, if it has established permanently a prospect of metabolic change of 1 with regard to some metabolic source whose support does sustain its metabolic level above minimum, and if it has established permanently a prospect of metabolic change of 0 with all metabolic sinks. That means the ideal state of an individual is to eliminate space between itself and at least one sustaining metabolic source, and to introduce infinite space between itself and all metabolic sinks. An essential consequence is, that once the individual has attained such an ideal state, all of its movement will cease. Movement was assumed to be only necessary to redefine relations with regard to metabolic sources or sinks. Such redefinition becomes unnecessary once an ideal state is reached. Once an ideal state is reached we can, therefore, conclude that space for the

individual ceases to exist. But so does time. Time has for the individual only relevance by the existential metabolic decay rule (and other decay rules due to certain movement strategies). In an ideal state however the existential metabolic decay is compensated for by the immediate contact with the sustaining metabolic source. Therefore, the following can be stated: *A metabolic individual has reached an ideal state once it has completely eliminated its subjective time and space.* Thus the evolution of a species will be considered as having reached an apex, if by mutation and selection the individuals of that species became removed from time and space. The "purpose" of evolution is, therefore, the elimination of the biological relevance of time and space.

What I have introduced here is a subjective - or individualistic - notion of space. Movement of an individual, put in terms of changes in prospect of metabolic change, can be seen as the individual transforming its space and - taking modification in speed of movement into account - its time. The individual can be interpreted as a space-time transformer, who thrives to eliminate space and time.

Chapter 2.   Axioms

      The following axioms are motivated by the discussion in chapter 1. Additional

discussion is added below the axioms in brackets [...]. I will use the interaction between

zebras and lion as an example to motivate the axioms. It is the most simple system and

thought experiments can be done with it very easily. Generalization to piranhas or other

species is straightforward. In later chapters further axioms will be added as necessary.

The system of axioms given here is further on referred to as the "Fundamental System

of Axioms", and is abbreviated by 'FundAx'. All axioms used in this thesis are listed

without additional comments in appendix 1.

2.1.   Fundamental Axiomatic System (FundAx)

      The fundamental axiomatic system is given by the following eight axioms:

A)   **Existential Axiom:**

      FundAx 1:

      There exist the following three types of objects: individuals,

      metabolic sources, and metabolic sinks.

      [Biological individuals are dependent on metabolic energy in order to

      stay alive and functioning. They obtain this metabolic energy from

      realizations of metabolic sources. For example, the species 'zebra' is

      a metabolic source for each individual lion. An individual zebra is a

      realization of that metabolic source. The species 'lion', on the other

hand, is a metabolic sink for each individual zebra. An individual lion is a realization of that metabolic sink. A metabolic sink for an individual has the potential to lower the amount of metabolic energy available to that individual.]

B) Relational Axioms:

Let $\mathscr{I}$ be the finite set of all individuals. Let Γ be a metabolic source or sink with regard to each individual of the set $\mathscr{I}$.

FundAx 2 (Existence of encounter events):

Let $S \subseteq \mathscr{I}$ and $S \neq \varnothing$. There is a non empty set E_S^Γ of events called *encounter between S and* Γ.

Formally: $\forall S \subseteq \mathscr{I} : S \neq \varnothing \Leftrightarrow E_S^\Gamma \neq \varnothing$

[An encounter is meant to be the first contact between a set of individuals S and the metabolic source or sink Γ via a realization of Γ]

FundAx 3 (Superset closure of encounter events):

Let $S, W \subseteq \mathscr{I}$ and $S, W \neq \varnothing$. Then: $S \subset W \Rightarrow E_S^\Gamma \subset E_W^\Gamma$.

[Any encounter in E_S^Γ is also an encounter in E_W^Γ for all $W \supset S$. An encounter between a set of individuals and a metabolic source or sink is also an encounter between any superset of individuals and this metabolic source or sink. For example, an encounter between five

zebras of a herd and a lion is also an encounter between any part of the herd containing those five zebras, including the entire herd, and the lion. It is not, however, an encounter between a part of the herd which does not contain all five zebras and the lion (This statement follows from FundAx 2 and FundAx3 and will be proven in section 1.4). I should also note that the five zebras being encountered does not imply that each single one of those five is encountered. What this axiom does, however, imply is that for each encounter there is a smallest set of individuals encountered. In Lemma 2 in section 1.4, Theorem 1, it will be shown that this smallest set exists, is unique and not empty. This set is called the 'set of total encounter'.]

FundAx 4 (Existence of focus events):

Let $S \subseteq \mathscr{T}$, and $S \neq \varnothing$. There is a set Φ_S^Γ of events called *focus between S and Γ*. Formally: $\forall S \subseteq \mathscr{T} : \Phi_S^\Gamma \neq \varnothing$

[An encounter exposes a set of individuals and a metabolic source or sink to each other. A focus is a 'homing in' between certain individuals and the metabolic source or sink. During an encounter between a herd of zebras and a lion the lion might not be aware of any of the individual zebras. The lion is facing a 'cloud' of zebras. In order to hunt one of the zebras down the lion needs to 'focus' on one of them. He needs to overcome the confusion and dilution created by the herd, or at least make a choice which zebra to capture. In general, it cannot be assumed that a focus will be established merely between one individual and the metabolic source and sink. Usually

there is a focus between, for instance, many piranhas and one cow (cow being the metabolic source). Another example is the saw fish. A predator preying on schooling fish kills many individuals during a successful attack.

It is essential to distinguish between an encounter and a focus. An encounter concerns a set of individuals, e.g. a zebra herd, and a representation of a metabolic source or sink, e.g. a lion. Once encountered the herd can dilute the predator's attempt to gain focus. This ability to dilute is a property of the herd, not a property of a single zebra. If the herd is successful in diluting the predator's attack, no single zebra is forced to face the lion. However, a zebra will be forced to face the attack once there is a focus event between this zebra and the lion. Once a focus event happened it is entirely up to the abilities of the zebra and the lion whether a capture will happen or not. In order to obtain a survival probability, which is in this setup identical to fitness, one can therefore adjust two parameters: the ability of the herd to dilute predator attacks, or the individual ability of the zebra to escape.

Confusion and dilution can also be present in the encounter between individuals and a metabolic source. Confusion results from "competition" for focus. If a lion encounters a herd of zebras the confusion effect due to the sameness of the individuals can be interpreted as the individual zebras competing for the focus of the lion, and in doing so blocking the lion from focusing. Similarly, two individuals encountering one fooditem might fight over that item. This lowers the probability of focus between that item and each of

those individuals. This lowering of probability of focus is confusion.]

FundAx 5 (Subset Closure of focus events):

Let $S, W \subseteq \mathscr{T}$, and $S, W \neq \varnothing$. Then, $S \subset W \Rightarrow \Phi_S^\Gamma \supset \Phi_W^\Gamma$.

[If $S \subset W$ then any focus in Φ_W^Γ is also a focus in Φ_S^Γ. An event

$f \in \Phi_w^\Gamma$ is, therefore, a focus between any subset of W and Γ.

Therefore, a specific $f \in \Phi_S^\Gamma$ is not necessarily a focus exclusively

between individuals in S and Γ. What can be said, however, is that

it is a focus between *at least* the individuals in S and Γ. If $\alpha \in \mathscr{T}$

then $\Phi_{\{\alpha\}}^\Gamma$ is the set of focus events between at least α and Γ. The

largest set of focus events containing all Φ_S^Γ is $\Phi_\varnothing^\Gamma$.

Any focus between zebras and a lion will only concern exactly

one zebra. Therefore the zebra-lion system does not serve as a good

example here. The cow-piranha example is better: Each piranha is

attracted by the cow, and so are all the subsets of the overall set of

attracted piranha. If one is given a set of attracted piranha (as the cow

is at any time point of the attack) one cannot definitely claim that

there are no more piranhas attracted. Attraction is here equivalent to

focus.

Analogous to the set of total encounter for each encounter event

there is a 'set of total focus' for each focus event. This is the largest

set of individuals involved in the focus event. Existence and

uniqueness of the non-empty set of total focus for each focus event is

proven in section 1.4, Theorem 2.]

FundAx 6 (Existence of reception events):

Let $S \neq \varnothing$. There exists a set P_S^{Γ} of events called *reception of* Γ *by*

S. Formally: $\forall S \subseteq \mathscr{T} : S \neq \varnothing \Leftrightarrow \Phi_S^{\Gamma} \neq \varnothing$

[A reception event is an event by which an individual experiences a
change in its metabolic level due to a metabolic source or sink. A
zebra captured by a lion looses all its metabolic energy. The capture
itself is the reception of the lion by the zebra. The devouring of a
cow by a school of piranha is a reception of the cow by the piranhas.

Between an encounter and the successive focus event there is
interaction between the encountered set of individuals and the
realization of the metabolic source or sink. Once a focus event
happens the probability of whether there is a reception of the
metabolic source or sink by the individuals is determined by the
individuals themselves. Once a focus event happens all individuals in
the set associated with the focus are exposed to the metabolic source
or sink independently of all the other individuals. Their probability
of experiencing metabolic change is only affected by how many other
individuals share the same focus event, and the performance of the
metabolic source or sink.]

FundAx 7 (Subset closure of reception events):

Let $S, W \subseteq \mathscr{T}$, and $S, W \neq \varnothing$. Then, $S \subset W \Rightarrow P_S^{\Gamma} \supset P_W^{\Gamma}$.

[If $S \subset W$ then any reception in P_W^{Γ} is also a reception in P_S^{Γ}. An
event $r \in P_w^{\Gamma}$ is, therefore, a reception between any subset of W and

Γ. Therefore, a specific $r \in \mathrm{P}_S^\Gamma$ is not necessarily a reception exclusively between individuals in S and Γ. What can be said, however, is that it is a reception between *at least* the individuals in S and Γ. If $\alpha \in \mathscr{T}$ then $\mathrm{P}_{\{\alpha\}}^\Gamma$ is the set of reception events between at least α and Γ.

Focus events and reception events have the same axiomatic structure. The same set theoretical ideas apply to focus and reception events.]

FundAx 8 (Existence of a resignation event):

There exists an event $\omega_{\mathscr{T}}^\Gamma$ called the *resignation between $\mathscr{T}$ and Γ*.

[Not every encounter between a zebra herd and a lion will result in the lion capturing a zebra. More often the lion will abort the hunt. Reasons for resignation are confusion or being outperformed after focus by the zebra. Resignation means that the current attack is terminated.]

In the following section I derive some lemmas and theorems implied by the axioms.

2.2. Ramifications

The first three lemmas in this section explore the concept of 'encounter'. Very essential is the concept of the 'set of total encounter' which will allow the definition of the central concept of 'accumulation' in the next chapter.

First, I generalize FundAx 3 in Lemma 1. Lemma 1 and Lemma 2 will be used to

proof Lemma 3, which is essential for understanding the concept of encounter. Lemma 1 and Lemma 2 are then used to proof the existence and uniqueness theorem of the set of total encounter.

To proof those statements we need FundAx 1-3.

Lemma 1: Let $S, W \subseteq \mathcal{I}$ and $S, W \neq \varnothing$. Then, $S \subset W \Leftrightarrow \mathrm{E}_S^\Gamma \subset \mathrm{E}_W^\Gamma$.

Proof: FundAx 3 states that $S \subset W \Rightarrow \mathrm{E}_S^\Gamma \subset \mathrm{E}_W^\Gamma$, which implies that

$$S \subseteq W \Rightarrow \mathrm{E}_S^\Gamma \subseteq \mathrm{E}_W^\Gamma \tag{1}$$

It remains to be shown that $\mathrm{E}_S^\Gamma \subset \mathrm{E}_W^\Gamma \Rightarrow S \subset W$.

Let $\mathrm{E}_S^\Gamma \subset \mathrm{E}_W^\Gamma$. Assume $S \supseteq W$. Then, by FundAx 3 and equation 1, $\mathrm{E}_S^\Gamma \supseteq \mathrm{E}_W^\Gamma$. This contradicts the condition $\mathrm{E}_S^\Gamma \subset \mathrm{E}_W^\Gamma$. Therefore $S \supseteq W$ is false, thus

$\mathrm{E}_S^\Gamma \subset \mathrm{E}_W^\Gamma \Rightarrow S \subset W$. ❑

Lemma 2: Let $S, W \subseteq \mathcal{I}$. Then, $\mathrm{E}_{W \cap S}^\Gamma = \mathrm{E}_W^\Gamma \cap \mathrm{E}_S^\Gamma$.

Proof: In order to prove the Lemma I will show that $\mathrm{E}_{W \cap S}^\Gamma \subseteq \mathrm{E}_W^\Gamma \cap \mathrm{E}_S^\Gamma$ and $\mathrm{E}_{W \cap S}^\Gamma \supseteq \mathrm{E}_W^\Gamma \cap \mathrm{E}_S^\Gamma$ are both true.

(1)   Show that $\mathrm{E}_{W \cap S}^\Gamma \subseteq \mathrm{E}_W^\Gamma \cap \mathrm{E}_S^\Gamma$.

By FundAx 3 $\mathrm{E}_{W \cap S}^\Gamma \subseteq \mathrm{E}_W^\Gamma$ and $\mathrm{E}_{W \cap S}^\Gamma \subseteq \mathrm{E}_S^\Gamma$, since $W \cap S \subseteq W$ and $W \cap S \subseteq S$.

Therefore: $\mathrm{E}_{W \cap S}^\Gamma \subseteq \mathrm{E}_W^\Gamma \cap \mathrm{E}_S^\Gamma$. ❑

(2)   Show that $\mathrm{E}_{W \cap S}^\Gamma \supseteq \mathrm{E}_W^\Gamma \cap \mathrm{E}_S^\Gamma$.

There are two cases: $W \cap S = \varnothing$ and $W \cap S \neq \varnothing$.

(a)   Let $W \cap S = \varnothing$. Assume $\mathrm{E}_W^\Gamma \cap \mathrm{E}_S^\Gamma \neq \varnothing$. Let $e \in \mathrm{E}_W^\Gamma \cap \mathrm{E}_S^\Gamma$. It follows by FundAx 2, that $\exists J \subseteq \mathcal{I}, J \neq \varnothing : \{e\} = \mathrm{E}_J^\Gamma$. Clearly $\mathrm{E}_J^\Gamma \subseteq \mathrm{E}_W^\Gamma \cap \mathrm{E}_S^\Gamma$. It follows then by FundAx 3 that $J \subseteq W$ and $J \subseteq S$. Therefore $J \subseteq W \cap S$

and $J \neq \varnothing$. This contradicts the condition $W \cap S = \varnothing$. Therefore the assumption $E_W^\Gamma \cap E_S^\Gamma \neq \varnothing$ is false, thus $W \cap S = \varnothing \Rightarrow E_{W \cap S}^\Gamma \supseteq E_W^\Gamma \cap E_S^\Gamma$.

❑

(b)   Let $W \cap S \neq \varnothing$. Then by FundAx 2 $E_{W \cap S}^\Gamma \neq \varnothing$. By FundAx 3

$E_{W \cap S}^\Gamma \subseteq E_W^\Gamma$ and $E_{W \cap S}^\Gamma \subseteq E_S^\Gamma$. Therefore $E_W^\Gamma \cap E_S^\Gamma \neq \varnothing$. Let $e \in E_W^\Gamma \cap E_S^\Gamma$.

It follows by FundAx 2, that $\exists J \subseteq \mathscr{I}, J \neq \varnothing : \{e\} = E_J^\Gamma$. Clearly

$E_J^\Gamma \subseteq E_W^\Gamma \cap E_S^\Gamma$. Lemma 1 yields $J \subseteq W$ and $J \subseteq S$. Therefore

$J \subseteq W \cap S$. By FundAx 3 it follows that $E_J^\Gamma \subseteq E_{W \cap S}^\Gamma$. Since

$e \in E_W^\Gamma \cap E_S^\Gamma$ was arbitrarily chosen and $\{e\} = E_J^\Gamma$, it follows that

$E_W^\Gamma \cap E_S^\Gamma \subseteq E_{W \cap S}^\Gamma$, which is statement (2) of this Lemma.   ❑

This proves the Lemma.   ❑

Lemma 3: Let $S, W \subseteq \mathscr{I}$ and $S, W \neq \varnothing$. Then, $W \cap S = \varnothing \Leftrightarrow E_W^\Gamma \cap E_S^\Gamma = \varnothing$.

Proof: By FundAx 2 $W \cap S = \varnothing \Leftrightarrow E_{W \cap S}^\Gamma = \varnothing$. By Lemma 2 $E_{W \cap S}^\Gamma = E_W^\Gamma \cap E_S^\Gamma$.

This proves the Lemma.   ❑

Lemma 3 is an explicit statement of a comment made in the discussion of FundAx 3. If $W \cap S = \varnothing$ then any encounter in E_W^Γ is not an encounter in E_S^Γ. If there is an encounter between five zebras of a herd and a lion, then this is not an encounter between the lion and any set that does not contain all the five zebras. Consider, for example, two different herds of zebras. If there is an encounter between one of these herds and a lion, then this encounter is not an encounter between the other herd and the lion. On the other hand, if there is an encounter between one of the herds and the lion, then this encounter is also an encounter between both herds together and the lion.

The superset closure of encounter events stated by FundAx 3 implies that for each encounter there is a smallest set of individuals which is encountered. I call this smallest

set the 'set of total encounter'. The set of total encounter is an essential concept which will be used to define the concepts of cluster, accumulation and solitary individual in chapter 3. A formal definition follows.

Definition (Set of total encounter): Let an encounter $e \in E_S^\Gamma$ be given. Let $H \subseteq S : (e \in E_H^\Gamma) \wedge (\forall K \subset H : e \notin E_K^\Gamma)$. Then H is called the *set of total encounter by* e. It is denoted by $\hat{e}$. ▲

The following theorem shows that for each encounter the total set of encounter exists and is unique. The theorem also gives a procedure to construct that total set of encounter.

Theorem 1 (Existence and uniqueness of the set of total encounter): Let $S \subseteq \mathcal{I}$ and $S \neq \varnothing$. Then, the set $\hat{e}$ of total encounter by e exists for every $e \in E_S^\Gamma$. It is unique and not empty.

Proof: Let $S_e := \{K \mid e \in E_K^\Gamma\}$. Define $H := \bigcap_{K \in S_e} K$. We show that $H \neq \varnothing$ and that $H = \hat{e}$.

(1) Show that $H \neq \varnothing$.

$e \in E_K^\Gamma$ for all $K \in S_e$. It follows from Lemma 2 that

$$H = \bigcap_{K \in S_e} K \Rightarrow E_H^\Gamma = \bigcap_{K \in S_e} E_K^\Gamma.$$ Therefore $e \in E_H^\Gamma$ and thus $E_H^\Gamma \neq \varnothing$. By FundAx 2 this yields $H \neq \varnothing$. ❑

(2) Show that $H = \hat{e}$.

$\hat{e}$ as the set of total encounter by $e \in E_S^\Gamma$ was defined to be $\hat{e} \subseteq S : e \in E_{\hat{e}}^\Gamma \wedge e \notin E_K^\Gamma \forall K \subset \hat{e}$. Since $S \in S_e$ and $H = \bigcap_{K \in S_e} K$ it follows that $H \subseteq S$. In Part (1) of the proof it was shown that $e \in E_H^\Gamma$.

Assume that $H \neq \hat{e}$. Then there is a $G \subset H$ such that $e \in E_G^\Gamma$. Therefore

$G \in S_e$ since $S_e = \{K \mid e \in \mathrm{E}_K^\Gamma\}$. Since $H = \bigcap_{K \in S_e} K$ it follows that $H \subseteq G$. This contradicts the statement $G \subset H$ which followed directly from the assumption $H \neq \hat{e}$. Therefore $H = \hat{e}$. ❑

The proof of this lemma is complete. ❑

If a lion encounters a herd of zebras, the total set of encounter might consist of ten zebras. With the encounter between the herd and the lion, also an encounter between the whole zebra population and the lion has happened. Since the total set of encounter consists of ten zebras, all the encounters between any set containing those ten zebras and the lion have also occurred. What has not occurred is an encounter between the lion and any proper subset of the ten zebras.

Notation. Let $\hat{\mathrm{E}}_S^\Gamma := \{e \in \mathrm{E}_{\mathscr{I}}^\Gamma \mid \hat{e} = S\}$ denote the set of encounter events which have S as set of total encounter. This implies that: $\forall S \subseteq \mathscr{I} : \hat{\mathrm{E}}_S^\Gamma \subseteq \mathrm{E}_S^\Gamma$

It was already stated in the comment to FundAx 7 that focus and encounter events follow the same axiomatic structure. Therefore any statement about one type of event has the same truth value as the analogous statement about the other type of event. I will, therefore, prove those statements simultaneously. Lemmas analogous to the lemmas for encounter events will be proven.

First I generalize FundAx 5 and FundAx 7.

Lemma 4: Let $\mathrm{X} \in \{\Phi, \mathrm{P}\}$. Let $S, W \subseteq \mathscr{I}$ and $S, W \neq \varnothing$. Then,
$S \subset W \Leftrightarrow \mathrm{X}_S^\Gamma \supset \mathrm{X}_W^\Gamma$.

Proof: FundAx 5/7 states that $S \subset W \Rightarrow \mathrm{X}_S^\Gamma \supset \mathrm{X}_W^\Gamma$, which implies that

$$S \subseteq W \Rightarrow X_S^\Gamma \supseteq X_W^\Gamma \qquad\qquad (2)$$

It remains to be shown that $X_S^\Gamma \subset X_W^\Gamma \Rightarrow S \supset W$. Let $X_S^\Gamma \subset X_W^\Gamma$. Assume $S \subseteq W$. Then, by FundAx 5/7 and equation 2, $X_S^\Gamma \supseteq X_W^\Gamma$. This contradicts the condition $X_S^\Gamma \subset X_W^\Gamma$. Therefore $S \subseteq W$ is false, thus $X_S^\Gamma \subset X_W^\Gamma \Rightarrow S \supset W$. □

Corrolary: Let $X \in \{\Phi, P\}$. Let $S \subseteq \mathscr{I}$. Then, $X_S^\Gamma \subseteq X_\varnothing^\Gamma$.

Lemma 5: Let $X \in \{\Phi, P\}$. Let $S, W \subseteq \mathscr{I}$. Then, $X_{W \cup S}^\Gamma = X_W^\Gamma \cap X_S^\Gamma$.

Proof: In order to prove this Lemma I will show that both statements,

$X_{W \cup S}^\Gamma \subseteq X_W^\Gamma \cap X_S^\Gamma$ and $X_{W \cup S}^\Gamma \supseteq X_W^\Gamma \cap X_S^\Gamma$, are true.

(1)   Show that $X_{W \cup S}^\Gamma \subseteq X_W^\Gamma \cap X_S^\Gamma$.

By FundAx 5/7 $X_{W \cup S}^\Gamma \subseteq X_W^\Gamma$ and $X_{W \cup S}^\Gamma \subseteq X_S^\Gamma$, since $W \cup S \supseteq W$ and $W \cup S \supseteq S$. Therefore: $X_{W \cup S}^\Gamma \subseteq X_W^\Gamma \cap X_S^\Gamma$. □

(2)   Show that $X_{W \cup S}^\Gamma \supseteq X_W^\Gamma \cap X_S^\Gamma$.

Nothing has to be shown if $X_W^\Gamma \cap X_S^\Gamma = \varnothing$. Therefore let $X_W^\Gamma \cap X_S^\Gamma \neq \varnothing$. Let $e \in X_W^\Gamma \cap X_S^\Gamma$. Then $e \in X_W^\Gamma$ and $e \in X_S^\Gamma$. Thus e is a focus/reception event between Γ and both subsets W and S. This means, however, that $e \in X_{W \cup S}^\Gamma$ and, therefore, that $X_{W \cup S}^\Gamma \supseteq X_W^\Gamma \cap X_S^\Gamma$. □

The proof of this lemma is complete. □

The subset closure of focus events stated by FundAx 5 implies that for each focus there exists a largest set of focused individuals. I call this largest set the 'set of total focus'. A formal definition follows.

Definition (Set of total focus): Let an focus $f \in \Phi_S^\Gamma$ be given.

Let $H \supseteq S : (f \in \Phi_H^\Gamma) \wedge (\forall K \supset H : f \notin \Phi_K^\Gamma)$. Then H is called the *set of total focus by* f. It is denoted by $\hat{f}$. ▲

As in the case of the set of total encounter the set of total focus exists and is unique.

Theorem 2 (Existence and uniqueness of the set of total focus): Let $S \subseteq \mathcal{T}$, and $S \neq \varnothing$. Then: The set $\hat{f}$ of total focus by f exists for every $f \in \Phi_S^\Gamma$. It is unique and not empty.

Proof: Let $S_f := \{K \mid f \in \Phi_K^\Gamma\}$. Define $H := \bigcup_{K \in S_f} K$. We show that $H = \hat{f}$.

$\hat{f}$ as the set of total focus by $f \in \Phi_S^\Gamma$ was defined to be

$$\hat{f} \supseteq S : (f \in \Phi_{\hat{f}}^\Gamma) \wedge (\forall K \supset \hat{f} : f \notin \Phi_K^\Gamma)$$

Since $S \in S_e$ and $H = \bigcup_{K \in S_f} K$ it follows that $H \supseteq S$. Clearly $f \in \Phi_H^\Gamma$. Assume that $H \neq \hat{f}$. Then there is a $G \supset H$ such that $e \in E_G^\Gamma$. Therefore $G \in S_f$ since $S_f = \{K \mid f \in \Phi_K^\Gamma\}$. Since $H = \bigcup_{K \in S_f} K$ it follows that $H \supseteq G$. This contradicts $G \supset H$ which followed directly from the assumption $H \neq \hat{f}$.

Therefore $H = \hat{f}$. ❑

Notation. Let $\hat{\Phi}_S^\Gamma := \{f \in \Phi_S^\Gamma \mid \hat{f} = S\}$ denote the set of focus events which have S as set of total focus.

Analogously to the 'set of total focus' I define the 'set of total reception'. The proof of the respective existence and uniqueness theorem is analogous to the one for the

set of total focus and is omitted.

Definition (Set of total reception): Let a reception $r \in P_S^\Gamma$ be given.

Let $H \supseteq S : (r \in P_H^\Gamma) \wedge (\forall K \supset H : r \notin P_K^\Gamma)$. Then H is called the *set of total reception by* r. It is denoted by $\hat{r}$. ▲

Theorem 3 (Existence and uniqueness of the set of total reception): Let $S \subseteq \mathscr{T}$ and $S \neq \varnothing$. Then, the set $\bar{r}$ of total reception by r exists for every $r \in P_S^\Gamma$. It is unique and not empty.

Notation. Let $\hat{P}_S^\Gamma := \{r \in P_S^\Gamma \mid \hat{r} = S\}$ denote the set of reception events which have S as set of total reception.

2.3.   Discussion

On encounter with a herd of zebras a lion might be hungry or not. In case he is not hungry (or for some reason unable to hunt), immediatly after encounter there will be a termination of orientation event which is not a focus. In the discussion of the Red-Bellied Piranha it was mentioned that larger schools of pirnaha can attack their predators. Therefore, a crocodile encountering a large school of piranha might choose not to attack, even if hungry.

In order to simplify calculation I restrict all future discussion involving encounters to encounters with metabolic sources or sinks that are available for focus. Therefore, an encounter between a satiated or injured lion and a herd of zebras does not count as an encounter between the zebras and the lion as a metabolic sink. This makes sense, since a satiated lion is not actually a realization of a metabolic sink for the zebras.

the situation is more complicated in the case of the Red-Bellied piranha. If we ignore predators (i.e., crocodiles) as metabolic sinks, if they are not available for focus, the probability of encounter becomes variable; in case of the piranha it is dependent on the school size. A large school will have a lower exposure to predators than a small school. In conclusion: Encounters with metabolic sources or sinks are exclusively encounters involving metabolic sources or sinks available for focus.

We assume that, if a focus event between multiple individuals and Γ happens after an encounter with a set, this focus event happens simultaneously for all individuals. An earth-quake for example might kill 20% of a zebra herd over a period of a couple minutes. Nevertheless in our approach there is no time interval assumed between encounter of the first and of the last zebra by the earth-quake. There is also no time interval assumed between the death of the first and the death of the last zebra. Certain predators, like the sawfish, swim into schools of prey fish and use their sword to kill many individuals per attack. Also in this case we assume the focus between individuals and the predator to be simultaneous, and so are the individual receptions.

2.4.   Graphical Representations

I explicitly do not presume that the space occupied by individuals and metabolic sources and sinks is Euclidean. Nevertheless the Euclidean two-dimensional space can be used to illustrate the relation between individuals and realizations of metabolic sources and sinks. Figure 2.3 shows the graphical representation of a metabolic source or sink Γ and an individual α. A realization of Γ and the individual α are each given by two concentric circular vicinities whose centers are the coordinates of that realization of Γ and of α in space. The inner vicinity is called the *existential vicinity*, the outer one, the *relational vicinity*. The existential vicinity can be seen as the biological body,

the relational vicinity as a range of awareness. Further there is an optional set of *focus arrows* assigned to the center of the vicinities. Encounter, focus and reception events can be introduced as follows: As soon as the existential vicinity of at least one individual $\alpha \in S$ intersects with the relational vicinity of the realization of Γ we say that an encounter event of S with Γ has happened. As soon as the existential vicinity of α intersects with the relational vicinity of the realization of Γ and is pointed at by one of the focus arrows of the realization of Γ, we say that a focus event between $\{\alpha\}$ and Γ has happened. As soon as the existential vicinity of α intersects with the existential vicinity of the realization of Γ and a focus arrow points from the realization of Γ to α, we say that a reception event has happened.

With these graphical conventions we can illustrate more relations between metabolic objects than described in the axioms. For example, we can introduce the concept of 'encounter between individuals'. This is, however, not supported by the the axiomatic system so far. Also note that with the existence of encounter, focus and reception events there is the possibility introduced for representations of metabolic sources or sinks to change their position relative to the individuals. However, there is no concept of motion of individuals relative to each other introduced yet.

realization of Γ

focus arrows

α

relational vicinity

existential vicinity
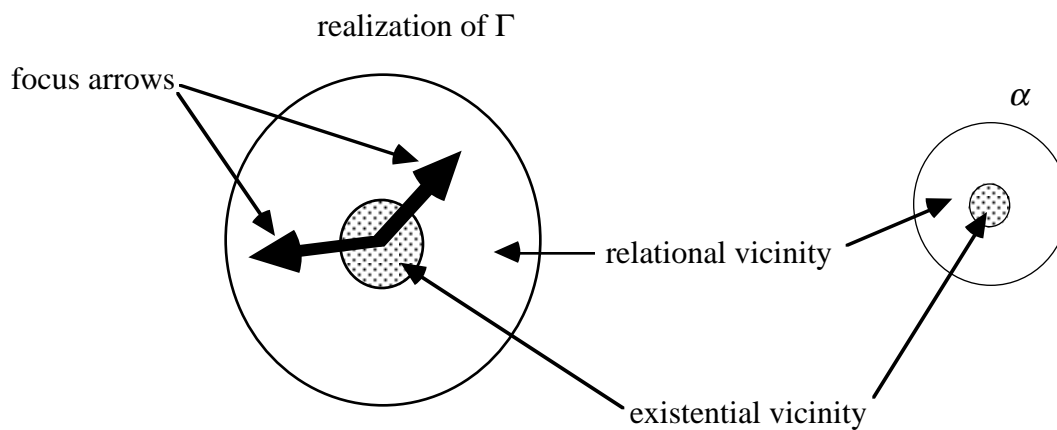
Figure 2.3. : Graphical representation of a metabolic object (an individual or a metabolic source or sink).

Figures 2.4 - 2.6 illustrate different situations involving a set of individuals S, certain subsets of S, and a metabolic source or sink Γ. Relational vicinities of individuals in S are omitted.

Γ

S

α

β
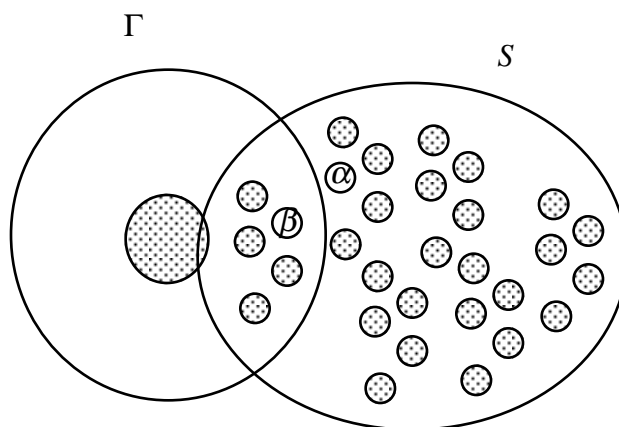
Figure 2.4. : Graphical representation of an encounter between S and Γ. There is no focus between indivduals α or β and Γ.
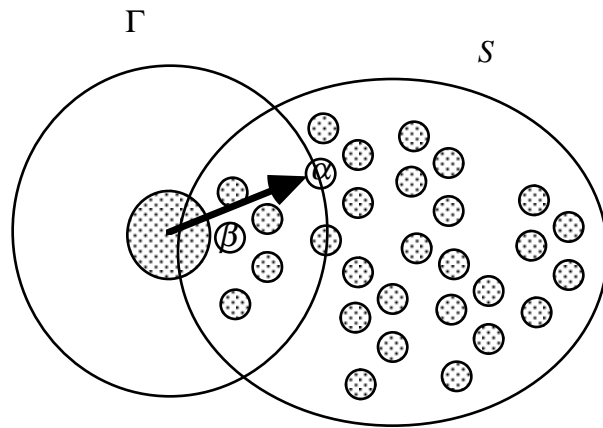
Figure 2.5. : There is a focus between α and Γ, but no focus between β and Γ.
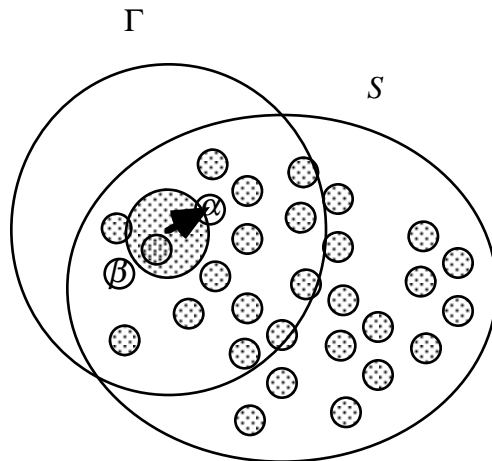
Figure 2.6. : Reception of Γ by α. There is no other reception since there is no other focus.

Chapter 3.   Solitary Individuals, Clusters, and Accumulations

In this chapter I introduce the concepts of 'cluster', 'accumulation' and 'solitary individual'. Some facts related to these concepts are derived. These concepts are based solely on the concepts of encounter and total encounter between a set of individuals and a metabolic source or sink. No other concepts are used to define them. In particular, I do not introduce an explicit notion of space. Introducing a notion of space will deter us from understanding the *meaning* of space for an individual. This meaning is given solely by the extent and the likelihood of a metabolic change to the individual caused by a metabolic source or sink, and not, for instance, by a euclidean distance from the metabolic sink or source per se.

The concepts of 'cluster' and 'accumulation' are concepts of spatial closeness. Individuals are considered spatially close under a metabolic source or sink if all of them can be encountered simultaneously. This idea gives rise to the concept of a 'cluster'. Another concept is that of an 'accumulation'. A set is considered to be an accumulation if it is a union of clusters which are themselves "close to each other" in the sense just mentioned. While within a cluster all individuals can be encountered simultaneously, this is not necessarily true for an accumulation. On the other hand two different clusters might share individuals. However, two different accumulations are spatially clearly separated from each other. They do not have any individuals in common.

A solitary individual is an individual who is not an element of a cluster. And since accumulations are unions of clusters, a solitary individual can never be an element of an accumulation either.

3.1.   Theory

Let $\mathscr{I}$ be the finite set of all individuals. Let $S \subseteq \mathscr{I}$. Let Γ be a metabolic source or sink with regard to each individual of the set S.

Notation for encounter probabilities (exposures). Let $S, W \subseteq \mathscr{I}$. Recall that an encounter event in E_S^Γ is an encounter which has S or a subset of S as its set of total encounter. Encounters between Γ and subsets of $\mathscr{I}$ are assumed to happen with certain probabilities. This establishes the existence of a probability space $(\mathrm{E}_\mathscr{I}^\Gamma, \mathscr{A}_\mathscr{I}^\Gamma, P)$, where $\mathrm{E}_\mathscr{I}^\Gamma$ is the sample space, $\mathscr{A}_\mathscr{I}^\Gamma$ is the σ-algebra generated by $\{\mathrm{E}_S^\Gamma \mid S \subseteq \mathscr{I}\}$ (see Bauer (1990)), and P the probability measure. This probability space gives rise to the probability space $(\mathscr{I}, P\{\mathscr{I}\}, \eta^\Gamma)$, where $\eta_S^\Gamma := P[e \in \mathrm{E}_S^\Gamma \mid e \in \mathrm{E}_\mathscr{I}^\Gamma]$. η_S^Γ is the probability that an encounter event is in E_S^Γ and is called the *exposure of S to Γ*. η^Γ is a probability measure on $P\{\mathscr{I}\}$, because:

    i.) $\eta_S^\Gamma \geq 0$ for all $S \subseteq \mathscr{I}$

    ii.)   Let $\mathrm{E}_S^\Gamma \cap \mathrm{E}_W^\Gamma = \varnothing$, then

$$\eta_{S \cup W}^\Gamma = P[e \in \mathrm{E}_S^\Gamma \mid e \in \mathrm{E}_\mathscr{I}^\Gamma] + P[e \in \mathrm{E}_W^\Gamma \mid e \in \mathrm{E}_\mathscr{I}^\Gamma] = \eta_S^\Gamma + \eta_W^\Gamma.$$

        According to lemma 3 in section 2.2 we have

$$\mathrm{E}_S^\Gamma \cap \mathrm{E}_W^\Gamma = \varnothing \Leftrightarrow S \cap W = \varnothing.$$

        Therefore: $S \cap W = \varnothing \Rightarrow \eta_{S \cup W}^\Gamma = \eta_S^\Gamma + \eta_W^\Gamma$

    iii.) $\eta_\mathscr{I}^\Gamma = P[e \in \mathrm{E}_\mathscr{I}^\Gamma \mid e \in \mathrm{E}_\mathscr{I}^\Gamma] = 1$

Since η^Γ is a probability measure we obtain $\eta_\varnothing^\Gamma = 0$.

Since the concepts of solitary individual, cluster and accumulation are based on the concept of set of total encounter, it is necessary to have a notation for the probability

that an encounter event is between S and Γ and has S as its set of total encounter. This probability is denoted by $\hat{\eta}_S^\Gamma$, thus $\hat{\eta}_S^\Gamma := P[e \in \hat{\mathrm{E}}_S^\Gamma \mid e \in \mathrm{E}_{\mathscr{I}}^\Gamma]$, and is called *total exposure of S to* Γ. Recall that an event that has S as its set of total encounter is an encounter event between Γ and S which is not an encounter event between Γ and any proper subset of S. Recall that $\mathrm{E}_{\mathscr{I}}^\Gamma = \dot{\bigcup_{S \subseteq \mathscr{I}}} \hat{\mathrm{E}}_S^\Gamma$, thus $\mathrm{E}_{\mathscr{I}}^\Gamma$ is partitioned into sets of total encounter events. This is true for each E_S^Γ, namely $\mathrm{E}_S^\Gamma = \dot{\bigcup_{H \subseteq S}} \hat{\mathrm{E}}_H^\Gamma$. We obtain therefore $\eta_S^\Gamma = \sum_{H \subseteq S} \hat{\eta}_H^\Gamma$, and $\sum_{S \subseteq \mathscr{I}} \hat{\eta}_S^\Gamma = 1$. This shows that we can construct a probability measure η^Γ by assigning to each element S of $P\{\mathscr{I}\}$ a non-negative number $\hat{\eta}_S^\Gamma$ all of which have to add up to 1.

From the non-negativity of η^Γ and $\eta_\varnothing^\Gamma = 0$ follows the non-negativity of $\hat{\eta}^\Gamma$ and that $\hat{\eta}_\varnothing^\Gamma = 0$. The non-negativity of $\hat{\eta}^\Gamma$ and the equation $\eta_S^\Gamma = \sum_{H \subseteq S} \hat{\eta}_H^\Gamma$ imply that $H \subseteq S \Rightarrow \eta_H^\Gamma \leq \eta_S^\Gamma$. The probability measure η^Γ is therefore generated by the function $\hat{\eta}^\Gamma$, and we describe this fact by writing $\eta^\Gamma = \left\langle \hat{\eta}^\Gamma \right\rangle_{prob}$.

Cluster. For the following definition recall from chapter 2 the definition of the set of total encounter and Theorem 1 which states that the set of total encounter is not empty and is unique for each encounter. The concepts of 'cluster' and 'accumulation' are based on the concept of 'set of total encounter'.

Definition (Cluster under Γ): A set $S \subseteq \mathscr{I}$ of individuals, with $|S| > 1$, is called a *cluster (of individuals) under* Γ if and only if there is $H \subseteq \mathscr{I}$ such that $S \subseteq H$ and $\hat{\eta}_H^\Gamma \neq 0$. If S is a cluster under Γ, then we denote S by S_{clust}^Γ. If S is not a cluster under Γ, then $S_{clust}^\Gamma := \varnothing$. ▲

This means that a cluster is a subset of a set of total encounter which can be encountered by Γ. Whether a set of individuals is a cluster or not depends on Γ. For

example: A herd of zebras is not a cluster under a lion, it might however be a cluster under an earthquake.

In order to illustrate the concept of a cluster we can use the graphical representation introduced in section 2.4. A set of individuals will form a cluster if we can position Γ so that all existential vicinities of the individuals intersect simultaneously with the Γ's relational vicinity. Note that the possibility of individuals moving relatively to each other is not yet defined. However, encounter, focus, and reception events imply motion between individuals and metabolic sources or sinks. This can be illustrated in the graphical representation given in section 2.4 as Γ is moving,while keeping the locations of all individuals fixed. A type of movement between individuals will be introduced in the next chapter in the form of migration events between, towards and away from accumulations.

Conclusion 1: Let $S_{clust}^{\Gamma} \neq \varnothing$. Then, there is an event $e \in \mathrm{E}_S^{\Gamma}$ such that $S_{clust}^{\Gamma} \subseteq \hat{e}$.

❑

Conclusion 2: Let $S_{clust}^{\Gamma} \neq \varnothing$, and let $H \subseteq S_{clust}^{\Gamma}$ with $|H| > 1$. Then $H = H_{clust}^{\Gamma}$. Therefore, every subset of a cluster containing at least two individuals is a cluster as well. ❑

Conclusion 3: Because of conclusion 2 any intersection of two clusters containing at least two individuals is again a cluster. The set of all clusters is, therefore, closed under those intersections:

Let $S_{clust}^{\Gamma} \neq \varnothing$ and $H_{clust}^{\Gamma} \neq \varnothing$. If $|S_{clust}^{\Gamma} \cap H_{clust}^{\Gamma}| > 1$ then $S_{clust}^{\Gamma} \cap H_{clust}^{\Gamma} = (S \cap H)_{clust}^{\Gamma}$. ❑

Conclusion 4: The union of two clusters may not be a cluster. ❑

In figure 3.1 the concepts of solitary individual and cluster are illustrated in two-dimensional space using some of the graphical conventions introduced in section 2.4.
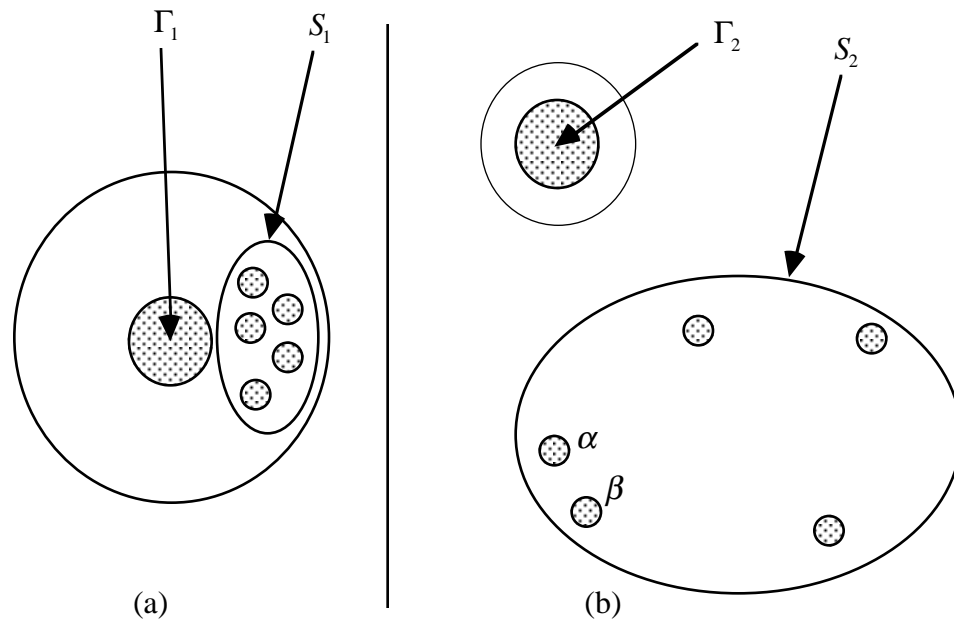
Figure 3.1.: In part (a) the set S_1 forms a cluster under Γ_1. However, S_2 in part (b) does not form a cluster under Γ_2, because Γ_2 cannot be positioned such that all individuals within Γ_2's relational vicinity. The set $\{\alpha, \beta\}$, however, forms a cluster under Γ_2. For explanations regarding the meaning of the graphical elements see section 2.4.

The relation $\underset{clust}{\sim}$ **.** Let H be a cluster under Γ. Let $\alpha, \beta \in H$. Then we write $\alpha \overset{\Gamma}{\underset{clust}{\sim}} \beta$ (α clustered with β, or α clust β), or shortly, if there is no ambiguity with regard to Γ, $\alpha \underset{clust}{\sim} \beta$. The relation $\underset{clust}{\sim}$ is reflexive and symmetric, however not necessarily transitive.

Accumulation. I will define now the concept of an 'accumulation' which is a "spatially connected union of clusters". In order to accomplish that, we extend the relation $\underset{clust}{\sim}$ to the relation $\underset{accum}{\sim}$ which is reflexive, symmetric and transitive.

Definition (Accumulation under Γ): Let S be a set of individuals with $|S| > 1$ satisfying the following condition:

Let $\alpha \in S$ and $\beta \in \mathscr{I}$. If there is a finite sequence of individuals

$\omega_1, \omega_2, ..., \omega_n$ with $\omega_i \in \mathscr{I}$ for all $i = 1, 2, ..., n$, such that

$$\alpha \underset{clust}{\sim} \omega_1, \omega_1 \underset{clust}{\sim} \omega_2, ..., \omega_{n-1} \underset{clust}{\sim} \omega_n, \omega_n \underset{clust}{\sim} \beta,$$

then $\omega_1, \omega_2, ..., \omega_n, \beta \in S$.

Then S is called an *accumulation (of individuals) under* Γ and is denoted by S_{accum}^{Γ}. ▲

The next theorem lists a few properties of an accumulation.

Theorem 1: If the set S of individuals, with $|S| > 1$, is an accumulation under Γ, then all of the following conditions are satisfied:

i.) An accumulation is the union of its clusters: $S = \bigcup_{H \subseteq S} H_{clust}^{\Gamma}$

ii.) Cluster connectivity: Let $S_1, S_2 \subseteq S$, $S_1 \cup S_2 = S$, $S_1 \cap S_2 = \varnothing$. Then there is a cluster $H \subseteq S$ under Γ such that $H \cap S_1 \neq \varnothing$ and $H \cap S_2 \neq \varnothing$.

iii.) Cluster closure: Let $H = H_{clust}^{\Gamma}$ and $H \neq \varnothing$. If $H \cap S \neq \varnothing$ then $H \subseteq S$.

Proof: Let S be an accumulation under Γ.

i.) S can be written as a union of sets of individuals which are

linked by finite chains. Two individuals related to each other by

$\underset{accum}{\sim}$ form a cluster, and therefore $S = \bigcup_{\substack{H \subseteq S, \\ |H|=2}} H^{\Gamma}_{clust}$. If $| H^{\Gamma}_{clust} | > 2$

then, according to conclusion 1, there are clusters K with

$| K |= 2$, such that $H^{\Gamma}_{clust} = \bigcup_{\substack{K \text{ is cluster,} \\ |K|=2}} K$. Therefore $S = \bigcup_{H \subseteq S} H^{\Gamma}_{clust}$.   ❑

ii.) Let $S_1, S_2 \subseteq S$, $S_1 \cup S_2 = S$, $S_1 \cap S_2 = \varnothing$. Let $\alpha \in S_1$ and $\beta \in S_2$.

Then there are individuals $\omega_1, \omega_2, ..., \omega_n$ in S, such that

$$\alpha \underset{clust}{\sim} \omega_1, \omega_1 \underset{clust}{\sim} \omega_2, ..., \omega_{n-1} \underset{clust}{\sim} \omega_n, \omega_n \underset{clust}{\sim} \beta.$$

Since $S_1 \cap S_2 = \varnothing$ and $S_1 \cup S_2 = S$ there has to be a first index k,

such that $\omega_k \in S_1$ and $\omega_{k+1} \in S_2$. The set $H := \{\omega_k, \omega_{k+1}\}$ is a

cluster satisfying $H \cap S_1 \neq \varnothing$ and $H \cap S_2 \neq \varnothing$.   ❑

iii.) Let $H = H^{\Gamma}_{clust}$, $H \neq \varnothing$ and $H \cap S \neq \varnothing$. Let $\alpha \in H \cap S$. Then for

all $\beta \in H$ it holds that $\alpha \underset{clust}{\sim} \beta$. Therefore by the definition of

accumulation it follows that $H \subseteq S$.   ❑

That completes the proof of the theorem.   ❑

Condition ii.) in Theorem 2 relates to "spatial connectedness" of accumulations,

while condition iii.) relates to a "distance between accumulations". Two individuals

from two different accumulations are never in the same cluster. Two individuals in the

same cluster are always in the same accumulation.

Corollary: Let S_1 and S_2 be two accumulations under Γ. Then,

$S_1 \cap S_2 \neq 0 \Rightarrow S_1 = S_2$.   ❑

It follows from the definition of 'accumulation' that any cluster is either an accumulation, or is a subset of an accumulation. The following lemma states that for each cluster there is a unique embedding accumulation.

Lemma 1: Let $H = H_{clust}^{\Gamma}$ with $H \neq \emptyset$. Then, there is an S_{accum}^{Γ} such that $H \subseteq S_{accum}^{\Gamma}$. S_{accum}^{Γ} is unique.

Proof: Define S to be the following set:

$$S = \{\beta | \exists \omega_i \in I, i = 1, 2, ..., n : \alpha \underset{clust}{\sim} \omega_1 \wedge \omega_1 \underset{clust}{\sim} \omega_2 \wedge ... \wedge \omega_{n-1} \underset{clust}{\sim} \omega_n \wedge \omega_n \underset{clust}{\sim} \beta \wedge \alpha \in H\}.$$

Then S is clearly an accumulation, and $H \subseteq S_{accum}^{\Gamma}$. Because of the corollary to Theorem 2, there can be only one accumulation containing H. Therefore S_{accum}^{Γ} is unique.   ❑

It is essential that the set H in the Lemma 1 is indeed a cluster or an accumulation if $|H| > 1$. Let H, e.g., be the union of two different accumulations. Then S as constructed in the theorem will still be the union of these two accumulations yielding $S = H$ which is not an accumulation. On the other hand, H in Lemma 1 can be a single individual α. Using the set formation given in Lemma 1 we can easily generate a unique accumulation containing α, assuming α belongs to a cluster.

Corollary: Let $\alpha \in \mathscr{T}$. If there is a set H such that $\alpha \in H_{clust}^{\Gamma}$, then there is a unique accumulation S_{accum}^{Γ} such that $\alpha \in S_{accum}^{\Gamma}$.   ❑

Lemma 1 and the Corollary to Lemma 1 motivate a notation for the accumulation containing a cluster or an individual.

Notation. Let

$$\langle\alpha\rangle_{accum} := \{\beta | \exists\omega_i \in I, i=1,2,...,n : \alpha \underset{clust}{\sim} \omega_1 \wedge \omega_1 \underset{clust}{\sim} \omega_2 \wedge ... \wedge \omega_{n-1} \underset{clust}{\sim} \omega_n \wedge \omega_n \underset{clust}{\sim} \beta\}$$

then $<\alpha>_{accum}$ is the accumulation containing α. Let $H = H^{\Gamma}_{clust}$ with $H \neq \varnothing$. Let

$$\langle H\rangle_{accum} = \{\beta | \exists\omega_i \in I, i=1,2,...,n : \alpha \underset{clust}{\sim} \omega_1 \wedge \omega_1 \underset{clust}{\sim} \omega_2 \wedge ... \wedge \omega_{n-1} \underset{clust}{\sim} \omega_n \wedge \omega_n \underset{clust}{\sim} \beta \wedge \alpha \in H\}$$

then $\langle H\rangle_{accum}$ is the accumulation containing H.

The relation $\underset{accum}{\sim}$ **.** Let S be an accumulation under Γ. Let $\alpha, \beta \in S$. Then we write $\alpha \overset{\Gamma}{\underset{accum}{\sim}} \beta$ (α accumulated with β (under Γ), or α accum β), or shortly, if there is no ambiguity with regard to Γ, $\alpha \underset{accum}{\sim} \beta$. The relation $\underset{accum}{\sim}$ is reflexive and symmetric, because the relation $\underset{clust}{\sim}$ has these properties. Furthermore $\underset{accum}{\sim}$ is, in contrast to $\underset{clust}{\sim}$, transitive. $\underset{accum}{\sim}$ is therefore an equivalence relation.

Solitary individuals. If an $\alpha \in \mathscr{I}$ is not an element of any cluster, then it is also not an element of any accumulation. This fact constitutes the concept of a 'solitary individual'.

Definition (Solitary under Γ): An individual α is called *solitary under* Γ if and only if $\forall S \subseteq \mathscr{I} : \alpha \in S \Rightarrow S^{\Gamma}_{clust} = \varnothing$. $\blacktriangle$

Conclusion 5: Let α be an individual. Then under Γ α is either solitary or it is an element of a cluster. $\square$

Theorem 2: Let α be an individual. Then under Γ α is either solitary or it is an

element of an accumulation.

Proof: This follows from Lemma 1 and Conclusion 5. ❑

Since $\underset{accum}{\sim}$ is an equivalence relation the following theorem is immediately implied.

Theorem 3: Any given metabolic source or sink Γ defines a unique partition on $\mathscr{I}$ into accumulations and solitary individuals. ❑

Exposure of accumulations: The set $\mathscr{I}$ is uniquely partitioned into accumulations and solitary individuals under a probability measure $\hat{\eta}^{\Gamma}$. Denote with $P(\hat{\eta}^{\Gamma})$ the partition of $\mathscr{I}$ into solitary individuals and accumulations under the metabolic sink or source Γ, thus:

$$P(\hat{\eta}^{\Gamma}) := \{S \mid S = S_{accum}^{\Gamma}\} \cup \{\alpha \mid \forall S \subseteq \mathscr{I} : \alpha \in S \Rightarrow S_{clust}^{\Gamma} = \varnothing\}$$

Let $S \in P(\hat{\eta}^{\Gamma})$. Recall that $\eta_S^{\Gamma} = \sum_{H \subseteq S} \hat{\eta}_H^{\Gamma}$. Then η^{Γ} is a probability measure on $P(\hat{\eta}^{\Gamma})$. η_S^{Γ} is called the *exposure of the accumulation (or solitary individual) S to* Γ. η_S^{Γ} is the probability that an encounter between the accumulation S and Γ happens. Also: $S \in P(\hat{\eta}^{\Gamma}) \Rightarrow \eta_S^{\Gamma} \neq 0$.

3.2.   Discussion

I have now set the stage to address certain sets of individuals, namely accumulations, as entities under encounter by a metabolic source or sink. Recall that the axioms in FundAx assumed encounter, focus, and reception with regard to arbitrary sets of individuals. In future we can restrict encounters to those of solitary individuals

and accumulations. This is, indeed, an essential conceptual progress. Note that there are no ambiguities possible, since the relation $\underset{accum}{\sim}$ is an equivalence relation. For each metabolic source or sink there is a partition of the set of individuals into accumulations and solitary individuals, and this partition is unique.

The following line of thought shows the connection between the concept of total set of encounter and the concept of accumulation. Let's assume that a set of individuals is encountered. Then there is a smallest set of individuals being encountered, namely the set of total encounter. This set of total encounter is either a cluster or a solitary individual. If it is a cluster, then there exists a unique accumulation containing this cluster (by Lemma 1 in this section). According to FundAx 3 (Superset closure of encounter events) the encounter of the cluster also means that the cluster's accumulation has been encountered. Therefore, encountering an arbitrary set of individuals is equivalent to encountering either a solitary individual or an accumulation via the set of total encounter.

3.3.   Extension of FundAx to AccumAx, Interactive Process

In chapters 1 and 2 I discussed the procedure during which a realization of a metabolic source or sink can induce a metabolic change in an individual. First, there will be an encounter between individuals and the metabolic source or sink, then a focus event might occur, and finally a reception of the metabolic source or sink by one or more individuals may happen. FundAx and the concept of accumulation developed in this chapter allow for capturing such procedures in the form of a stochastic process.

Assume that an encounter involving an accumulation happens. Then it cannot be concluded from the axioms in FundAx that a successive focus event will involve a subset of that same accumulation. If there is an encounter between a herd of zebras and

a lion, then the successive event will either be a focus event between a zebra of the herd and the lion, or a resignation. Before there can be a focus between the lion and a solitary zebra or a zebra from another herd, there has to be a resignation involving the herd that was just encountered. To capture this fact it is necessary to introduce another axiom, which makes sure that after an encounter with an accumulation focus cannot occur beyond that accumulation before a resignation involving this accumulation happens. The following definition captures this fact:

Definition (Stories): Let $S_1, S_2, S_3 \subseteq \mathscr{I}$. Let S_1 be an accumulation or a solitary individual. Let $S_1 \supseteq S_2 \supseteq S_3$. Then the set $\Sigma_{\mathscr{I}}^{\Gamma}$ of *stories concerning $\mathscr{I}$ and* Γ is defined as follows:

i)   Let $e \in \mathrm{E}_{S_1}^{\Gamma}$. Then: $[e \to \omega_{\mathscr{I}}^{\Gamma}] \in \Sigma_{\mathscr{I}}^{\Gamma}$.

ii)   Let $e \in \mathrm{E}_{S_1}^{\Gamma}$ and $f \in \hat{\Phi}_{S_2}^{\Gamma}$. Then: $[e \to f \to \omega_{\mathscr{I}}^{\Gamma}] \in \Sigma_{\mathscr{I}}^{\Gamma}$.

iii)   Let $e \in \mathrm{E}_{S_1}^{\Gamma}$ $f \in \hat{\Phi}_{S_2}^{\Gamma}$, and $r \in \hat{\mathrm{P}}_{S_3}^{\Gamma}$. Then: $[e \to f \to r] \in \Sigma_{\mathscr{I}}^{\Gamma}$.

iv)   (Closure under story concatenation)

Let $[\sigma_1] \in \Sigma_{\mathscr{I}}^{\Gamma}$ and $[\sigma_2] \in \Sigma_{\mathrm{I}}^{\Gamma}$. Then: $[\sigma_1 \to \sigma_2] \in \Sigma_{\mathscr{I}}^{\Gamma}$.

v)   (Completeness of the set of stories)

If $[\sigma] \in \Sigma_{\mathscr{I}}^{\Gamma}$, then $[\sigma]$ is of either of the forms given in i)-iv).   ▲

Extension to AccumAx. The definition of a story allows us to extend FundAx.

Axiomatic System for Accumulations (AccumAx)

Let $\mathscr{I}$ be the finite set of all individuals. Let Γ be a metabolic source or sink with regard to each individual of the set $\mathscr{I}$. Then,

AccumAx consists of FundAx and the following axiom:

AccumAx 1 (Existence of stories):

There exists a non empty set $\Sigma_{\mathscr{I}}^{\Gamma}$ of stories concerning $\mathscr{I}$ and Γ.

This set is complete, i.e., if $[\sigma]$ is a story concerning $\mathscr{I}$ and Γ

according to the definition of the concept 'story', then $[\sigma] \in \Sigma_{\mathscr{I}}^{\Gamma}$.

The concept of a story defines sequencing (time) and causation between events. A story is a sequence of events such that before a reception event can occur there has to be a focus event and before a focus event can occur there has to be an encounter event. Encounters only happen to solitary individuals or accumulations. Focus happens only to subsets of sets encountered. Reception happens only to subsets of sets of focus.

In the context of a story the concepts 'before' and 'after' can be defined.

Definition (Event happens before another event, event happens after another event): Let a and b be two events, and let $[a_1 \to a_2 \to ... \to a_n]$ be a story. We say that *a happens before b in* $[a_1 \to a_2 \to ... \to a_n]$ or, equivalently, that *b happens after a in* $[a_1 \to a_2 \to ... \to a_n]$, if and only if there are indices $i, j \in \{1, 2, ..., n\}$ such that $a = a_i$ and $b = b_j$ and $i < j$. $\blacktriangle$

The following notation concerning probabilities of events will be used in the definition of the concept of 'interactive process' and later on in deriving fitness functions. An interactive process is a stochastic process on stories. In stories of type ii.) an encounter and a focus event occur consecutively. Which individuals will be subjected to focus depends on which accumulation or solitary individual has been encountered. In stories of type iii.) a focus and a reception event occur consecutively.

Which individuals will be subjected to reception depends on which individuals were subjected to focus.

Notation for focus probabilities (acceptances). Let $S, W, H \subseteq \mathscr{I}$. Recall that a focus event in Φ_S^Γ is a focus which has S or a superset of S as its set of total focus. Focuses between Γ and subsets of $\mathscr{I}$ are assumed to happen with certain probabilities. Recall also, that $\Phi_\varnothing^\Gamma$ is the set of all focus events (see corollary to lemma 4 in section 2.2). This establishes the existence of a certain probability space $(\Phi_\varnothing^\Gamma, \mathscr{B}_\mathscr{I}^\Gamma, Q)$, where $\Phi_\varnothing^\Gamma$ is the sample space, $\mathscr{B}_\mathscr{I}^\Gamma$ is the σ-algebra generated by $\{\hat{\Phi}_S^\Gamma \mid S \subseteq \mathscr{I}\}$ (see Bauer (1990)), and Q the probability measure. This probability space gives rise to the probability space $(\mathscr{I}, P\{\mathscr{I}\}, \mu^\Gamma)$. The probability measure μ^Γ is not as easily obtained from Q as the probability measure η^Γ from P in case of definition of the probability space of encounters.

Given a certain subset H of $\mathscr{I}$ it is of interest to obtain the probability of a focus event being in Φ_H^Γ. The probability that a focus event is in Φ_H^Γ is denoted by φ_H^Γ, thus $\varphi_H^\Gamma := Q[f \in \Phi_H^\Gamma \mid f \in \Phi_\varnothing^\Gamma]$. φ_H^Γ is called the *acceptance of* Γ *by* H. φ_H^Γ is the probability that a focus event occurs between at least H and Γ. However, φ^Γ is not a probability measure on $\mathscr{I}$, because of the biconditional $S \subseteq W \Leftrightarrow \varphi_S^\Gamma \geq \varphi_W^\Gamma$ (follows from lemma 4 in section 2.2). φ_H^Γ can be expressed in terms of μ^Γ for all $H \subseteq \mathscr{I}$, because for all $H \subseteq \mathscr{I}$ the set $\{f \in \Phi_H^\Gamma \mid f \in \Phi_\varnothing^\Gamma\}$ is in the σ-algebra $\mathscr{B}_\mathscr{I}^\Gamma$. This can be seen by expressing Φ_H^Γ by using sets in $\{\hat{\Phi}_S^\Gamma \mid S \subseteq \mathscr{I}\}$ by stating the fact that $\Phi_H^\Gamma = \bigcup_{K \supseteq H} \hat{\Phi}_K^\Gamma$. Since $\mathscr{I}$ is a finite set Φ_H^Γ is, therefore, indeed in $\mathscr{B}_\mathscr{I}^\Gamma$.

The probability $\hat{\varphi}_H^\Gamma := Q[f \in \hat{\Phi}_H^\Gamma \mid f \in \Phi_\varnothing^\Gamma]$ is called the *total acceptance of* Γ *by* H. Acceptance and total acceptance are related by the equation $\varphi_H^\Gamma = \sum_{K \supseteq H} \hat{\varphi}_K^\Gamma$.

In the stories of type ii.) and iii.) focus events happen after encounter events. An encounter event is always an encounter with an accumulation or a solitary individual.

That means, that an encounter event can be interpreted as the set of all possible focuses on subsets of the encountered accumulation. Let S be an accumulation under Γ. Then the probability that H is the set of total focus under the condition that S was encountered is denoted by $\hat{\varphi}_{H|S}^{\Gamma}$. Once S is encountered only sets $K \subseteq S$ can be sets of total focus. Therefore $\hat{\varphi}_{H|S}^{\Gamma}$ is defined by $\hat{\varphi}_{H|S}^{\Gamma} := \dfrac{\hat{\varphi}_H^{\Gamma}}{\sum\limits_{K \subseteq S} \hat{\varphi}_S^{\Gamma}}$. The overall probability of focus between a set H and Γ is therefore $\eta_S^{\Gamma} \cdot \hat{\varphi}_{H|S}^{\Gamma}$, where $H \subseteq S$, and S is an accumulation. This probability is denoted by $\hat{\varphi}_{H:S}^{\Gamma}$, and called the *total acceptance of H through S*. Thus $\hat{\varphi}_{H:S}^{\Gamma} := \eta_S^{\Gamma} \cdot \hat{\varphi}_{H|S}^{\Gamma}$.

The probability that accumulation S is encountered and successively a focus occurs between (at least) individual $\alpha \in S$ and Γ is denoted by $\varphi_{\{\alpha\}:S}^{\Gamma}$. Then

$$\varphi_{\{\alpha\}:S}^{\Gamma} := \eta_S^{\Gamma} \cdot \sum_{\substack{H \subseteq S, \\ \alpha \in H}} \hat{\varphi}_{H|S}^{\Gamma} .$$

Notation for reception probabilities (receptances). Completely analogous to the probability spaces defined in case of focus the probability spaces $(P_{\mathscr{G}}^{\Gamma}, \mathscr{C}_{\mathscr{G}}^{\Gamma}, R)$ and $(\mathscr{I}, P\{\mathscr{I}\}, \nu^{\Gamma})$ can be defined in case of reception.

The probability that a reception event is in P_H^{Γ} is denoted by ρ_H^{Γ}, thus $\rho_H^{\Gamma} := P[r \in P_H^{\Gamma} \mid r \in \bigcup\limits_{S \subseteq \mathscr{I}} P_S^{\Gamma}]$. ρ_H^{Γ} is called the *receptance of Γ by H*. ρ_H^{Γ} is the probability that a reception event occurs between at least H and Γ. Because of the subset closure of reception events (FundAx 7) we obtain: $H \subseteq S \Rightarrow \rho_H^{\Gamma} \geq \rho_S^{\Gamma}$ (which also means that ρ^{Γ} is not a proabability measure, but is deried from the probability measure ν^{Γ}). The probability $\hat{\rho}_H^{\Gamma}$ that H is the set of total reception for a reception event, thus $\hat{\rho}_H^{\Gamma} := P[r \in \hat{P}_H^{\Gamma} \mid r \in \bigcup\limits_{S \subseteq \mathscr{I}} P_S^{\Gamma}]$. Recall that an event that has H as its set of total reception is not a reception event for any proper superset of H.

$\hat{\rho}^{\Gamma}$ is a probability measure on the powerset of $\mathscr{I}$, which means that $\sum\limits_{S \subseteq \mathscr{I}} \hat{\rho}_S^{\Gamma} = 1$ and $\hat{\rho}_H^{\Gamma} \geq 0$ for all $H \subseteq \mathscr{I}$. $\hat{\rho}_H^{\Gamma}$ is called the *total receptance of Γ by H*. Note that the

probability measure $\hat{\rho}^{\Gamma}$ is dependent on Γ and $\mathscr{I}$. It is for example not necessary that if $H \neq \varnothing$ that there is any subset of $K \subseteq H$ such that $\hat{\rho}_K^{\Gamma} \neq 0$.

Receptance and total receptance are related by the equation $\rho_H^{\Gamma} = \sum_{K \supseteq H} \hat{\rho}_K^{\Gamma}$. For completeness define $\hat{\rho}_{\varnothing}^{\Gamma} = 0$. This implies that $\rho_{\varnothing}^{\Gamma} = 0$ as well.

In the stories of type ii.) and iii.) reception events happen after focus events. A focus event gives rise to the set of possible receptions, because the receptions have to be chosen from the set of total focus given by that focus event. I denote with $\hat{\rho}_{H|S}^{\Gamma}$ the probability that H is the set of total reception under the condition that S is the preceeding set of total focus. $\hat{\rho}_{H|S}^{\Gamma}$ is called the *total receptance of Γ by H after total focus between S and Γ*. Once S is focused on only sets $K \subseteq S$ can be sets of total reception. The overall probability of reception of Γ by H is therefore

$\eta_S^{\Gamma} \cdot \sum_{K \subseteq S} (\hat{\varphi}_{K|S}^{\Gamma} \cdot \sum_{H \subseteq K} \hat{\rho}_{H|K}^{\Gamma})$, where $H \subseteq S$, and S is an accumulation. This probability is denoted by $\hat{\rho}_{H:S}^{\Gamma}$, and called the *total receptance of Γ by H through accumulation S*.

Thus $\hat{\rho}_{H:S}^{\Gamma} := \eta_S^{\Gamma} \cdot \sum_{K \subseteq S} (\hat{\varphi}_{K|S}^{\Gamma} \cdot \sum_{H \subseteq K} \hat{\rho}_{H|K}^{\Gamma})$.

The probability that accumulation S is encountered, successively a focus occurs between individual $\alpha \in S$ and Γ, and after that a reception of Γ by (at least) α happens is denoted by $\rho_{\{\alpha\}:S}^{\Gamma}$. Then $\rho_{\{\alpha\}:S}^{\Gamma} := \eta_S^{\Gamma} \cdot \sum_{\substack{K \subseteq S, \\ \alpha \in K}} (\hat{\varphi}_{K|S}^{\Gamma} \cdot \sum_{\substack{H \subseteq K, \\ \alpha \in H}} \hat{\rho}_{H|K}^{\Gamma})$. $\rho_{\{\alpha\}:S}^{\Gamma}$ is called the *receptance of Γ by individual α through accumulation S*. This type of probability will become essential once individual fitness functions are introduced in chapter 4.

Interactive process. An interactive process generates random sequences of stories. The process concatenates stories. Hence the process has to be defined only on the shortest stories. The set of shortest stories is defined as follows:

Definition (Shortest stories): Let $S_1, S_2, S_3 \subseteq \mathscr{I}$. Let S_1 be an accumulation or a solitary individual. Let $S_1 \supseteq S_2 \supseteq S_3$. Let Γ be a metabolic source or sink for all

individuals in $\mathscr{I}$. Then the set $\check{\Sigma}^{\Gamma}_{\mathscr{I}}$ of *shortest stories concerning* $\mathscr{I}$ *and* Γ is defined as follows*:*

    i)   Let $e \in \mathrm{E}^{\Gamma}_{S_1}$. Then, $[e \rightarrow \omega^{\Gamma}_{\mathscr{I}}] \in \check{\Sigma}^{\Gamma}_{\mathscr{I}}$.

    ii)   Let $e \in \mathrm{E}^{\Gamma}_{S_1}$ and $f \in \hat{\Phi}^{\Gamma}_{S_2}$. Then, $[e \rightarrow f \rightarrow \omega^{\Gamma}_{\mathscr{I}}] \in \check{\Sigma}^{\Gamma}_{\mathscr{I}}$.

    iii)   Let $e \in \mathrm{E}^{\Gamma}_{S_1}$ $f \in \hat{\Phi}^{\Gamma}_{S_2}$, and $r \in \hat{\mathrm{P}}^{\Gamma}_{S_3}$. Then, $[e \rightarrow f \rightarrow r] \in \check{\Sigma}^{\Gamma}_{\mathscr{I}}$.

    vi)   If $[\sigma] \in \check{\Sigma}^{\Gamma}_{\mathscr{I}}$, then $[\sigma]$ is of the form given in i), ii), or iii).

$\blacktriangle$

The definition of 'shortest story' is identical to the definition of 'story' but excludes closure under concatenation. Therefore, $\check{\Sigma}^{\Gamma}_{\mathscr{I}} \subset \Sigma^{\Gamma}_{\mathscr{I}}$. Also, $[a_1 \rightarrow a_2 \rightarrow ... \rightarrow a_n] \in \check{\Sigma}^{\Gamma}_{\mathrm{I}}$ if and only if $n = 2 \vee n = 3$. $\check{\Sigma}^{\Gamma}_{\mathscr{I}}$ generates $\Sigma^{\Gamma}_{\mathscr{I}}$ under concatenation.

The stage is now set to define the concept of 'interactive process'.

Definition (Interactive process between $\mathscr{I}$ and Γ): Define the random variables $X_t, t \in \mathbb{N}_0$ with values in $\check{\Sigma}^{\Gamma}_{\mathscr{I}}$ in the following way:

For all $i = 1,2,3,...$

    i) $P[X(i) \in \{[e \rightarrow \omega^{\Gamma}_{\mathscr{I}}] \mid e \in \mathrm{E}^{\Gamma}_{S_1}] := \eta^{\Gamma}_{S_1} \cdot (1 - \sum_{K \subseteq S_1} \hat{\varphi}^{\Gamma}_{K|S_1})$.

    ii)

$P[X(i) \in \{[e \rightarrow f \rightarrow \omega^{\Gamma}_{\mathscr{I}}] \mid e \in \mathrm{E}^{\Gamma}_{S_1} \wedge S_1 \supseteq S_2 : f \in \hat{\Phi}^{\Gamma}_{S_2}] := \eta^{\Gamma}_{S_1} \cdot \hat{\varphi}^{\Gamma}_{S_2|S_1} \cdot (1 - \sum_{K \subseteq S_2} \hat{\rho}^{\Gamma}_{K|S_2})$.

    iii)

$P[X(i) \in \{[e \rightarrow f \rightarrow r] \mid e \in \mathrm{E}^{\Gamma}_{S_1} \wedge S_1 \supseteq S_2 : f \in \hat{\Phi}^{\Gamma}_{S_2} \wedge S_2 \supseteq S_3 : r \in \hat{\mathrm{P}}^{\Gamma}_{S_3}] := \eta^{\Gamma}_{S_1} \cdot \hat{\varphi}^{\Gamma}_{S_2|S_1} \cdot \hat{\rho}^{\Gamma}_{S_3|S_2}$.

Then, a sequence $\{X(i)\}_{i=1,2,3,...}$ of random variables, such that each realization $[x(1)],[x(2)],...,[x(n)]$ of any subsequence of the form $X(1), X(2),..., X(n)$ forms an

allowable sequence when written in the form $[x(1) \to x(2) \to ... \to x(n)]$ is called an

interactive process between $\mathscr{I}$ *and* Γ. ▲

Chapter 4.   Incentives for Accumulation

In this chapter I return to the original question: Under which conditions will solitary individuals competing over metabolic sources form accumulations? In order to tackle this question, some constructions have to be made. Note first, that individuals do not have the ability (AccumAx) to "form accumulations". Accumulations and solitary individuals, as introduced in chapter 3, are fixed. Second, even if this ability to form accumulations is introduced individuals have to have an incentive to form them. Both, the ability to form accumulations and the incentive to form them, are introduced in the following.

4.1.   Movement and migration

Movement. The concept of accumulation (introduced and discussed in chapter 3) is based on the concept of encounter (FundAx 2 and 3). The properties of accumulation are derived from the properties of the set of total encounter (Definition and Theorem 1 in chapter 2). Theorem 4 in chapter 3 states that any given metabolic source or sink defines, on any given set of individuals, a unique partition into accumulations and solitary individuals. There is at this point of the development of the theory no possibility for individuals to migrate between accumulations. In order to introduce such a possibility the following has to be established:

(1)   Define the possibility that under the same metabolic source or sink different partitions in accumulations and solitary individuals are possible, and

(2)   define migration events and introduce a time-line along which those events

happen.

In order to accomplish (1) note that a metabolic source or sink Γ is given with regard to a finite set of individuals $\mathscr{I}$ by the probability spaces $(\mathscr{I}, P\{\mathscr{I}\}, \eta^\Gamma)$ (η_S^Γ is the probability that an encounter event is in E_S^Γ), $(\mathscr{I}, P\{\mathscr{I}\}, \mu^\Gamma)$ (with φ_H^Γ is the probability that a focus event is in Φ_H^Γ), and $(\mathscr{I}, P\{\mathscr{I}\}, \nu^\Gamma)$ (with ρ_K^Γ is the probability that a reception event is in P_K^Γ), and the associated sets of events [see chapter 3 for the notation regarding these probability spaces]. Until now it was not required that encounter events exist in E_S^Γ for which, e.g., any $\{\alpha\} \subset S$ is the set of total encounter. However, if, for instance, we want to have the possibility of α leaving an accumulation and becoming solitary, there has to be an encounter such that $\{\alpha\}$ is the set of total encounter. Therefore, the following closure property for encounter events is required to implement the possibility of free movement. This gives rise to an extension of AccumAx.

Extension to MoveAx.

Axiomatic System for Movements (MoveAx)

Let $\mathscr{I}$ be the finite set of all individuals. Let Γ be a metabolic source or sink with regard to each individual of the set $\mathscr{I}$. Then,

MoveAx consists of AccumAx and the following axiom:

MoveAx 1 (Closure of total encounter events):
$$\forall S \subseteq \mathscr{I}\ \exists e \in \mathrm{E}_S^\Gamma : S = \hat{e}$$

[This means that each subset of individuals can be a set of total encounter]

Recall that $\hat{E}_S^\Gamma$ denotes the set of encounter events which have S as the set of total encounter. The set of all encounters $E_{\mathscr{I}}^\Gamma$ is partitioned by the set $\{\hat{E}_S^\Gamma \mid S \subseteq \mathscr{I}\}$. In chapter 3 it was shown that $\hat{\eta}_S^\Gamma = P[e \in \hat{E}_S^\Gamma \mid e \in E_{\mathscr{I}}^\Gamma]$ is a probability measure on $P\{\mathscr{I}\}$. The idea now is to represent movement of individuals as sequences of probability measures on the powerset of $P\{\mathscr{I}\}$.

Consider the following example: Let $\hat{\eta}^{\Gamma,1}, \hat{\eta}^{\Gamma,2}$ be probability measures on $\mathscr{I}$. Let's assume that individual α is solitary under Γ with $\hat{\eta}^{\Gamma,1}$ and that α is not solitary under Γ with $\hat{\eta}^{\Gamma,2}$. Assume further that $\hat{\eta}_S^{\Gamma,1} = \hat{\eta}_S^{\Gamma,2}$ for all $S \subseteq \mathscr{I}$ with $\alpha \notin S$. Then $\hat{\eta}_S^{\Gamma,1} = 0$ for all $S \subseteq \mathscr{I}$ with $\{\alpha\} \subset S$ since α is solitary under Γ with $\hat{\eta}^{\Gamma,1}$. On the other hand, there has to be $S \subseteq \mathscr{I}$ with $\alpha \in S$ such that $\hat{\eta}_S^{\Gamma,2} \neq 0$, since α is not solitary under Γ with $\hat{\eta}^{\Gamma,1}$. Therefore, the short sequence $\hat{\eta}^{\Gamma,1}, \hat{\eta}^{\Gamma,2}$ stands for a process during which a solitary α joins an accumulation. It is, indeed, α who is joining the accumulation and not the accumulation joining α, since α is the only individual that moved (due to the condition that $\hat{\eta}_S^{\Gamma,1} = \hat{\eta}_S^{\Gamma,2}$ for all $S \subseteq \mathscr{I}$ with $\alpha \notin S$, and that there is at least one $S \subseteq \mathscr{I}$ with $\{\alpha\} \subset S$ such that $\hat{\eta}_S^{\Gamma,1} = 0 \wedge \hat{\eta}_S^{\Gamma,2} \neq 0$).

This example shows that movement between accumulations and movement of solitary individuals towards or away from accumulations can be created by a sequence of redefinitions of clusters under Γ via probability measures. A set $S \subseteq \mathscr{I}$ of individuals with $|S| > 1$ is a cluster under Γ with $\hat{\eta}^{\Gamma,1}$ if and only if $\hat{\eta}_S^{\Gamma,1} \neq 0$. Because of conclusion 2 in chapter 3 it follows that $\forall H \subseteq S_{clust}^\Gamma \wedge |H| > 1 : \hat{\eta}_H^{\Gamma,1} \neq 0$. Define $\hat{\eta}^{\Gamma,2}$ so that $\hat{\eta}_S^{\Gamma,2} = 0$ and $\hat{\eta}_H^{\Gamma,2} = \hat{\eta}_H^{\Gamma,1}$ for all $H \neq S$. Then the sequence $\hat{\eta}^{\Gamma,1}, \hat{\eta}^{\Gamma,2}$ stands for a dispersal of S. Note that proper subsets of S will still form clusters under Γ with $\hat{\eta}^{\Gamma,2}$ as they did under Γ with $\hat{\eta}^{\Gamma,1}$. Therefore, not only movement between accumulations

can be characterized by sequences of probability distributions. Movement within accumulations can be captured by this method as well. This gives rise to the following definition.

Definition (Movement): Let $\{\hat{\eta}^{\Gamma,i}\}_{i=1,...,n}$ with $n > 1$ be a sequence of probability measures on $\{\hat{E}_S^\Gamma \mid S \subseteq \mathcal{I}\}$. Then $\{\hat{\eta}^{\Gamma,i}\}_{i=1,...,n}$ is called a *movement in* $\mathcal{I}$. ▲

With this definition of movement also a time-line along which movement occurs has been introduced. That takes partially care of point (2) above. It is, however, prudent to integrate movement with the concept of a story. This will be done towards the end of the chapter. At this point the time-line for movement is unrelated to the time-line for stories.

The concept of movement given in the definition is very general. Of interest at this point are special movements, namely the movement of a single individual leaving, joining or commuting between accumulations. These types of movement are called 'migrations'. In this thesis no other kind of movement will be investigated, although the framework has the potential to define them.

Definition (Migration between accumulations): A movement $\{\hat{\eta}^{\Gamma,i}\}_{i=1,...,n}$ is called a *migration of individual* α *from accumulation* S_1 *to accumulation* $S_2 \setminus \{\alpha\}$ if the following conditions are met:

i.) $\alpha \in S_1 \cap S_2$

ii.) S_1 is an accumulation under Γ with $\hat{\eta}^{\Gamma,1}$, but not with $\hat{\eta}^{\Gamma,n}$.

iii.) S_2 is an accumulation under Γ with $\hat{\eta}^{\Gamma,n}$, but not with $\hat{\eta}^{\Gamma,1}$.

iv.) $S_2 \setminus \{\alpha\}$ is an accumulation or a solitary individual under Γ with

$\hat{\eta}^{\Gamma,1}$.

v.) $S_1 \setminus \{\alpha\}$ is an accumulation or a solitary individual under Γ with $\hat{\eta}^{\Gamma,2}$.   ▲

The first three conditions in this definition make sure that α originates from an accumulation and ends up within another one. The last two conditions state that individuals by 'migrating between accumulations' do not arbitrarily generate new or destroy old accumulations.

Definition (Migration into solitude): A movement $\{\hat{\eta}^{\Gamma,i}\}_{i=1,...,n}$ is called a *migration of individual* α *from accumulation* S *into solitude* if the following conditions are met:

i.) $\alpha \in S$

ii.) S is an accumulation under Γ with $\hat{\eta}^{\Gamma,1}$, but not with $\hat{\eta}^{\Gamma,n}$.

iii.) α is a solitary individual under Γ with $\hat{\eta}^{\Gamma,n}$, but not with $\hat{\eta}^{\Gamma,1}$.

iv.) $S \setminus \{\alpha\}$ is an accumulation or a solitary individual under Γ with $\hat{\eta}^{\Gamma,n}$.   ▲

Definition (Migration from solitude into an accumulation): A movement $\{\hat{\eta}^{\Gamma,i}\}_{i=1,...,n}$ is called a *migration of individual* α *from solitude into an accumulation* S if the following conditions are met:

i.) $\alpha \in S$

ii.) α is a solitary individual under Γ with $\hat{\eta}^{\Gamma,1}$, but not with $\hat{\eta}^{\Gamma,n}$.

iii.) S is a accumulation under Γ with $\hat{\eta}^{\Gamma,n}$, but not with $\hat{\eta}^{\Gamma,1}$.

iv.) $S \setminus \{\alpha\}$ is an accumulation or a solitary individual under Γ with

$\hat{\eta}^{\Gamma,1}$. ▲

Definition (Isolated Migration): A migration $\{\hat{\eta}^{\Gamma,i}\}_{i=1,\dots,n}$ of individual α is called an *isolated migration of individual* α if the following conditions are met:

i.) $\forall S \subseteq \mathscr{I} \wedge \alpha \notin S : \hat{\eta}_S^{\Gamma,1} = \hat{\eta}_S^{\Gamma,n}$

ii.) $\exists S \subseteq \mathscr{I} \wedge \alpha \in S : \hat{\eta}_S^{\Gamma,1} \neq \hat{\eta}_S^{\Gamma,n}$ ▲

A probability distribution $\hat{\eta}^{\Gamma}$ on $\{\hat{E}_S^{\Gamma} \mid S \subseteq \mathscr{I}\}$ defines a partition of $\mathscr{I}$ into accumulations and solitary individuals. This is stated by the following two propositions:

(1) α and β belong to the same cluster if and only if

$$\exists H \subseteq \mathscr{I} \wedge \{\alpha, \beta\} \subseteq H : \hat{\eta}_H^{\Gamma} \neq 0.$$

(2) α is solitary if and only if $\forall S \subseteq \mathscr{I} \wedge \{\alpha\} \subset S : \hat{\eta}_S^{\Gamma} = 0$.

For example, if $\hat{\eta}_S^{\Gamma} \neq 0$ for all $S \subseteq \mathscr{I}$ then the whole set $\mathscr{I}$ is a single accumulation. If $\hat{\eta}_S^{\Gamma} = 0$ for all $S \subseteq \mathscr{I}$ with $|S| > 1$, and $\hat{\eta}_{\{\alpha\}}^{\Gamma} \neq 0$ for all $\alpha \in \mathscr{I}$, then all individuals in $\mathscr{I}$ are solitary. If two individuals $\beta_1, \beta_2 \in \mathscr{I}$ form a cluster and all other individuals are solitary, then $\hat{\eta}_{\{\beta_1,\beta_2\}}^{\Gamma} \neq 0$, $\hat{\eta}_{\{\alpha\}}^{\Gamma} \neq 0$ for all $\alpha \in \mathscr{I} \setminus \{\beta_1, \beta_2\}$, and

$$\forall S \subseteq \mathscr{I} \wedge (|S| \neq 1 \wedge \{\beta_1, \beta_2\} \not\subset S) : \hat{\eta}_S^{\Gamma} = 0$$

describes the situation completely.

Incentive to migrate. An individual has to have an incentive to migrate. Such an incentive is given once an individual can improve its current situation by migration. Improvement refers here to improvement of the individual's *metabolic* situation. Right now there is, however, no explicit metabolic concept defined which could be used to define a concept like 'incentive'.

An individual is in a metabolically beneficial situation if the probability of reception of a metabolic source is large, and/or probability of reception of a metabolic sink is small. Incentive to move is given if, by moving, the individual can increase the probability of reception of a metabolic source and/or lower the probability of reception of a metabolic sink. Therefore receptance (as defined at the end of chapter 3) can be used to form a measure of incentive which in our context is the same as fitness.

Fitness in evolutionary biology is defined as the differential of survival and reproduction. A fitness function is any function which can be used to measure that differential. In a system like ours, which does not feature reproduction, fitness is equivalent with survival, i.e., metabolic benefit. An appropriate fitness function can then be created using probabilities for metabolic benefit or damage, i.e., receptance.

To investigate the conditions under which individuals will form accumulations it suffices to use as incentive fitness functions based on receptance. I will, therefore, not concern myself with specific calculations of expected metabolic benefits. In order to be complete I have however included in appendix 2 the definition of 'metabolic payoff function' which is based on the definition of stories in much the same way as the definition of the interactive process was.

In 3.2 I have defined receptance via sets of total encounter and/or focus. As I

stated above receptance will be used in constructing a measure of incentive or fitness. Part of the receptance via sets is a focus probability, or the acceptance. The following section discusses acceptance for the purpose of finding an algebraic expression for it.

4.2. Deriving a formula for the receptance of an individual via an accumulation

In this section I derive a formula of $\rho_{\{\alpha\}:S}^{\Gamma}$, which was defined in chapter 3 as

$$\rho_{\{\alpha\}:S}^{\Gamma} = \eta_S^{\Gamma} \cdot \sum_{\substack{K \subseteq S, \\ \alpha \in K}} (\hat{\varphi}_{K|S}^{\Gamma} \cdot \sum_{\substack{H \subseteq K, \\ \alpha \in H}} \hat{\rho}_{H|K}^{\Gamma})$$

$\rho_{\{\alpha\}:S}^{\Gamma}$ is the probability of reception of one realization of Γ by α through the accumulation S. When Γ is a metabolic source, $\rho_{\{\alpha\}:S}^{\Gamma}$ is a measure of α's fitness. When Γ is a metabolic sink, $1 - \rho_{\{\alpha\}:S}^{\Gamma}$ is a measure of α's fitness.

In the following I will derive successively more explicit expressions for $\hat{\rho}_{H|K}^{\Gamma}$,

$$\varphi_{\{\alpha\}|S}^{\Gamma} = \eta_S^{\Gamma} \cdot \sum_{\substack{K \subseteq S, \\ \alpha \in K}} \hat{\varphi}_{K|S}^{\Gamma},$$

The formula for $\hat{\rho}_{H|K}^{\Gamma}$. First I derive a formula for the probability $\hat{\rho}_{H|K}^{\Gamma}$ of H being the set of total reception under the condition that K was the preceeding set of total focus under Γ. Since a reception event of Γ by any individual can only happen after there was a focus event between that individual and Γ we have to set $\hat{\rho}_{H|K}^{\Gamma} = 0$ if $H \not\subset K$. Let $H \subseteq K$. Since reception events between individuals and Γ occur independently of each other we obtain for $\hat{\rho}_{H|K}^{\Gamma}$ the equation $\hat{\rho}_{H|K}^{\Gamma} = \prod_{\beta \in H} \hat{\rho}_{\{\beta\}|\{\beta\}}^{\Gamma} \cdot \prod_{\beta \in K \setminus H} (1 - \hat{\rho}_{\{\beta\}|\{\beta\}}^{\Gamma})$. The following simplification will yield more manageable formulas:

(Equal performance of individuals under metabolic sources and sinks): Let Γ be a metabolic source or sink. Then: $\exists \rho^{\Gamma} > 0 \forall \alpha \in \mathscr{S} : \hat{\rho}^{\Gamma}_{\{\alpha\}|\{\alpha\}} = \rho^{\Gamma}$.

With this simplification we obtain $\hat{\rho}^{\Gamma}_{H|K} = \begin{cases} 0 & \text{, if } H \not\subset K \\ (\rho^{\Gamma})^{|H|} \cdot (1-\rho^{\Gamma})^{|K|-|H|} & \text{, if } H \subseteq K \end{cases}$.

The formula for $\displaystyle\sum_{\substack{H \subseteq K, \\ \alpha \in H}} \hat{\rho}^{\Gamma}_{H|K}$. $\displaystyle\sum_{\substack{H \subseteq K, \\ \alpha \in H}} \hat{\rho}^{\Gamma}_{H|K}$ is the probability that a reception event of Γ by at least α occurs under the condition that K was the preceeding set of total focus under Γ. This probability is denoted by $\rho^{\Gamma}_{\{\alpha\}|K}$. If $\alpha \notin K$ then $\rho^{\Gamma}_{\{\alpha\}|K} = 0$. Otherwise there are $\binom{|K|-1}{|H|-1}$ possibilities to choose a set of size $|H|$ from a set of size $|K|$ given that α has to be contained in the chosen set. There are overall $2^{|K|} - 1$ non-empty subsets in K. So the probability of choosing a set of size $|H|$ containing α is $\dfrac{\binom{|K|-1}{|H|-1}}{2^{|K|} - 1}$. The probability that such a set is a set of total reception is $(\rho^{\Gamma})^{|H|} \cdot (1-\rho^{\Gamma})^{|K|-|H|}$. From this we obtain

$$\rho^{\Gamma}_{\{\alpha\}|K} = \sum_{\substack{H \subseteq K, \\ \alpha \in H}} \hat{\rho}^{\Gamma}_{H|K} = \sum_{i=1}^{|K|} (\rho^{\Gamma})^{i} \cdot (1-\rho^{\Gamma})^{|K|-i} \cdot \frac{\binom{|K|-1}{i-1}}{2^{|K|} - 1},$$

which simplifies to $\rho^{\Gamma}_{\{\alpha\}|K} = \dfrac{\rho^{\Gamma}}{2^{|K|} - 1}$. Therefore we obtain overall

$$\rho^{\Gamma}_{\{\alpha\}|K} = \begin{cases} 0 & \text{, if } \alpha \in K \\ \dfrac{\rho^{\Gamma}}{2^{|K|} - 1} & \text{, if } \alpha \in K \end{cases}.$$

Acceptance in terms of confusion and dilution. Let $S \subseteq \mathscr{S}$ be an accumulation under the metabolic source or sink Γ and let $\alpha \in S$. I denoted with $\varphi^{\Gamma}_{\{\alpha\}:S}$ acceptance of Γ by at least α through S, which is the probability that the next focus event in an interactive

process is a focus between at least α and Γ.

One reason for an encounter not to be succeeded by a focus is the ability of the set S to dilute the focus between α and Γ. A lion will be less successful when attacking a herd of zebras than attacking a number of widely dispersed zebras, since on encounter of the second constellation of zebras the predator will face only one zebra at a time and will not have to deal with confusion and dilution generated by the closeness of others. Confusion is the ability of zebras to move about in a fashion which makes it difficult for the predator to keep track of any single zebra. Dilution is the the effect that the probability of being captured by a lion is for any given zebra lower in a group simply because the danger is divided. Given that an encounter has happened, the probability that a focus within accumulation S will not occur because of confusion is denoted with γ_S^Γ. The index S indicates that confusion is considered to be a property of the accumulation S.

$\varphi_{\{\alpha\}:S}^\Gamma$ is, therefore, the probability of the event (1) overcoming the confusion of Γ by S, and (2) overcoming the dilution of Γ by S capturing at least α. (2) means the probability of focus due to random drawing between at least individual α and Γ ignoring the confusion effect of S. Therefore, $\varphi_{\{\alpha\}:S}^\Gamma = (1 - \gamma_S^\Gamma) \cdot f_{\{\alpha\}:S}^\Gamma$, and analogously $\hat{\varphi}_{\{\alpha\}:S}^\Gamma = (1 - \gamma_S^\Gamma) \cdot \hat{f}_{\{\alpha\}:S}^\Gamma$, γ_S^Γ being the probability of confusion of Γ by S, $f_{\{\alpha\}:S}^\Gamma$ is the probability of drawing at least individual α in S, and $\hat{f}_{\{\alpha\}:S}^\Gamma$ is the probability of drawing only individual α in S. The probability of overcoming dilution, $f_{\{\alpha\}:S}^\Gamma$, is dependent on the number of individuals in S and on the maximum number m^Γ of individuals possibly involved within a focus with Γ, i.e., the focus capacity of Γ. After overcoming confusion at least one individual is chosen from S. If there is no confusion, which means that $\gamma_S^\Gamma = 0$, then $\varphi_{\{\alpha\}:S}^\Gamma = f_{\{\alpha\}:S}^\Gamma$. In that case focus is simply a random drawing of sets of individuals according to a probability distribution which depends on the focus capacity of Γ. If $\gamma_S^\Gamma = 1$, then for all $\beta \in S : \varphi_{\{\beta\}:S}^\Gamma = 0$ which means that there will never

be a focus of any $\beta \in S$ with Γ through S since confusion is perfect.

Since confusion is the only reason that a focus event after encounter will not

happen we get $\sum\limits_{\substack{H \subseteq S, \\ H \neq \varnothing}} \hat{f}_{H|S}^{\Gamma} = 1$. $\sum\limits_{\substack{H \subseteq S, \\ H \neq \varnothing}} \hat{\varphi}_{H|S}^{\Gamma}$ is the probability that there is a focus event

between at least one individual in S and Γ. From here

$\sum\limits_{\substack{H \subseteq S, \\ H \neq \varnothing}} \hat{\varphi}_{H|S}^{\Gamma} = \sum\limits_{\substack{H \subseteq S, \\ H \neq \varnothing}} (1 - \gamma_S^{\Gamma}) \cdot \hat{f}_{H|S}^{\Gamma} = (1 - \gamma_S^{\Gamma}) \cdot \sum\limits_{\substack{H \subseteq S, \\ H \neq \varnothing}} \hat{f}_{H|S}^{\Gamma} = 1 - \gamma_S^{\Gamma}$. So the probability of confusion

of Γ by S can be written as $\gamma_S^{\Gamma} = 1 - \sum\limits_{\substack{H \subseteq S, \\ H \neq \varnothing}} \hat{\varphi}_{H|S}^{\Gamma}$.

A short remark on solitary individuals under Γ is in order. There is no confusion

in solitary individuals. That means that $\forall \alpha \in \mathcal{T} : \gamma_{\{\alpha\}}^{\Gamma} = 0$. This also means that

$f_{\{\alpha\}:S}^{\Gamma} = \hat{f}_{\{\alpha\}:S}^{\Gamma} = \varphi_{\{\alpha\}:S}^{\Gamma} = \hat{\varphi}_{\{\alpha\}:S}^{\Gamma} = 1$ if α is solitary.

Illustrating confusion. A reception of Γ by $\alpha \in S$ through the accumulation S can be

illustrated as follows: The probability of the encounter is η_S^{Γ}. Once the encounter has

occurred, Γ will face confusion. Confusion is overcome with a probability of $1 - \gamma_S^{\Gamma}$,

after which an individual $\alpha \in S$ is chosen with probability $f_{\{\alpha\}:S}^{\Gamma}$. Figure 4.1 illustrates

this.

$$\varphi_{\{\alpha\}:S}^{\Gamma} = (1 - \gamma_S^{\Gamma}) \cdot f_{\{\alpha\}:S}^{\Gamma}$$

$$\Gamma \xrightarrow{\ \hat{\eta}_S^{\Gamma}\ }$$

Encounter between Γ and S

$$1 - \gamma_S^{\Gamma}$$
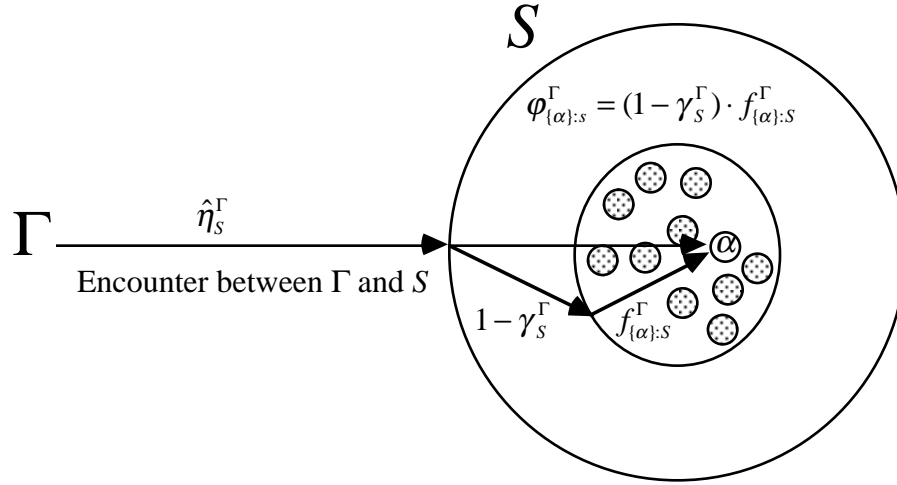
$$f_{\{\alpha\}:S}^{\Gamma}$$

Figure 4.1.: Illustration of the concept of confusion

The acceptance formula. It is now possible to find a formula for the acceptance $\varphi_{\{\alpha\}:S}^{\Gamma}$.

We know that $\varphi_{\{\alpha\}:S}^{\Gamma} = (1 - \gamma_S^{\Gamma}) \cdot f_{\{\alpha\}:S}^{\Gamma} = (1 - \gamma_S^{\Gamma}) \cdot \sum_{\substack{H \subseteq S, \\ \alpha \in H}} \hat{f}_{H|S}^{\Gamma}$. If $|H_1| = |H_2|$ then $\hat{f}_{H_1|S}^{\Gamma} = \hat{f}_{H_2|S}^{\Gamma}$.

There are $\binom{|S|-1}{|H|-1}$ possibilities to draw sets of size $|H|$ from a set of size $|S|$ under the condition that α has to be in all of them. The probability that α is in a set of size i is therefore $\dfrac{\binom{|S|-1}{i-1}}{2^n - 1}$, since there are $2^n - 1$ non-empty subsets in a set of size n.

First assume that the probabilities of focus between Γ and any subset of S are the same. The formula for the acceptance is then $\varphi_{\{\alpha\}:S}^{\Gamma} = (1 - \delta_S^{\Gamma}) \cdot \sum_{i=1}^{|S|} \dfrac{\binom{|S|-1}{i-1}}{2^{|S|} - 1}$ which can be simplified to $\varphi_{\{\alpha\}:S}^{\Gamma} = (1 - \gamma_S^{\Gamma}) \cdot \dfrac{2^{|S|-1}}{2^{|S|} - 1}$.

However, in general, the probability of focus between Γ and subsets of individuals of S will vary with the size of those subsets. For example, focus occurs only between a lion and a single zebra, not two, or three or more. The probability that a

lion focuses on more than one zebra is 0. The probability of focus depends on m^{Γ}, the focus capacity of Γ. The focus capacity of Γ can be represented by a focus weight function. A focus weight function assigns to each set seize i the probability of focus for a set of that size. Therefore, I define for Γ the focus weight function w_n^{Γ} as follows:

$$w_n^{\Gamma} : \begin{array}{ccc} \{1,2,...,n\} & \to & [0,1] \\ i & \mapsto & w_n^{\Gamma}(i) \end{array}, \text{ and } \sum_{i=1}^{n} w_n^{\Gamma}(i) = 1$$

where n is the size of the encountered accumulation. In the zebra-lion example the accumulation size does not matter: The lion will focus always on exactly one zebra. Let's, however, postulate a predator who always focuses on five zebras. Then, when encountering a herd of at least five zebras the predator will focus on them with probability one. When an encounter with a group of less than five zebras happens, it is safe to assume that the predator will focus on all zebras present. w_n^{Γ} is, therefore, dependent on accumulation size only, if the accumulation size is below the focus capacity of Γ. If the focus capacity of Γ is ∞, then w_n^{Γ} will always be dependent on accumulation size. If there is focus exclusively between sets of a certain size j and Γ, then

(1) If $n \leq j$ then $w_n^{\Gamma}(n) = 1$ and $w_n^{\Gamma}(i) = 0$ for $i = 1,2,...,n-1$. Thus:

$$\varphi_{\{\alpha\}:S}^{\Gamma} = (1 - \delta_S^{\Gamma})$$

(2) If $n > j$ then $w_n^{\Gamma}(j) = 1$ and $w_n^{\Gamma}(i) = 0$ for $i \in \{1,2,...,n\}$ and $i \neq j$. Thus:

$$\varphi_{\{\alpha\}:S}^{\Gamma} = (1 - \delta_S^{\Gamma}) \cdot \frac{j}{|S|}$$

In general the formula for $\varphi^{\Gamma}_{\{\alpha\}:S}$ is given by $\varphi^{\Gamma}_{\{\alpha\}:S} = (1 - \delta^{\Gamma}_S) \cdot \sum_{i=1}^{|S|} w^{\Gamma}_{|S|}(i) \dfrac{\binom{|S|-1}{i-1}}{\binom{|S|}{i}}$

and simplified to $\varphi^{\Gamma}_{\{\alpha\}:S} = (1 - \delta^{\Gamma}_S) \cdot \sum_{i=1}^{|S|} w^{\Gamma}_{|S|}(i) \dfrac{i}{|S|}$, where $w^{\Gamma}_{|S|}(i) = 0$ for $i > m^{\Gamma}$. For

$|S| < m^{\Gamma}$ the weight is distributed in some to be specified fashion among the possible set

sizes.

Joining acceptance and receptance. We are now in the position to find an expression

for $\sum\limits_{\substack{K \subseteq S, \\ \alpha \in K}} (\hat{\varphi}^{\Gamma}_{K|S} \cdot \sum\limits_{\substack{H \subseteq K, \\ \alpha \in H}} \hat{\rho}^{\Gamma}_{H|K})$. Using the formulas for receptance and acceptance derived

earlier yields $(1 - \delta^{\Gamma}_S) \cdot \sum\limits_{i=1}^{|S|} \left(w^{\Gamma}_{|S|}(i) \dfrac{i}{|S|} \cdot \dfrac{\rho^{\Gamma}}{2^i - 1} \right)$. Overall we obtain for the receptance:

$$\rho^{\Gamma}_{\{\alpha\}:S} = \eta^{\Gamma}_S \cdot (1 - \delta^{\Gamma}_S) \cdot \rho^{\Gamma} \cdot \sum_{i=1}^{|S|} \frac{i \cdot w^{\Gamma}_{|S|}(i)}{|S| \cdot (2^i - 1)}$$

Because confusion is a mechanism which evolves *after* accumulations have

formed it is reasonable to assume ignore it for the remainder of this thesis. This means

$\delta^{\Gamma}_S = 0$. Thus $\rho^{\Gamma}_{\{\alpha\}:S}$ becomes $\rho^{\Gamma}_{\{\alpha\}:S} = \eta^{\Gamma}_S \cdot \rho^{\Gamma} \cdot \sum\limits_{i=1}^{|S|} \dfrac{i \cdot w^{\Gamma}_{|S|}(i)}{|S| \cdot (2^i - 1)}$ where $\alpha \in S$ and S is an

accumulation. The formula for acceptance becomes then $\varphi^{\Gamma}_{\{\alpha\}:S} = \sum\limits_{i=1}^{|S|} w^{\Gamma}_{|S|}(i) \dfrac{i}{|S|}$,

Example of focus always occurring between a certain number of individuals and

Γ. Assume there is an accumulation of n individuals. Define the weight function w^{Γ}_n

such that $w^{\Gamma}_n(j) = 1$ for a $j \in \{1, 2, ..., n\}$ $w^{\Gamma}_n(i) = 0$ for $i = 1, 2, ..., n \wedge i \neq j$.

Then $\rho^{\Gamma}_{\{\alpha\}:S} = \dfrac{j \cdot \eta^{\Gamma}_S \cdot \rho^{\Gamma}}{n \cdot (2^j - 1)}$. This example shows that in the case of one specific set size

$\rho^{\Gamma}_{\{\alpha\}:S}$ is a decreasing function in n. A more general result is stated in the theorem

below.

Let's apply the obtained formula to the zebra-lion example. Assume there is a herd of n zebras. Let Γ be the metabolic sink 'lion'. If a focus occurs, then for each realization of Γ the probability of focusing on exactly one zebra is 1 for all n. Focussing on any different number of zebras is 0. Thus $w_n^\Gamma(i) = 0$ for $i = 2,3,...,n$, and $w_n^\Gamma(1) = 1$. $\rho_{\{\alpha\}:S}^\Gamma$ is therefore here $\rho_{\{\alpha\}:S}^\Gamma = \dfrac{\eta_S^\Gamma \cdot \rho^\Gamma}{n}$. Hence the receptance is decaying proportionally to the reciprocal of the accumulation size. This is the fastest decay possible given $\rho_{\{\alpha\}:S}^\Gamma$.

The opposite extreme to the zebra-lion example is the case where focus happens only between all individuals and the metabolic source or sink. Assume there is an accumulation of n individuals. Define the weight function w_n^Γ such that $w_n^\Gamma(i) = 0$ for $i = 1,2,...,n-1$ and $w_n^\Gamma(n) = 1$. Then $\rho_{\{\alpha\}:S}^\Gamma = \dfrac{\eta_S^\Gamma \cdot \rho^\Gamma}{2^n - 1}$. A biological example would be the piranha-cow example, assuming that any school size could kill the cow.

Example of focus occurring with equal probability for all set sizes. This example is of technical interest. There is no apparent biological system for which this example can serve as a model. However, it is used to show a proof for the receptance which is decreasing as accumulation size increases. The method of proving that fact for this special case might also be used for more sophisticated ones. Especially, I will later assume that for an accumulation, whose size is below the focus capacity of a metabolic source or sink, the probabilities of focus for all subsets are equal. The following lemma guarantees then, that for accumulation sizes up to the focus capacity the receptance is decreasing.

The focus weight function for this example is defined by $w_n^\Gamma(i) = \dfrac{1}{2^n - 1}\dbinom{n}{i}$ for $i = 1,2,...,n$, and for all n.

Therefore $\rho^{\Gamma}_{\{\alpha\}:S} = \eta^{\Gamma}_S \cdot \rho^{\Gamma} \cdot \sum_{i=1}^{|S|}\left(\frac{w^{\Gamma}_{|S|}(i)}{2^i-1} \cdot \frac{\binom{|S|-1}{i-1}}{\binom{|S|}{i}} \right) = \frac{\eta^{\Gamma}_S \cdot \rho^{\Gamma}}{2^{|S|}-1} \cdot \sum_{i=1}^{|S|}\left(\frac{1}{2^i-1} \cdot \binom{|S|-1}{i-1} \right).$

Receptance Lemma 1: The sequence $\left\{ \frac{1}{2^n-1} \sum_{i=1}^{n} \frac{\binom{n-1}{i-1}}{2^i-1} \right\}_{n \in \mathbb{N}}$ is strictly decreasing.

Proof: Since $\frac{1}{2^n-1} \sum_{i=1}^{n} \binom{n-1}{i-1} = \frac{2^{n-1}}{2^n-1}$, the sequence

$\left\{ \frac{1}{2^n-1} \sum_{i=1}^{n} \binom{n-1}{i-1} \right\}_{n \in \mathbb{N}} = \left\{ \frac{2^{n-1}}{2^n-1} \right\}_{n \in \mathbb{N}}$ is certainly strictly decreasing

($\lim_{n \to \infty} \frac{1}{2^n-1} \sum_{i=1}^{n} \binom{n-1}{i-1} = \frac{1}{2}$). From this we conclude that the sequence

$\left\{ \frac{1}{2^n-1}\left(1 + \sum_{i=2}^{n} \frac{\binom{n-1}{i-1}}{2^2-1} \right) \right\}_{n \in \mathbb{N}}$ is strictly decreasing as well. In general: For all $N \in \mathbb{N}$

the sequence $\left\{ \frac{1}{2^n-1}\left(\sum_{i=1}^{n} \frac{\binom{n-1}{i-1}}{2^{\min\{N,i\}}-1} \right) \right\}_{n \in \mathbb{N}}$ is strictly decreasing. As $N \to \infty$ the strictly

decreasing sequences $\left\{ \frac{1}{2^n-1}\left(\sum_{i=1}^{n} \frac{\binom{n-1}{i-1}}{2^{\min\{N,i\}}-1} \right) \right\}_{n \in \mathbb{N}}$ approach the sequence

$\left\{ \frac{1}{2^n-1} \sum_{i=1}^{n} \frac{\binom{n-1}{i-1}}{2^i-1} \right\}_{n \in \mathbb{N}}$ which is, therefore, strictly decreasing as well. $\square$

The following second receptance lemma addresses the situation in which there is a finite focus capacity.

Receptance Lemma 2: Let m^Γ be the focus capacity of Γ. Let $n = |S|$, $n \geq m^\Gamma$, $w^\Gamma(i) = 0$ for $i > m^\Gamma$, and $w^\Gamma(i) \geq 0$ for $i \leq m^\Gamma$. Let $\rho_{\{\alpha\}:S}^\Gamma = \dfrac{\eta_S^\Gamma \cdot \rho^\Gamma}{n} \cdot \sum_{i=1}^{n} \left(\dfrac{i \cdot w^\Gamma(i)}{2^i - 1} \right)$.

Then $\rho_{\{\alpha\}:S}^\Gamma$ is a strictly decreasing function in $n \geq m^\Gamma$, and

$$\rho_{\{\alpha\}:S}^\Gamma = \frac{\eta_S^\Gamma \cdot \rho^\Gamma}{n} \cdot \sum_{i=1}^{m^\Gamma} \left(\frac{i \cdot w^\Gamma(i)}{2^i - 1} \right).$$

Proof: Let $n \geq m^\Gamma$. Then $w_n^\Gamma(i) = w_m^\Gamma(i) = w^\Gamma(i)$ for all $i \in \mathbb{N}$. Clearly, $\dfrac{i \cdot w^\Gamma(i)}{n \cdot (2^i - 1)} > \dfrac{i \cdot w^\Gamma(i)}{(n+1) \cdot (2^i - 1)}$ for $i = 1, 2, ..., n+1$ and for $w^\Gamma(i) > 0$. Thus, it remains to be shown that

$$\sum_{i=1}^{n} \left(\frac{i \cdot w^\Gamma(i)}{n \cdot (2^i - 1)} \right) > \sum_{i=1}^{n+1} \left(\frac{i \cdot w^\Gamma(i)}{(n+1) \cdot (2^i - 1)} \right) \qquad (1)$$

Since $n \geq m^\Gamma$ we obtain that $w_{n+1}^\Gamma(n+1) = 0$. Therefore,

$$\sum_{i=1}^{n} \left(\frac{i \cdot w^\Gamma(i)}{n \cdot (2^i - 1)} \right) = \sum_{i=1}^{m^\Gamma} \left(\frac{i \cdot w^\Gamma(i)}{n \cdot (2^i - 1)} \right) > \sum_{i=1}^{m^\Gamma} \left(\frac{i \cdot w^\Gamma(i)}{(n+1) \cdot (2^i - 1)} \right) = \sum_{i=1}^{n+1} \left(\frac{i \cdot w^\Gamma(i)}{(n+1) \cdot (2^i - 1)} \right)$$

which is clearly true. ❑

Corollary: Let $\rho_{\{\alpha\}:S}^\Gamma = \dfrac{\eta_S^\Gamma \cdot \rho^\Gamma}{n} \cdot \sum_{i=1}^{n} \left(w_n^\Gamma(i) \cdot i \cdot \dfrac{(1 + \rho^\Gamma)^{i-1}}{2^i - 1} \right)$, where $n = |S|$, be the receptance of α through accumulation S. Let $0 \leq \rho^\Gamma \leq 1$. Let m^Γ be the focus capacity of Γ, and let the weight function w_n^Γ be defined in the following way:

(1) If $n \leq m^\Gamma$ then $w_n^\Gamma(i) = \dfrac{1}{2^n - 1} \dbinom{n}{i}$ for $i = 1, 2, ..., n$.

(2) If $n > m^\Gamma$ then $w_n^\Gamma(i) = \dfrac{1}{2^{m^\Gamma} - 1} \dbinom{m^\Gamma}{i}$ for $i = 1, 2, ..., m^\Gamma$,

and $w_n^\Gamma(i) = 0$ for $i = m^\Gamma + 1, m^\Gamma + 2, ..., n$.

Then $\rho_{\{\alpha\}:S}^\Gamma$ is decreasing in n. ❑

Definition (Standard Receptance): If the receptance $\rho_{\{\alpha\}:S}^{\Gamma}$ of α through accumulation S satisfies conditions (1) and (2) in the corollary above, then $\rho_{\{\alpha\}:S}^{\Gamma}$ is called the *standard receptance of α through accumulation S*. The standard receptance is denoted by $\overline{\rho}_{\{\alpha\}:S}^{\Gamma}$, and is

$$\overline{\rho}_{\{\alpha\}:S}^{\Gamma} = \frac{\min(|S|,m^{\Gamma}) \cdot \eta_S^{\Gamma} \cdot \rho^{\Gamma}}{|S| \cdot (2^{\min(|S|,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(|S|,m^{\Gamma})} \frac{\binom{\min(|S|,m^{\Gamma})-1}{i-1}}{2^i - 1}$$

Conclusion. As the accumulation size increases, the standard receptance of Γ by any individual in the accumulation decreases. The decrease is hyperbolic for $n > m^{\Gamma}$ and will be slower for $n \leq m^{\Gamma}$. Therefore, if Γ is a metabolic sink, then individuals always have an incentive to accumulate under the standard receptance of Γ. If Γ is a metabolic source, then individuals always have an incentive to become solitary under the standard receptance of Γ.

Variations. Only the first of the following variations will be investigated further (more than one realization for the metabolic source or sink). I will not be concerned in this thesis with the change of the individual receptance ρ^{Γ}. It is assumed here to be constant.

(1)   Assume that there are p realizations of Γ. Assume that the reception events due to those realizations are independent of each other. The probability that a reception of Γ by α happens equals the probability that a reception event between at least one of those realizations and α happens. Denote this probability by $\rho_{\{\alpha\}:S}^{\Gamma,p}$. Then $\rho_{\{\alpha\}:S}^{\Gamma,1} = \rho_{\{\alpha\}:S}^{\Gamma}$, and $\rho_{\{\alpha\}:S}^{\Gamma,p} = 1 - \left[1 - \rho_{\{\alpha\}:S}^{\Gamma,1}\right]^p$. The receptance is therefore increasing in the number of realizations of Γ which is a result clearly supported by intuition.

The standard receptance under p realizations of Γ is denoted by $\bar{\rho}_{\{\alpha\}:S}^{\Gamma,p}$.

(2)   It is possible that the individual receptance ρ^Γ itself is dependent on the number of realizations of Γ. For example, a zebra in a herd of any size is easier hunted down by 5 lions than by only one. This is not only due to the number of lions alone but also due to coordination between the lions. This contradicts the assumption made in (1) of independence of reception by different realizations. A growing number of lions will eventually decrease the receptance of a zebra, as competition between lions will interfere with their ability to cooperate.

(3)   The success of a school of piranhas to devour a cow depends on the size of that school. A small school is less successful than a large one. The individual receptance ρ^Γ changes with the size of the school. For small schools ρ^Γ is decreasing, because the cow will escape. For larger schools ρ^Γ will increase until a certain value at which the cow is brought down with probability 1. After that the individual receptance will remain the same, although $\rho_{\{\alpha\}:S}^\Gamma$ will decrease due to the size of the school.

Zebra-grass Example. Assume there is a herd of n zebras. Let the metabolic source 'grass' be given. Assume that the grass is given as p realizations in the form of grass bushels.

Let's first assume, like in the zebra-lion example, that a focus is only possible between at most one grass bushel and a single zebra. Then $\rho_{\{\alpha\}:S}^{\Gamma,p} = 1 - \left[1 - \dfrac{\eta_s^\Gamma \cdot \rho^\Gamma}{|S|}\right]^p$.

Assume now that there can be a focus between up to six zebras and a single grass bushel. Further assume that any number of zebras up to six can experience focus with a grass bushel with the same probability.

Let first $|S| \geq 6$. Then the receptance $\rho_{\{\alpha\}:S}^{\Gamma,p}$ becomes

$$\rho_{\{\alpha\}:S}^{\Gamma,p} = 1 - \left[1 - \frac{\eta_S^\Gamma \cdot \rho^\Gamma}{|S|} \cdot \sum_{i=1}^{|S|} \left(\frac{i \cdot w_{|S|}^\Gamma(i)}{2^i - 1} \right) \right]^p$$

where $w_{|S|}^\Gamma(i) = \dfrac{\binom{6}{i}}{2^6 - 1}$ for $i = 1, 2, ..., 6$, and $w_{|S|}^\Gamma(i) = 0$ for $i > 6$. $\rho_{\{\alpha\}:S}^{\Gamma,p}$ simplifies to

$$\rho_{\{\alpha\}:S}^{\Gamma,p} = 1 - \left[1 - \frac{6 \cdot \eta_S^\Gamma \cdot \rho^\Gamma}{|S| \cdot (2^6 - 1)} \cdot \sum_{i=1}^{6} \left(\frac{\binom{5}{i-1}}{2^i - 1} \right) \right]^p$$

Let now $|S| < 6$. Then, still assuming that any number of zebras can experience focus with a grass bushel with the same probability, we obtain for $w_{|S|}^\Gamma(i)$ equations

$$w_{|S|}^\Gamma(i) = \frac{\binom{|S|}{i}}{2^{|S|} - 1} \text{ for } i = 1, 2, ..., |S|. \quad \rho_{\{\alpha\}:S}^{\Gamma,p} \text{ is then}$$

$$\rho_{\{\alpha\}:S}^{\Gamma,p} = 1 - \left[1 - \frac{\eta_S^\Gamma \cdot \rho^\Gamma}{(2^{|S|} - 1)} \cdot \sum_{i=1}^{|S|} \left(\frac{\binom{|S|-1}{i-1}}{2^i - 1} \right) \right]^p$$

Figure 4.2 compares graphs of the receptance dependent on the number of realizations of the metabolic source. Assumed is a single accumulation. The graphs show that there is no incentive for any individual to remain in this accumulation, since the receptance of a solitary individual is always the highest.
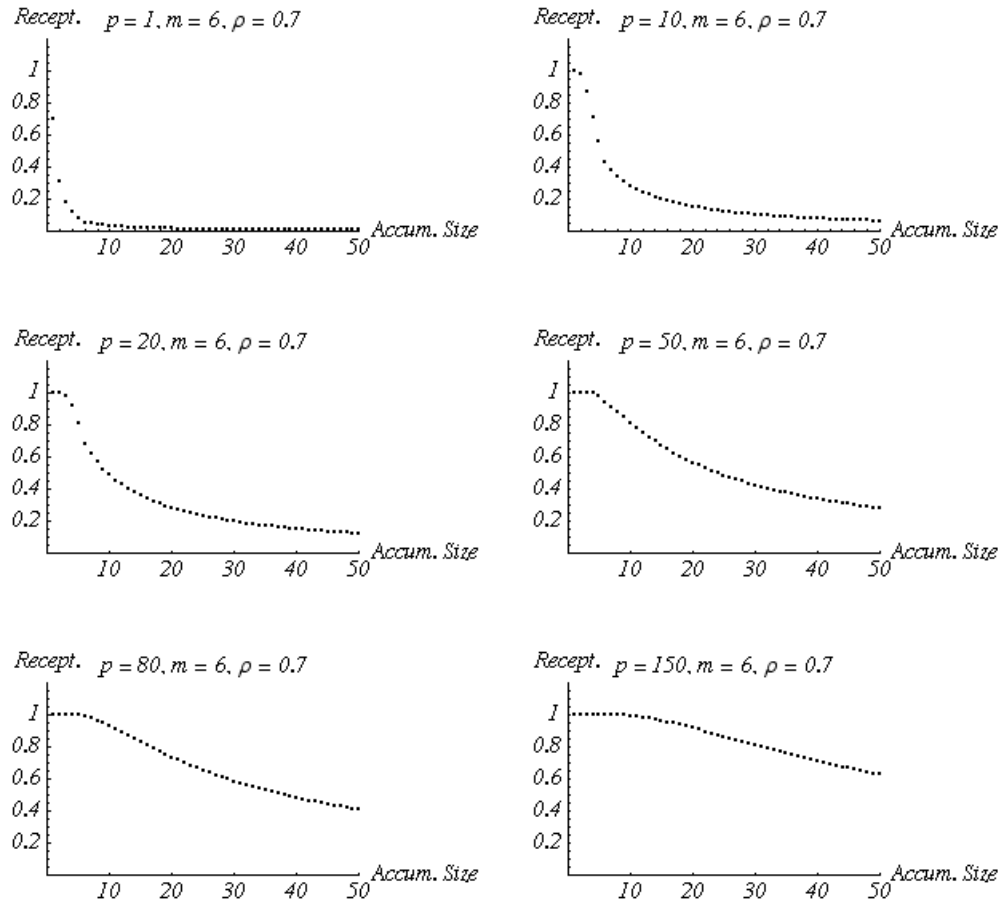
Figure 4.2.: Graphs for the zebra - grass example. p is the number of representations of Γ, m is the focus capacity of Γ, and $\rho = \rho^\Gamma$ is the individual receptance. The receptance is decreasing with accumulation size. With increasing p the overall receptance approaches 1. The probability of encounter is assumed to be 1.

4.3.   Example: Dispersion under a metabolic source

My approach in this thesis is based on the assumption that originally all individuals are highly competitive over metabolic sources. This assumption leads to the suspicion that under the original selective regime solitary individuals must have the highest fitness. Below, I will discuss an example which shows that even though all individuals will eventually be solitary the solitary fitness will not be the highest one. The complete solitary state is a globally approachable and attractive equilibrium (actually a Nash-equilibrium) with suboptimal payoff. Migration into solitude is, therefore, an evolutionary stable strategy (ESS; For two summaries on ESS theory see Hines, 1987, and Weibull, 1998). A more illustrative example is given in appendix 3. This example makes however certain assumptions regarding the structure of space (partitions of space), and is less general than the one given below. The example in appendix 3 is a model which demonstrates how under a predator prey individuals will eventually accumulate without gain or even with loss in fitness.

For the example regarding the accumulation behavior under a metabolic source the following list of assumptions are made:

(1) Γ is a metabolic source for all individuals in $\mathscr{T}$.

(2) Γ is assumed to be a metabolic source with only one realization for each probability measure on $\{\hat{E}_S^\Gamma \,|\, S \subseteq \mathscr{T}\}$.

(3)   The focus capacity of Γ is 1.

(4) $\mathscr{T}$ is fully accumulated under $\hat{\eta}^{\Gamma,1}$. That means that $\mathscr{T}$ itself is an accumulation.

(5)   If there are k accumulations and solitary individuals present, then the probability that a certain accumulation or solitary individual is

encountered next is $\dfrac{1}{k}$.

[This means that the probability of encounter is independent of the size of the accumulation. A single cow is a realization of the metabolic source 'cow' for the piranha. If there is only one cow available then the exposure of a certain piranha school to at least this cow is $\dfrac{1}{k}$ if there are k schools and solitary individuals assuming the encounter is uniformly distributed over the schools and solitary individuals. If there are p cows under the same conditions, then the probability that there is an encounter between at least one of them with a given piranha school is $1-\left(1-\dfrac{1}{k}\right)^{p}$. If $p \rightarrow \infty$, then the exposure approaches 1. Note that the probability measures η^{Γ} are dependent on the metabolic source and not on its realizations. Even if there are many cows there is always only one probability measure η^{Γ} at the time. Another example is that of zebra and grass. A realization of grass is a single bushel of grass. If there is a total encounter between maximally one zebra and a single bushel of grass, then zebras are solitary. This is the case when there is abundant supply of grass. The exposure of the zebra to grass is $1-\left(1-\dfrac{1}{k}\right)^{p}$, where p is the number of bushels of grass and k is the number of zebras. If grass is sparse, then total encounter between a bushel of grass and more than one zebra is expected. If this is the case, accumulations of zebra under the metabolic source 'grass' exist. However, the zebras will then have an incentive to decrease the probability of encountering a single piece of grass simultaneously. They will disperse and approach solitude again.]

(6)   The size of the focus set is limited to 1. That means that focus will occur between the metabolic source and at most one individual. The formula

for the receptance in that case is $\rho^{\Gamma}_{\{\alpha\}:S} = \dfrac{\eta^{\Gamma,t}_S \cdot \rho^{\Gamma}_{\alpha}}{n}$ for all $t \in \mathbb{N}$. Here we can distinguish between individual receptances since no complicating products of individual receptances are present.

(7) Closure of total encounter events is assumed.

[Each subset of $\mathscr{I}$ can become a cluster under the appropriate probability measure on $\{\hat{E}^{\Gamma}_S \mid S \subseteq \mathscr{I}\}$]

Let $N := |\mathscr{I}|$. Then the probability of reception via set of encounter $\mathscr{I}$ under $\hat{\eta}^{\Gamma,1}$ is $\rho^{\Gamma}_{\alpha:\mathscr{I}} = \dfrac{1}{N} \cdot \rho^{\Gamma}_{\alpha}$, because $\eta^{\Gamma}_{\mathscr{I}} = 1$.

a) First individual leaving. Let's assume that a single individual α is leaving the accumulation of all individuals. Then α will become solitary and α's leaving defines a new probability measure $\hat{\eta}^{\Gamma,2}$ on $\{\hat{E}^{\Gamma}_S \mid S \subseteq \mathscr{I}\}$ in the following way:

$$\forall S \subseteq \mathscr{I} \wedge \{\alpha\} \subset S : \hat{\eta}^{\Gamma,2}_S = 0 \text{ and } \forall S \subseteq \mathscr{I} \wedge \alpha \notin S : \hat{\eta}^{\Gamma,2}_S = \hat{\eta}^{\Gamma,1}_S$$

Because of assumption (2) we get $\eta^{\Gamma,2}_{\{\alpha\}} = \dfrac{1}{2}$, and $\eta^{\Gamma,2}_{\mathscr{I}\setminus\{\alpha\}} = \dfrac{1}{2}$. Therefore, the probability of reception via set of encounter $\{\alpha\}$ under $\hat{\eta}^{\Gamma,2}$ is $\rho^{\Gamma}_{\alpha:\{\alpha\}} = \dfrac{1}{2} \cdot \dfrac{1}{|\{\alpha\}|} \cdot \rho^{\Gamma}_{\alpha} = \dfrac{\rho^{\Gamma}_{\alpha}}{2}$. For any $\beta \in \mathscr{I}\setminus\{\alpha\}$ we get $\rho^{\Gamma}_{\beta:\mathscr{I}\setminus\{\alpha\}} = \dfrac{1}{2} \cdot \dfrac{1}{|\mathscr{I}\setminus\{\alpha\}|} \cdot \rho^{\Gamma}_{\alpha} = \dfrac{\rho^{\Gamma}_{\alpha}}{2(N-1)}$. Remember now that Γ is a metabolic source. By leaving the accumulation $\mathscr{I}$ individual α has changed the probability of focus between itself and the metabolic sink from $\dfrac{1}{N}$ to $\dfrac{1}{2}$. If $N > 2$, then $\dfrac{1}{N} < \dfrac{1}{2}$ which means that α had indeed an incentive to leave. On the other hand, if $N > 2$, then $\dfrac{1}{N} > \dfrac{1}{2(N-1)}$. Therefore, α's leaving has decreased the probability of focus between each other individual and the metabolic source. If $N > 2$, then α has increased its own fitness and decreased everyone else's by leaving the original

accumulation. If $N = 2$, no change in fitness occurs by leaving.

b) Second individual leaving. Let $\alpha_1 := \alpha$ and assume that a second individual α_2 is now leaving accumulation $\mathscr{T} \setminus \{\alpha\}$ under $\hat{\eta}^{\Gamma,2}$. Let $N > 2$. Then α_2 has two options: It can form an accumulation with α_1 or become solitary. If α_2 forms an accumulation with α_1, then two accumulations exist overall, and, therefore,

$$\rho^\Gamma_{\alpha_i:\{\alpha_1,\alpha_2\}} = \frac{1}{2} \cdot \frac{1}{|\{\alpha_1,\alpha_2\}|} \cdot \rho^\Gamma_{\alpha_i} = \frac{\rho^\Gamma_{\alpha_i}}{4} \text{ for } i = 1,2. \text{ Further}$$

$$\rho^\Gamma_{\beta:\mathscr{T}\setminus\{\alpha_1,\alpha_2\}} = \frac{1}{2} \cdot \frac{1}{|\mathscr{T} \setminus \{\alpha_1,\alpha_2\}|} \cdot \rho^\Gamma_\beta = \frac{\rho^\Gamma_\beta}{2(N-2)}$$

Certainly α_1's fitness has decreased by accumulating with α_2. α_2's probability of focus went from $\frac{1}{2(N-1)}$ to $\frac{1}{4}$. This is an increase in fitness if and only if $N > 3$. If $N > 3$ then α_2 has an incentive to accumulate with α_1. If $N = 3$ then there is no incentive for α_2 to accumulate with α_1 (α_2 forms already an accumulation with one other individual). $N = 2$ was already covered.

For a $\beta \in \mathscr{T} \setminus \{\alpha_1,\alpha_2\}$ the probability of focus went from $\frac{1}{2(N-1)}$ to $\frac{1}{2(N-2)}$. This is an increase in fitness. Therefore, if a second individual is leaving the accumulation $\mathscr{T} \setminus \{\alpha\}$ forming an accumulation with α, then, in general, this will lower α's fitness and increase the fitness of everyone else.

The second possibility for α_2 is to become solitary. Then, there are three accumulations and solitary individuals and we get $\rho^\Gamma_{\alpha_i:\{\alpha_i\}} = \frac{1}{3} \cdot \frac{1}{|\{\alpha_i\}|} \cdot \rho^\Gamma_{\alpha_i} = \frac{\rho^\Gamma_{\alpha_i}}{3}$ for $i = 1,2$. Further $\rho^\Gamma_{\beta:\mathscr{T}\setminus\{\alpha_1,\alpha_2\}} = \frac{1}{3} \cdot \frac{1}{|\mathscr{T} \setminus \{\alpha_1,\alpha_2\}|} \cdot \rho^\Gamma_\beta = \frac{\rho^\Gamma_\beta}{3(N-2)}$.

α_1's fitness has decreased since the focus probability dropped from $\frac{1}{2}$ to $\frac{1}{3}$. α_2's probability of focus went from $\frac{1}{2(N-1)}$ to $\frac{1}{3}$. This is an increase in fitness if and only if $N > 2$. This is here always the case. For a $\beta \in \mathscr{T} \setminus \{\alpha_1,\alpha_2\}$ the probability of focus

went from $\dfrac{1}{2(N-1)}$ to $\dfrac{1}{3(N-2)}$. This is an increase in fitness only if $N < 4$. If $N > 4$, then fitness for $\beta \in \mathcal{T} \setminus \{\alpha_1, \alpha_2\}$ decreases if α_2 becomes solitary.

In summary, if the second individual leaves, then it should choose to become solitary. This would increase its fitness as long as $N > 2$. Everyone else will suffer a decrease in fitness if the second individual becomes solitary.

c) **Migration into solitude.** Will fitness of an individual always increase if that individual becomes solitary? In order to answer this question let's assume that individual α migrates from accumulation S into solitude. Let $n := |S|$. Let there be k accumulations and solitary individuals before α. Then the probability of focus between α and the metabolic source in accumulation S is $\dfrac{1}{k \cdot n}$. After migration into solitude the probability of focus between α and the metabolic source will be $\dfrac{1}{k+1}$. This is an increase in fitness if and only if $\dfrac{1}{k+1} > \dfrac{1}{k \cdot n}$. This is always the case except for $n = 2$ and $k = 1$. When $n = 2$ and $k = 1$ there is no difference in fitness between the fully accumulated and fully dispersed situation. Hence, given a metabolic source, migration into solitude increases in general the fitness of an individual.

Migration into solitude will always lower the fitness of individuals in accumulations not involved in the migration and that of other solitary individuals. Now the question becomes: Will an individual migrating into solitude always lower the fitness of individuals in the accumulation which it has left? The probability of focus between an individual $\beta \in S \setminus \{\alpha\}$ and the metabolic source before migration is $\dfrac{1}{k \cdot n}$. After α's migration into solitude, it is $\dfrac{1}{(k+1) \cdot (n-1)}$. Fitness before migration for $\beta \in S \setminus \{\alpha\}$ is higher than after migration if and only if $\dfrac{1}{k \cdot n} > \dfrac{1}{(k+1) \cdot (n-1)}$. Simplifying this inequality yields $n > k+1$. Thus, as long as $n > k+1$ the leaving of one individual into solitude lowers the fitness of the others in the accumulation. If $n < k+1$ the leaving of an individual into solitude will increase the fitness of the others

in the accumulation.

d) Migration between accumulations. An individual will have an incentive to migrate from one accumulation to another if and only if before migration the accumulation of the individual contains at least 2 individuals more than the accumulation the individual wants to migrate to.

Conclusion. The example demonstrated that under a metabolic source (given certain conditions) dispersal of accumulations will happen. In the final state all individuals will be solitary. The most interesting point is that the receptance in the fully accumulated situation is exactly the same as in the fully dispersed situation for any individual. In the fully accumulated situation the receptance for an individual α is $\rho_{\alpha:\mathscr{I}}^{\Gamma} = 1 \cdot \frac{1}{N} \cdot \rho_{\alpha}^{\Gamma} = \frac{\rho_{\alpha}^{\Gamma}}{N}$. In the fully dispersed situation the receptance for α is $\rho_{\alpha:\{\alpha\}}^{\Gamma} = \frac{1}{N} \cdot 1 \cdot \rho_{\alpha}^{\Gamma} = \frac{\rho_{\alpha}^{\Gamma}}{N}$. From the way $\rho_{\alpha:\mathscr{I}}^{\Gamma}$ and $\rho_{\alpha:\{\alpha\}}^{\Gamma}$ are formed it follows that dispersal of individuals is, indeed, dispersal of encounter and concentration of focus. The more individuals are dispersed the higher the probability of focus between a single individual and the metabolic source once it, or its accumulation, is encountered.

If we interpret receptance under a metabolic source as a measure of fitness, then this example shows that an evolutionary game is possible in which individuals thriving to increase their individual fitness will end up with the same or even lower fitness than in the beginning. The reason is that in some vicinity of the globally approachable and attractive equilibrium every individual by increasing its own fitness will be decreasing everyone else's. The first individual leaving has the highest benefit (it will acquire a receptance of .5). However, later in the game it will suffer loss in receptance while others will be migrating into solitude. This is true for each individual: It can only improve its fitness as long as it has not migrated into solitude. Once that has happened,

any further migration of any other individual into solitude will lower the receptance of solitary individuals. Eventually all individuals will reach the same fitness as they had in the beginning.

Although the fully dispersed situation provides the same fitness for each individual as the fully accumulated one, the fully dispersed situation will be the one the system will converge on. The fully dispersed situation is a globally attractive ESS. This follows from the fact that an individual will always benefit from leaving its accumulation, as long as there are at least three individuals in it.

Assume now that the individual receptance for all individuals is the same. Thus $\rho_\alpha^\Gamma = \rho^\Gamma$ for all individuals α. How does the average receptance change as the dispersal proceeds? At a certain stage of the system there are k accumulations and solitary individuals. Let n_i be the number of individuals in the i-th set, which can be an accumulation or a solitary individual. Let the overall number of individuals be N. Then the average receptance is given by $\dfrac{1}{N} \sum_{i=1}^{k} n_i \cdot \dfrac{\rho^\Gamma}{k \cdot n_i} = \dfrac{\rho^\Gamma}{N}$. This means the average receptance in this example does not change during the process of dispersal, if all the individual receptances are the same.

I did not include confusion in this example. Including confusion will, indeed, result in higher fitness for individuals at the end of the dispersal compared to the beginning. Complete dispersal will still, however, happen.

Note that no condition regarding competitive strategies, nor any damage to individuals due to the competition over the metabolic source, was assumed. The only assumption regarding dispersal which factors into our investigation is the assumption that the encounter probabilities for all accumulations and solitary individuals are the same. This assumption can be weakened to the following: If S_1, S_2 are accumulations in $\mathscr{S}$ under $\hat{\eta}^{\Gamma,i}$. Then the statement:

For all $i \in \mathbb{N}$: If S_1, S_2 are accumulations in $\mathscr{S}$ under $\hat{\eta}^{\Gamma,i}$. Then:

$$|S_1| < |S_2| \Longrightarrow \frac{\eta_{S_1}^{\Gamma,i}}{|S_1|} > \frac{\eta_{S_2}^{\Gamma,i}}{|S_2|}$$

implies that the fully dispersed state will be a globally attractive ESS. $\dfrac{\eta_{S_1}^{\Gamma,i}}{|S_1|}$ is the

product of exposure and acceptance, and is called *per-capita exposure under* $\eta^{\Gamma,i}$.

Therefore, the fully dispersed state is a globally attractive equilibrium situation if the

per-capita exposure is decreasing in accumulation size for every probability measure

$\hat{\eta}^{\Gamma,i}$ used.

4.4.   Fitness functions

In this section I continue to assume that each accumulation or solitary individual

is encountered with the same probability by a realization of a metabolic source or sink.

That means that there is no increase in exposure with increasing accumulation size, and

decrease of per-capita exposure as accumulation size increases. As before, confusion is

ignored.

Let $S \subseteq \mathscr{S}$ be an accumulation under the metabolic source or sink Γ given a

probability measure $\hat{\eta}^{\Gamma}$ and let $\alpha \in S$. Let $m^{\Gamma} \geq 1$ be the focus capacity of Γ. I assume

that all sets that can be sets of total focus are so with equal probability (see the zebra-

grass example above). Therefore $\rho_{\{\alpha\}:S}^{\Gamma} = \overline{\rho}_{\{\alpha\}:S}^{\Gamma}$. In the following I discuss how to use

$\overline{\rho}_{\{\alpha\}:S}^{\Gamma}$, as derived in section 4.2, in order to get fitness functions. First, I consider the

two marginal cases, where there is only one metabolic source or sink Γ. Next, I

consider the combined case with a metabolic source and a metabolic sink together.

Assume that there are p realizations of Γ. If there are k accumulations and

solitary individuals, then $\overline{\rho}_{\{\alpha\}:S}^{\Gamma}$ can be written as

$$\overline{\rho}^{\Gamma}_{\{\alpha\}:S} = 1 - \left(1 - \frac{\min(|S|,m^{\Gamma}) \cdot \rho^{\Gamma}}{k \cdot |S| \cdot (2^{\min(|S|,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(|S|,m^{\Gamma})} \binom{\min(|S|,m^{\Gamma}) - 1}{i - 1} \cdot \frac{(1 + \rho^{\Gamma})^{i-1}}{2^i - 1}\right)^p$$

4.4.1. Fitness under a metabolic source

If Γ is a metabolic source then receptance is beneficial. Therefore, $\overline{\rho}^{\Gamma}_{\{\alpha\}:S}$ can be used directly as a fitness function. Define the fitness function as follows:

$$F_{\alpha,\Gamma}(n,k,p) := 1 - \left(1 - \frac{\min(n,m^{\Gamma}) \cdot \rho^{\Gamma}}{k \cdot n \cdot (2^{\min(n,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma}) - 1}{i - 1} \cdot \frac{(1 + \rho^{\Gamma})^{i-1}}{2^i - 1}\right)^p$$

where $n, k, p \in \mathbb{N}$, and where n is the accumulation size. k the number of accumulations and solitary individuals, and p the number of realizations of the metabolic source. If $n = 1$ then $F_{\alpha,\Gamma}(n,k,p)$ is a solitary individuals fitness, and

$$F_{\alpha,\Gamma}(1,k,p) = 1 - \left(1 - \frac{\rho^{\Gamma}}{k}\right)^p \,, \quad k, p \in \mathbb{N}.$$

The following statements are obvious:

(1) $F_{\alpha,\Gamma}(n,k,p)$ is decreasing in n

(2) $F_{\alpha,\Gamma}(n,k,p)$ is decreasing in k

(3) $F_{\alpha,\Gamma}(n,k,p)$ is increasing in p

In the following I will first investigate the two cases $p = \infty$ and $p = 1$. All the other cases will then be covered using the first two ones. I denote with N the overall number of individuals.

Case $p = \infty$. Then $F_{\alpha,\Gamma}(n,k,\infty) = 1$, $n,k \in \mathbb{N}$. In this case there is no difference in fitness between solitary and accumulated individuals. There is, therefore, neither incentive for accumulation nor for dispersal.

Case $p = 1$. In that case

$$F_{\alpha,\Gamma}(n,k,1) = \frac{\min(n,m^{\Gamma}) \cdot \rho^{\Gamma}}{k \cdot n \cdot (2^{\min(n,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma}) - 1}{i-1} \cdot \frac{(1 + \rho^{\Gamma})^{i-1}}{2^i - 1} , \quad n,k \in \mathbb{N}$$

Assume first that α migrates from one accumulation to another. This means that there will be no change in the number k of accumulations. Hence α has an incentive to migrate from an accumulation of size n_1 to an accumulation of size n_2 if and only if

$$F_{\alpha,\Gamma}(n_2 + 1, k, 1) > F_{\alpha,\Gamma}(n_1, k, 1)$$

Since $F_{\alpha,\Gamma}(n,k,1)$ is decreasing in n, this means that $n_2 + 1 < n_1$. This means that there is always an incentive to migrate from an accumulation of size $n_1 > 1$ to an accumulation of size $n_2 < n_1 - 1$.

Assume now that individual α migrates from an accumulation of size n into solitude. Then the number of accumulations and solitary individuals grows from k to $k + 1$. $F_{\alpha,\Gamma}(n,k,1)$ is decreasing in n as well as in k. With regard to n α's fitness has, therefore, increased. With regard to k, however, it has increased. So, we have to look closer into this case. α's fitness after migrating into solitude is $F_{\alpha,\Gamma}(1, k+1, 1) = \frac{\rho^{\Gamma}}{k+1}$, $k \in \mathbb{N}$. α's fitness before migration is $F_{\alpha,\Gamma}(n,k,1)$. α has an incentive to migrate from an accumulation of size n into solitude if and only if

$$\frac{\rho^{\Gamma}}{k+1} > \frac{\min(n,m^{\Gamma}) \cdot \rho^{\Gamma}}{k \cdot n \cdot (2^{\min(n,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma}) - 1}{i-1} \cdot \frac{(1+\rho^{\Gamma})^{i-1}}{2^i - 1}$$

Solving for k yields

$$k > \frac{\dfrac{\min(n,m^{\Gamma})}{n \cdot (2^{\min(n,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma}) - 1}{i-1} \cdot \dfrac{(1+\rho^{\Gamma})^{i-1}}{2^i - 1}}{1 - \dfrac{\min(n,m^{\Gamma})}{n \cdot (2^{\min(n,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma}) - 1}{i-1} \cdot \dfrac{(1+\rho^{\Gamma})^{i-1}}{2^i - 1}} \qquad (1)$$

We note that $\dfrac{x}{1-x}$ is increasing in x. The expression

$\dfrac{\min(n,m^{\Gamma})}{n \cdot (2^{\min(n,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma}) - 1}{i-1} \cdot \dfrac{(1+\rho^{\Gamma})^{i-1}}{2^i - 1}$ is globally maximized for $n = 1$.

The next largest value is obtained for $n = 2$. Therefore consider

$$F_{\alpha,\Gamma}(2,k,1) = \frac{\min(2,m^{\Gamma}) \cdot \rho^{\Gamma}}{k \cdot 2 \cdot (2^{\min(2,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(2,m^{\Gamma})} \binom{\min(2,m^{\Gamma}) - 1}{i-1} \cdot \frac{(1+\rho^{\Gamma})^{i-1}}{2^i - 1} \ , \ k \in \mathbb{N}$$

Then there are two cases, namely $m^{\Gamma} = 1$ or $m^{\Gamma} > 1$.

(1) $\qquad\qquad m^{\Gamma} = 1$: Then $n = 2$ yields

$$\frac{\min(2,1)}{2 \cdot (2^{\min(2,1)} - 1)} \cdot \sum_{i=1}^{\min(2,1)} \binom{\min(2,1) - 1}{i-1} \cdot \frac{(1+\rho^{\Gamma})^{i-1}}{2^i - 1} = \frac{1}{2}$$

Therefore inequality (1) becomes $k > \dfrac{\dfrac{1}{2}}{1 - \dfrac{1}{2}} = 1$.

(2) $\qquad\qquad m^{\Gamma} > 1$: Then $n = 2$ yields

$$\frac{\min(2,m^{\Gamma})}{2\cdot(2^{\min(2,m^{\Gamma})}-1)}\cdot\sum_{i=1}^{\min(2,m^{\Gamma})}\binom{\min(2,m^{\Gamma})-1}{i-1}\cdot\frac{(1+\rho^{\Gamma})^{i-1}}{2^{i}-1}=\frac{1}{3}\cdot\left(1+\frac{(1+\rho^{\Gamma})}{3}\right)<\frac{5}{9}$$

Therefore inequality (1) becomes $k>\dfrac{\dfrac{5}{9}}{1-\dfrac{5}{9}}=\dfrac{5}{4}.$

Therefore, there is always an incentive for an individual to migrate into solitude if there are at least 2 accumulations or solitary individuals present. This is consistent with the analogous case treated in the example before.

Therefore, eventually all individuals will be solitary with fitness

$$F_{\alpha,\Gamma}(1,N,1)=\frac{\rho^{\Gamma}}{N}.$$

Case $1<p<\infty$. In that case

$$F_{\alpha,\Gamma}(n,k,p)=1-\left(1-\frac{\min(n,m^{\Gamma})\cdot\rho^{\Gamma}}{k\cdot n\cdot(2^{\min(n,m^{\Gamma})}-1)}\cdot\sum_{i=1}^{\min(n,m^{\Gamma})}\binom{\min(n,m^{\Gamma})-1}{i-1}\cdot\frac{(1+\rho^{\Gamma})^{i-1}}{2^{i}-1}\right)^{p}$$

with $n,k,p\in\mathbb{N}$.

Assume first that α migrates from one accumulation to another. This means that there will be no change in the number k of accumulations. α has, therefore, an incentive to migrate from an accumulation of size n_{1} to an accumulation of size n_{2} if and only if

$$F_{\alpha,\Gamma}(n_{2}+1,k,p)>F_{\alpha,\Gamma}(n_{1},k,p)$$

Since $F_{\alpha,\Gamma}(n,k,p)$ is decreasing in n, this means that $n_{2}+1<n_{1}$. This means that there is always an incentive to migrate from an accumulation of size $n_{1}>1$ to an

accumulation of size $n_2 < n_1 - 1$.

Assume now that individual α migrates from an accumulation of size n into solitude. Then the number of accumulations and solitary individuals grows from k to $k+1$. α's fitness after migrating into solitude is

$$F_{\alpha,\Gamma}(1, k+1, p) = 1 - \left(1 - \frac{\rho^\Gamma}{k+1}\right)^p , \quad k \in \mathbb{N}.$$ α's fitness before migration is $F_{\alpha,\Gamma}(n, k, p)$.

α has an incentive to migrate from an accumulation of size n into solitude if and only if

$$1 - \left(1 - \frac{\rho^\Gamma}{k+1}\right)^p > 1 - \left(1 - \frac{\min(n, m^\Gamma) \cdot \rho^\Gamma}{k \cdot n \cdot (2^{\min(n,m^\Gamma)} - 1)} \cdot \sum_{i=1}^{\min(n,m^\Gamma)} \binom{\min(n, m^\Gamma) - 1}{i - 1} \cdot \frac{(1 + \rho^\Gamma)^{i-1}}{2^i - 1}\right)^p$$

which can be rewritten to

$$\frac{\rho^\Gamma}{k+1} > \frac{\min(n, m^\Gamma) \cdot \rho^\Gamma}{k \cdot n \cdot (2^{\min(n,m^\Gamma)} - 1)} \cdot \sum_{i=1}^{\min(n,m^\Gamma)} \binom{\min(n, m^\Gamma) - 1}{i - 1} \cdot \frac{(1 + \rho^\Gamma)^{i-1}}{2^i - 1}$$

That means that exactly the same conclusions hold for the case $1 < p < \infty$ as for the case $p = 1$. Therefore, eventually all individuals will be solitary with fitness

$$F_{\alpha,\Gamma}(1, N, p) = 1 - \left(1 - \frac{\rho^\Gamma}{N}\right)^p$$

Summary. Under a metabolic source individuals will have the incentive to completely disperse and never to accumulate. The equilibrium in this case is given by all individuals being solitary.

4.4.2. Fitness under a metabolic sink

$\rho^{\Gamma}_{\{\alpha\}:S}$ is now a probability measuring damage. In order to obtain a fitness function this probability has to be transformed into a probability measuring benefits. Since

$$\text{Probability of benefit} = 1 - \text{probability of damage},$$

I denote as $\xi^{\Gamma}_{\{\alpha\}:S} := 1 - \rho^{\Gamma}_{\{\alpha\}:S}$ the *escapability of α from Γ through S*. Escapability is the probability that e.g., a zebra, for instance, can avoid being killed by a lion. We obtain for the standard escapability $\overline{\xi}^{\Gamma}_{\{\alpha\}:S} := 1 - \overline{\rho}^{\Gamma}_{\{\alpha\}:S}$ or more explicitly

$$\overline{\xi}^{\Gamma}_{\{\alpha\}:S} = \left(1 - \frac{\min(n,m^{\Gamma}) \cdot \rho^{\Gamma}}{k \cdot n \cdot (2^{\min(n,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma}) - 1}{i-1} \cdot \frac{(1 + \rho^{\Gamma})^{i-1}}{2^{i} - 1}\right)^{p}$$

There is still a probability of damage involved, namely ρ^{Γ}. Analogously to the definition of $\xi^{\Gamma}_{\{\alpha\}:S}$ we use the notation $\xi^{\Gamma} := 1 - \rho^{\Gamma}$. Then

$$\overline{\xi}^{\Gamma}_{\{\alpha\}:S} = \left(1 - \frac{\min(n,m^{\Gamma}) \cdot (1 - \xi^{\Gamma})}{k \cdot n \cdot (2^{\min(n,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma}) - 1}{i-1} \cdot \frac{(2 - \xi^{\Gamma})^{i-1}}{2^{i} - 1}\right)^{p}$$

ξ^{Γ} is the probability that individual α can avoid damage due to Γ, once a focus between α and Γ is established. ξ^{Γ} is the *individual escapability of α from Γ*. I define the following fitness function:

$$F_{\alpha,\Gamma}(n,k,p) := \left(1 - \frac{\min(n,m^{\Gamma}) \cdot (1 - \xi^{\Gamma})}{k \cdot n \cdot (2^{\min(n,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma}) - 1}{i-1} \cdot \frac{(2 - \xi^{\Gamma})^{i-1}}{2^{i} - 1}\right)^{p}$$

where $n, k, p \in \mathbb{N}$, and n is the accumulation size (if $n = 1$ then $F_{\alpha,\Gamma}(n, k, p)$ is a solitary individuals fitness, $F_{\alpha,\Gamma}(1, k, p) := \left(1 - \dfrac{(1-\xi^{\Gamma})}{k}\right)^{p}$, $k, p \in \mathbb{N}$), k the number of accumulations and solitary individuals, and p the number of realizations of the metabolic source.

The following statements are obvious:

(1) $F_{\alpha,\Gamma}(n, k, p)$ is increasing in n

(2) $F_{\alpha,\Gamma}(n, k, p)$ is increasing in k

(3) $F_{\alpha,\Gamma}(n, k, p)$ is decreasing in p

As in the case of the metabolic source I will first investigate the two cases $p = \infty$ and $p = 1$, before considering $1 < p < \infty$. Everything goes analogous to the case of the metabolic source.

Case $p = \infty$. Then $F_{\alpha,\Gamma}(n, k, \infty) = 0$, $n, k \in \mathbb{N}$. In this case there is no difference in fitness between solitary and accumulated individuals. Therefore there is neither incentive for accumulation nor for dispersal.

Case $p = 1$. In that case

$$F_{\alpha,\Gamma}(n, k, 1) = 1 - \frac{\min(n, m^{\Gamma}) \cdot (1 - \xi^{\Gamma})}{k \cdot n \cdot (2^{\min(n, m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n, m^{\Gamma})} \binom{\min(n, m^{\Gamma}) - 1}{i - 1} \cdot \frac{(2 - \xi^{\Gamma})^{i-1}}{2^{i} - 1} , \quad n, k \in \mathbb{N}$$

Assume first that α migrates from one accumulation to another. This means that there will be no change in the number k of accumulations. Hence α has an incentive to migrate from an accumulation of size n_1 to an accumulation of size n_2 if and only if

$$F_{\alpha,\Gamma}(n_2+1,k,1) > F_{\alpha,\Gamma}(n_1,k,1)$$

Since $F_{\alpha,\Gamma}(n,k,1)$ is increasing in n, this means that $n_2+1 > n_1$. This means that there is always an incentive to migrate from an accumulation of size $n_1 > 1$ to an accumulation of size $n_2 > n_1 - 1$.

Assume now that individual α migrates from an accumulation of size n into solitude. Then the number of accumulations and solitary individuals grows from k to $k+1$. α's fitness after migrating into solitude is $F_{\alpha,\Gamma}(1,k+1,1) = 1 - \dfrac{(1-\xi^{\Gamma})}{k+1}$, $k \in \mathbb{N}$. α's fitness before migration is $F_{\alpha,\Gamma}(n,k,1)$. α has an incentive to migrate from an accumulation of size n into solitude if and only if

$$1 - \frac{(1-\xi^{\Gamma})}{k+1} > 1 - \frac{\min(n,m^{\Gamma}) \cdot (1-\xi^{\Gamma})}{k \cdot n \cdot (2^{\min(n,m^{\Gamma})}-1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma})-1}{i-1} \cdot \frac{(2-\xi^{\Gamma})^{i-1}}{2^i-1}$$

thus

$$\frac{1}{k+1} < \frac{\min(n,m^{\Gamma})}{k \cdot n \cdot (2^{\min(n,m^{\Gamma})}-1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma})-1}{i-1} \cdot \frac{(2-\xi^{\Gamma})^{i-1}}{2^i-1}$$

Solving for k yields

$$k < \frac{\dfrac{\min(n,m^{\Gamma})}{n \cdot (2^{\min(n,m^{\Gamma})}-1)} \cdot \displaystyle\sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma})-1}{i-1} \cdot \dfrac{(2-\xi^{\Gamma})^{i-1}}{2^i-1}}{1 - \dfrac{\min(n,m^{\Gamma})}{n \cdot (2^{\min(n,m^{\Gamma})}-1)} \cdot \displaystyle\sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma})-1}{i-1} \cdot \dfrac{(2-\xi^{\Gamma})^{i-1}}{2^i-1}} \tag{1}$$

We note that $\dfrac{x}{1-x}$ is increasing in x. The expression

$\dfrac{\min(n,m^{\Gamma})}{n \cdot (2^{\min(n,m^{\Gamma})}-1)} \cdot \displaystyle\sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma})-1}{i-1} \cdot \dfrac{(2-\xi^{\Gamma})^{i-1}}{2^i-1}$ is globally minimized for $n=1$.

The next smallest value is obtained for $n = 2$. Therefore consider

$$F_{\alpha,\Gamma}(2,k,1) = 1 - \frac{\min(2,m^\Gamma)\cdot(1-\xi^\Gamma)}{k\cdot 2\cdot(2^{\min(2,m^\Gamma)}-1)}\cdot\sum_{i=1}^{\min(2,m^\Gamma)}\binom{\min(2,m^\Gamma)-1}{i-1}\cdot\frac{(2-\xi^\Gamma)^{i-1}}{2^i-1}, \ k \in \mathbb{N}$$

Then there are two cases, namely $m^\Gamma = 1$ or $m^\Gamma > 1$.

(1) $\qquad\qquad m^\Gamma = 1$: Then $n = 2$ yields

$$\frac{\min(2,1)}{2\cdot(2^{\min(2,1)}-1)}\cdot\sum_{i=1}^{\min(2,1)}\binom{\min(2,1)-1}{i-1}\cdot\frac{(2-\xi^\Gamma)^{i-1}}{2^i-1} = \frac{1}{2}$$

Therefore inequality (1) becomes $k < \dfrac{\frac{1}{2}}{1-\frac{1}{2}} = 1$.

(2) $\qquad\qquad m^\Gamma > 1$: Then $n = 2$ yields

$$\frac{\min(2,m^\Gamma)}{2\cdot(2^{\min(2,m^\Gamma)}-1)}\cdot\sum_{i=1}^{\min(2,m^\Gamma)}\binom{\min(2,m^\Gamma)-1}{i-1}\cdot\frac{(2-\xi^\Gamma)^{i-1}}{2^i-1} = \frac{1}{3}\cdot\left(1+\frac{(2-\xi^\Gamma)}{3}\right) > \frac{4}{9}$$

Therefore inequality (1) becomes $k < \dfrac{\frac{4}{9}}{1-\frac{4}{9}} = \frac{4}{5}$.

Therefore there is always an incentive for an individual to accumulate if there are at least 3 accumulations or solitary individuals present.

Therefore, eventually all individuals will form one accumulation with fitness

$$F_{\alpha,\Gamma}(N,1,1) = 1 - \frac{\min(N,m^\Gamma)\cdot(1-\xi^\Gamma)}{N\cdot(2^{\min(N,m^\Gamma)}-1)}\cdot\sum_{i=1}^{\min(N,m^\Gamma)}\binom{\min(N,m^\Gamma)-1}{i-1}\cdot\frac{(2-\xi^\Gamma)^{i-1}}{2^i-1}$$

Case $1 < p < \infty$. In that case

$$F_{\alpha,\Gamma}(n,k,p) = \left(1 - \frac{\min(n,m^{\Gamma}) \cdot (1-\xi^{\Gamma})}{k \cdot n \cdot (2^{\min(n,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma})-1}{i-1} \cdot \frac{(2-\xi^{\Gamma})^{i-1}}{2^i - 1} \right)^p$$

with $n,k,p \in \mathbb{N}$.

Assume first that α migrates from one accumulation to another. This means that there will be no change in the number k of accumulations. Hence α has an incentive to migrate from an accumulation of size n_1 to an accumulation of size n_2 if and only if

$$F_{\alpha,\Gamma}(n_2 + 1, k, p) < F_{\alpha,\Gamma}(n_1, k, p)$$

Since $F_{\alpha,\Gamma}(n,k,p)$ is increasing in n, this means that $n_2 + 1 < n_1$. This means that there is always an incentive to migrate from an accumulation of size $n_1 > 1$ to an accumulation of size $n_2 > n_1 - 1$.

Assume now that individual α migrates from an accumulation of size n into solitude. Then the number of accumulations and solitary individuals grows from k to $k+1$. α's fitness after migrating into solitude is

$$F_{\alpha,\Gamma}(1, k+1, p) = \left(1 - \frac{(1-\xi^{\Gamma})}{k+1} \right)^p \ , \ k \in \mathbb{N}$$

α's fitness before migration is $F_{\alpha,\Gamma}(n,k,p)$. α has an incentive to migrate from an accumulation of size n into solitude if and only if

$$\left(1 - \frac{(2-\xi^{\Gamma})}{k+1} \right)^p > \left(1 - \frac{\min(n,m^{\Gamma}) \cdot (1-\xi^{\Gamma})}{k \cdot n \cdot (2^{\min(n,m^{\Gamma})} - 1)} \cdot \sum_{i=1}^{\min(n,m^{\Gamma})} \binom{\min(n,m^{\Gamma})-1}{i-1} \cdot \frac{(2-\xi^{\Gamma})^{i-1}}{2^i - 1} \right)$$

which can be rewritten to

$$\frac{1}{k+1} < \frac{\min(n,m^\Gamma)}{k \cdot n \cdot (2^{\min(n,m^\Gamma)}-1)} \cdot \sum_{i=1}^{\min(n,m^\Gamma)} \binom{\min(n,m^\Gamma)-1}{i-1} \cdot \frac{(2-\xi^\Gamma)^{i-1}}{2^i-1}$$

That means that exactly the same conclusions hold for the case $1 < p < \infty$ as for the case $p = 1$.

Therefore, eventually all individuals will form a single accumulation with fitness

$$F_{\alpha,\Gamma}(N,1,1) = \left(1 - \frac{\min(N,m^\Gamma)\cdot(1-\xi^\Gamma)}{N\cdot(2^{\min(N,m^\Gamma)}-1)} \cdot \sum_{i=1}^{\min(N,m^\Gamma)} \binom{\min(N,m^\Gamma)-1}{i-1} \cdot \frac{(2-\xi^\Gamma)^{i-1}}{2^i-1}\right)^p$$

Summary. Under a metabolic sink individuals will always have the incentive to completely accumulate and never disperse. The equilibrium situation in this case is given by all individuals forming one accumulation.

4.4.3. Distributable and magnifyable metabolic sources and sinks

In chapter 1 the concept of distributable and magnifyable metabolic sources and sinks was introduced. Distributable means that by increasing the size of an accumulation the receptance will decrease. It is now possible to define these concepts properly.

Definition (Distributable and magnifyable metabolic source or sink): Let Γ be a metabolic source or sink. Let $F_{\alpha,\Gamma}(n,k,p)$ be the fitness function of an individual α under Γ through accumulation S. Then:

(1)   A metabolic source Γ is called *distributable for n individuals* if

$F_{\alpha,\Gamma}(n,k,p) > F_{\alpha,\Gamma}(n+1,k,p)$. If Γ is distributable for all $n \in \mathbb{N}$, then Γ is simply called *distributable*.

(2)   A metabolic sink Γ is called *distributable for n individuals* if $F_{\alpha,\Gamma}(n,k,p) < F_{\alpha,\Gamma}(n+1,k,p)$. If Γ is distributable for all $n \in \mathbb{N}$, then Γ is simply called *distributable*.

(3)   A metabolic source Γ is called *magnifyable for n individuals* if $F_{\alpha,\Gamma}(n,k,p) < F_{\alpha,\Gamma}(n+1,k,p)$. If Γ is magnifyable for all $n \in \mathbb{N}$, then Γ is simply called *magnifyable*.

(4)   A metabolic sink Γ is called *magnifyable for n individuals* if $F_{\alpha,\Gamma}(n,k,p) > F_{\alpha,\Gamma}(n+1,k,p)$.

If Γ is magnifyable for all $n \in \mathbb{N}$, then Γ is simply called *magnifyable*.   ▲

Given the standard receptance, individuals will always accumulate under a distributable metabolic sink and they will always disperse under a distributable metabolic source. A biological example for a not-distributable and not-magnifyable metabolic sink is a natural disaster like an earth quake. An example of a not-distributable and not-magnifyable metabolic source is the oxygen in the air.

4.4.4.   Combining fitness functions

In this section I investigate the situation in which individuals are under a metabolic source (e.g., zebras under grass) and under a metabolic sink (e.g., zebras under lion). A biological individual needs to forage (encounter metabolic sources) and needs to avoid its predators (avoid encounter with metabolic sinks). Individuals of the same species are threatened by the same predators and are interested in the same food. Due to the structure of the Euclidean space an accumulation of biological individuals

under their predators is also an accumulation under their food sources. This cannot be taken for granted in the setup where space and time are defined through the relations between individuals and metabolic sources and sinks. Therefore. I have to assume explicitly that any accumulation under the metabolic source is also an accumulation under the metabolic sink and vice versa.

Let $F_\alpha^+(n,k,p^+)$, $n,k,p^+ \in \mathbb{N}$ be the fitness function of α under the metabolic source and let $F_\alpha^-(n,k,p^-)$, $n,k,p^- \in \mathbb{N}$ be the fitness function of α under the metabolic sink. I assume that the escape from the metabolic sink and the reception of the metabolic source are independent events, and that the encounter probability measures of both of them are always the same. Then a first attempt in constructing a fitness function for the combined effect of the metabolic source and the metabolic sink on α is

$$F_\alpha(n,k,p^-,p^+) = F_\alpha^-(n,k,p^-) \cdot F_\alpha^+(n,k,p^+) , \ n,k,p^-,p^+ \in \mathbb{N} \qquad (1)$$

The two fitness functions $F_\alpha^-(n,k,p^-)$ and $F_\alpha^+(n,k,p^+)$ are called the *marginal fitness functions of $F_\alpha(n,k,p^-,p^+)$*. The fitness of individual α is then the probability that on encounter of the accumulation with the metabolic sink a reception is avoided, and that on encounter of the accumulation with the metabolic source a reception occurs. An appropriate fitness function will then be obtained if the benefit from escaping the metabolic sink is the same as the benefit from the reception of the metabolic source. This, however, in general is not the case. Hence, we need to introduce weights for the respective metabolic benefits. The fitness function would then measure the mean payoff weight. Since the fitness function in equation (1) is a product of probabilities, the geometric mean is the appropriate measure of fitness. Let $b^- \in \mathbb{R}^+$ be the benefit due to escaping from the metabolic sink, and $b^+ \in \mathbb{R}^+$ the benefit due to reception of the

metabolic source. I define the fitness function $F_\alpha(n,k,p^-,p^+)$ as the geometric mean of $F_\alpha^-(n,k,p^-)$ and $F_\alpha^+(n,k,p^+)$ given the weights b^- and b^+ respectively. Therefore

$$F_\alpha(n,k,p^-,p^+,b^-,b^+) := \left[F_\alpha^-(n,k,p^-)^{b^-} \cdot F_\alpha^+(n,k,p^+)^{b^+} \right]^{b^- b^+} , \quad n \in \mathbb{N}$$

or, simplified,

$$F_\alpha(n,k,p^-,p^+,b^-,b^+) = F_\alpha^-(n,k,p^-)^{\frac{1}{b^+}} \cdot F_\alpha^+(n,k,p^+)^{\frac{1}{b^-}} , \quad n \in \mathbb{N} \qquad (2)$$

Equation (2) is the special case where $b^- = b^+ = 1$.

Further we note that

$$\lim_{b^- \to \infty} F_\alpha(n,k,p^-,p^+,b^-,b^+) = F_\alpha^-(n,k,p^-)^{\frac{1}{b^+}},$$

and

$$\lim_{b^+ \to \infty} F_\alpha(n,k,p^-,p^+,b^-,b^+) = F_\alpha^+(n,k,p^+)^{\frac{1}{b^-}}$$

The goal is now to construct a combined fitness function $F_\alpha(n,k,p^-,p^+,b^-,b^+)$ under which a set of originally solitary individuals forms accumulations. This means that at least initially the fitness function has to be increasing. Therefore, at least for smaller accumulation sizes the fitness benefit due to accumulation under the metabolic sink has to outweigh the fitness damage due to accumulation under the metabolic source. Since $\lim_{n \to \infty} F_\alpha^+(n,k,p^+) = 0$ also $\lim_{n \to \infty} F_\alpha(n,k,p^-,p^+,b^-,b^+) = 0$. Thus for large accumulation sizes the damage due to accumulation under the metabolic source will outweigh the benefit due to accumulation under the metabolic sink.

I will give now a qualitative description of the combined fitness functions which

are of interest here. This qualitative description will suffice to develop some ideas

regarding the accumulation dynamics under such a combined fitness function. First, I

drop for the moment the restriction that accumulation sizes have to be natural numbers

and allow them to be real. The marginal fitness functions show hyperbolic decay or

growth, so $F_\alpha(n,k,p^-,p^+)$ can be approximately represented in the form

$$F_\alpha(x,k,p^-,p^+,b^-,b^+)=\left(1-\left(1-\frac{a}{k\cdot x}\right)^{p^+}\right)^{\frac{1}{b^-}}\left(1-\frac{b}{k\cdot x}\right)^{\frac{p^-}{b^+}}\quad\text{where } x\in\mathbb{R}\text{ is the}$$

accumulation size.

Investigate $\dfrac{d}{dx}F_\alpha(x,k,p^-,p^+,b^-,b^+)=0$. After simplifying, we obtain

$$a\cdot b^+\cdot p^+\cdot\left(1-\frac{a}{kx}\right)^{p^+-1}\left(1-\frac{b}{kx}\right)=b\cdot b^-\cdot p^-\cdot\left(1-\left(1-\frac{a}{kx}\right)^{p^+}\right)$$

The left-hand side of this equation is strictly increasing in x, the right-hand side is

strictly decreasing in x. That means that there is maximally one value x^* for the

variable x, such that $\dfrac{d}{dx}F_\alpha(x,k,p^-,p^+,b^-,b^+)\Big|_{x=x^*}=0$. With the additional condition

that $F_\alpha(x,k,p^-,p^+,b^-,b^+)$ is increasing for small x, and approaching 0 for large x, we

conclude that if there is a value x^* such that $\dfrac{d}{dx}F_\alpha(x,k,p^-,p^+,b^-,b^+)\Big|_{x=x^*}=0$. Then

this x^* is the unique value of the fitness maximizing accumulation size.

In the following investigation the specific algebraic form of

$F_\alpha(x,k)=F_\alpha(x,k,p^-,p^+,b^-,b^+)$ is irrelevant. Only the fact that there exists an x^* such

that $F_\alpha(x,k)$ is strictly increasing for $x<x^*$, and strictly decreasing for $x>x^*$ is

essential. This is captured by the following definitions.

Definition (Uniquely maximizing fitness function): A function $f_\alpha(x):D\rightarrow\mathbb{R}^+$,

for which $\exists x^*\in D\forall x\neq x^*\wedge x\in D:f_\alpha(x^*)>f_\alpha(x)$ is called a *uniquely maximizing*

fitness function (for α over D*)*. The number x^* is called the *ideal (uniquely)*

maximizing quantity under f_α.

Calling x^* an "ideal" quantity points out that x^* might actually no be realizable in a given system. For example, in our case x^* is an accumulation size and, therefore, in any given system it always is an integer. However, x^* does not need to be an integer. The definition of f_α works independently of f_α being differentiable or not.

The fitness functions of the type $F_\alpha(n,k,p^-,p^+,b^-,b^+)$ cannot necessarily be assumed to be uniquely maximizing, although a smooth approximation might be. If $F_\alpha(n,k,p^-,p^+,b^-,b^+)$ is not uniquely maximizing then there are at most two realizable maximizing quantities. I denote them by n_1^* and n_2^*, with $n_1^* < n_2^*$. If both of them exist, then $n_1^* = \lfloor x^* \rfloor$, and $n_2^* = \lfloor x^* \rfloor + 1$. If only one exists, then either one might be possible.

Definition (Subsized and supersized accumulations): Let a uniquely maximizing fitness function f_α on accumulation sizes be given. Let x^* be the ideal uniquely maximizing quantity under f_α. Then any accumulation of size $x < x^*$ is called *subsized* and any accumulation of size $x > x^*$ is called *supersized.*   ▲

Figure 4.3 illustrates the anatomy of a combined fitness function with dominating metabolic sink for small accumulation sizes. There are exactly two accumulation sizes for which the fitness is that of a solitary individual, namely 1 and ω with $\omega > n^* > 1$. Individuals will have an incentive to migrate into solitude whenever the size of their accumulation is greater than ω which means that their fitness is below the fitness of a solitary individual. On the other hand, if the accumulation size is less than ω, then an individual never has an incentive to migrate into solitude and has an incentive to migrate to another accumulation only under certain conditions. They will be discussed later. The following definition will allow me to capture those situations.

Definition (Conditional and unconditional migration supporting accumulation sizes): Let ω be the unique accumulation size such that $f_\alpha(\omega) = f_\alpha(1)$ and $\omega > 1$. An accumulation size x with $x > \omega$ is called an *unconditional migration supporting accumulation size* and an accumulation size x with $x < \omega$ is called a *conditional migration supporting accumulation size*. ▲
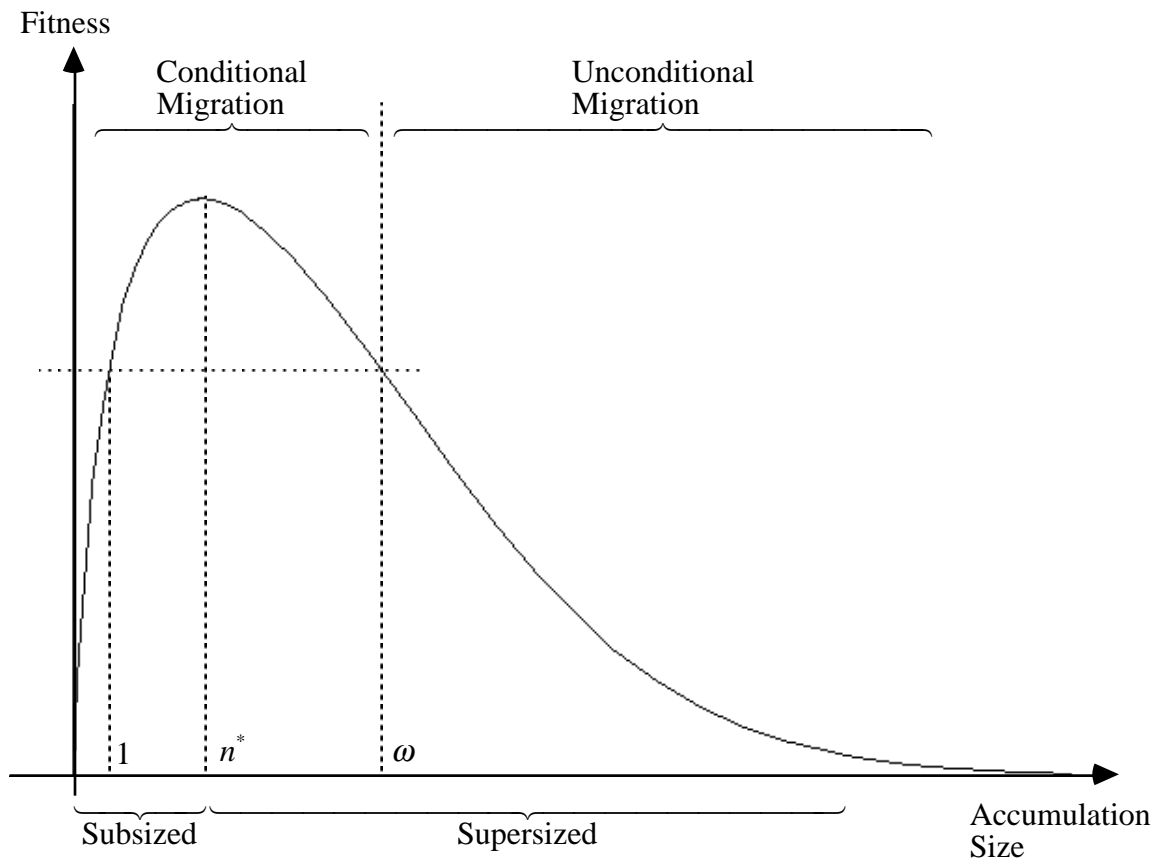

Figure 4.3.: Anatomy of a combined fitness function with the metabolic sink dominating for small accumulation sizes.

Let $F_\alpha(n,k) : \mathbb{N} \times \mathbb{N} \to \mathbb{R}$ be a uniquely maximizing fitness function in the first

component for each k. n^* is dependent on the number of accumulations and so is ω. In future this will be acknowledged in the notation when appropriate. Below I derive an equilibrium theorem for uniquely maximizing fitness functions.

The first equilibrium statement. Let a situation of k accumulations and/or solitary individuals be given and let there be at least two accumulations of equal size $\hat{n} > 1$ with $\hat{n} < \lfloor n_k^* - 1 \rfloor$, where $n_k^* > 2$ is the ideal maximizing accumulation size given k accumulations. Then, any individual migrating between two of these subsized accumulations would gain fitness and, therefore, a situation in which all accumulations are of size less than $\lfloor n_k^* - 1 \rfloor$ can never be an equilibrium. By a similar argument we can see that there is no equilibrium situation with at least two accumulations of different sizes less than $\lfloor n_k^* - 1 \rfloor$. In that case an individual can increase its fitness by migrating from a smaller of those groups to a larger one. From this we conclude:

Equilibrium statement 1: Let a situation of k accumulations and/or solitary individuals be given. Each equilibrium situation has at most one subsized accumulation of size

$$\hat{n} \leq \lfloor n_k^* - 1 \rfloor$$

Any situation consisting of exactly one conditional migration supporting accumulation is an equilibrium situation. ❑

If there is more than one accumulation in an equilibrium, then there are supersized or fitness maximized accumulations in that situation.

The second equilibrium statement. Type I equilibrium. Let a situation of k accumulations and/or solitary individuals be given. Let now all accumulations of a situation be of equal size $\hat{n} > \lfloor n_k^* - 1 \rfloor$ and let $\hat{n}$ be an accumulation size supporting conditional migration. That means that $\lfloor n_k^* - 1 \rfloor < \hat{n} < \omega_k$. Then, no individual can improve its fitness by migrating from one group to another and, therefore, this situation is an equilibrium. We conclude:

Equilibrium statement 2: Let a situation of k accumulations and/or solitary individuals be given. Let $\hat{n} > \lfloor n_k^* - 1 \rfloor$ and let $\hat{n}$ be an accumulation size supporting conditional migration, or let $\hat{n} = \lfloor n_k^* \rfloor$ and $F_\alpha(\lfloor n_k^* + 1 \rfloor, k) \leq F_\alpha(\lfloor n_k^* \rfloor, k)$. Let a situation be given with k accumulations all of the same size $\hat{n}$ and let $N = k \cdot \hat{n}$ be the overall number of individuals. Then this situation is an equilibrium. ❏

Definition (Type I equilibrium): An equilibrium as described in equilibrium statement 2 is called a *type I equilibrium*. ▲

A type I equilibrium situation is, therefore, an equilibrium consisting of supersized, conditional migration supporting accumulations of equal size.

The third equilibrium statement. Type II equilibrium. Let's assume that a situation of k accumulations and/or solitary individuals is given. Denote the smallest accumulation size by n_0. If n_0 is supersized, then all other accumulation sizes are supersized as well. Assume no accumulation size is unconditional migration supporting. That means that all accumulation sizes are less than or equal to ω_k . According to equilibrium statement 2, the situation is an equilibrium if all accumulations have size n_0 or size $n_0 + 1$ if $n_0 + 1 \leq \omega_k$. Then, there is no incentive for

migration from an accumulation of size n_0 to an accumulation of size $n_0 + 1$ (n_0 is supersized!) and there is also no incentive for migration from a group of size $n_0 + 1$ to a group of size n_0 since an individual undergoing that migration will have (after migration) the same fitness as before. There is also no incentive for migrating into solitude, since $n_0 + 1 \leq \omega_k$. Thus, a situation with conditional migration supporting supersized accumulations will be in equilibrium if those only differ by 1.

Equilibrium statement 3: Let a situation of k accumulations and/or solitary individuals be given. Let $k_1, k_2 \geq 1$ be positive integers, such that $k = k_1 + k_2$ and $N = \hat{n} \cdot k_1 + (\hat{n} + 1) \cdot k_2$. Then a situation with k_1 groups of size $\hat{n}$, and with k_2 groups of size $\hat{n} + 1$ is an equilibrium if $\hat{n}$ and $\hat{n} + 1$ are both supersized and conditional migration supporting accumulation sizes. ❑

Definition (Type II equilibrium): An equilibrium as described in equilibrium statement 3 is called a *type II equilibrium*. ▲

The fourth equilibrium statement. When deriving the third equilibrium statement we realized that there is no incentive for migration between two supersized and conditional migration supporting accumulations with a size difference of 1. However, if the size difference is larger than 1, then there is an incentive for migration from the larger to the smaller accumulation. This is captured in the next equilibrium statement.

Equilibrium statement 4: An equilibrium cannot contain two supersized accumulations with a size difference of more than one. ❑

The fifth equilibrium statement. Type III equilibrium. Let a situation of $k > 1$

accumulations and/or solitary individuals be given. Now I look into the case of a situation with exactly one subsized accumulation with size $n_0 \leq \lfloor n_k^* - 1 \rfloor$ and ask for conditions under which such a situation is an equilibrium. Let n_1 be the size of the smallest accumulation with $n_1 \geq \lfloor n_k^* \rfloor$. Equilibrium statement 4 implies that $n_1 + 1$ is the only other supersized accumulation size possible if the situation is assumed to be an equilibrium.

Assume now that the equilibrium consists of accumulations of the sizes $n_0, n_1, n_1 + 1$.

n_0 is a possible equilibrium accumulation size if and only if $F_\alpha(n_0, k) \geq F_\alpha(n_1 + 1, k)$, because then there is no incentive to migrate from an accumulation of size n_0 to neither an accumulation of size n_1 nor an accumulation of size $n_1 + 1$.

n_1 is a possible equilibrium accumulation size if and only if $F_\alpha(n_1, k) \geq F_\alpha(n_0 + 1, k)$, because then there is no incentive to migrate from an accumulation of size n_1 to neither an accumulation of size n_0 nor an accumulation of size $n_1 + 1$.

$n_1 + 1$ is a possible equilibrium accumulation size if and only if $F_\alpha(n_1 + 1, k) \geq F_\alpha(n_0 + 1, k)$. Only in that case there is no incentive for a migration from an accumulation of size $n_1 + 1$ to an accumulation of size n_0.

From these considerations we conclude that $F_\alpha(n_0, k) \geq F_\alpha(n_1 + 1, k) \geq F_\alpha(n_0 + 1, k)$. n_0 is subsized and $F_\alpha(n_0, k) \geq F_\alpha(n_0 + 1, k)$. This means that $n_0 + 1$ is supersized. n_1 was assumed to be greater than n_0. Therefore $n_1 + 1 > n_0 + 1$. This, however, is not possible since $n_0 + 1$ is supersized and $F_\alpha(n_1 + 1, k) \geq F_\alpha(n_0 + 1, k)$. $n_1 + 1$ is, therefore, not a possible equilibrium size. So, the only two possible equilibrium sizes are n_0, n_1. This means that the two inequalities $F_\alpha(n_0, k) \geq F_\alpha(n_1 + 1, k)$ and $F_\alpha(n_1, k) \geq F_\alpha(n_0 + 1, k)$ have to be satisfied. There are four possibilities. Either $n_0 = \lfloor n_k^* - 1 \rfloor$ is the realized fitness

maximizing accumulation size and $n_1 = n_0 + 1 = \lfloor n_k^* \rfloor$. Or, $n_0 = \lfloor n_k^* - 1 \rfloor$ and

$n_1 = n_0 + 1 = \lfloor n_k^* \rfloor$ is the realized fitness maximizing accumulation size. Or,

$n_0 = \lfloor n_k^* - 1 \rfloor$ and $n_1 = n_0 + 1 = \lfloor n_k^* \rfloor$ are both the realized fitness maximizing

accumulation sizes. Or, neither of those previous three possibilities. In the last case the

fitness function has to be skewed to the left: The decay for accumulation sizes larger

than n_k^* has to be steeper than the increase for accumulation sizes smaller than n_k^*.

Equilibrium statement 5: Let a situation of $k > 1$ accumulations and/or solitary

individuals be given. Let $n_0 \leq \lfloor n_k^* - 1 \rfloor$ and $n_1 \geq \lfloor n_k^* \rfloor$. Let $F_\alpha(n_0, k) \geq F_\alpha(n_1 + 1, k)$ and

$F_\alpha(n_1, k) \geq F_\alpha(n_0 + 1, k)$. Let $N = n_0 + n_1 \cdot (k - 1)$. Then a situation with one group of size

n_0 and with $k - 1$ groups of size n_1 is an equilibrium.

Definition (Type III equilibrium): An equilibrium as described in equilibrium

statement 5 is called a *type III equilibrium*. ▲

Dispersal. An individual will migrate into solitude if and only if the size of its

accumulation is unconditional migration supporting. In all other cases fitness is above

solitary fitness. This also means also that any equilibrium consists only of

accumulations of conditional migration supporting sizes.

All the equilibrium statements can be merged together to the following equilibrium

theorem.

Equilibrium Theorem for uniquely maximizing Fitness Functions: All equilibrium

situations are type I, II or III equilibria.

Figure 4.4.(a)

n_1 $n_1 + 1$ n_2 $n_2 + 1$

no incentive to migrate

Figure 4.4.(b)

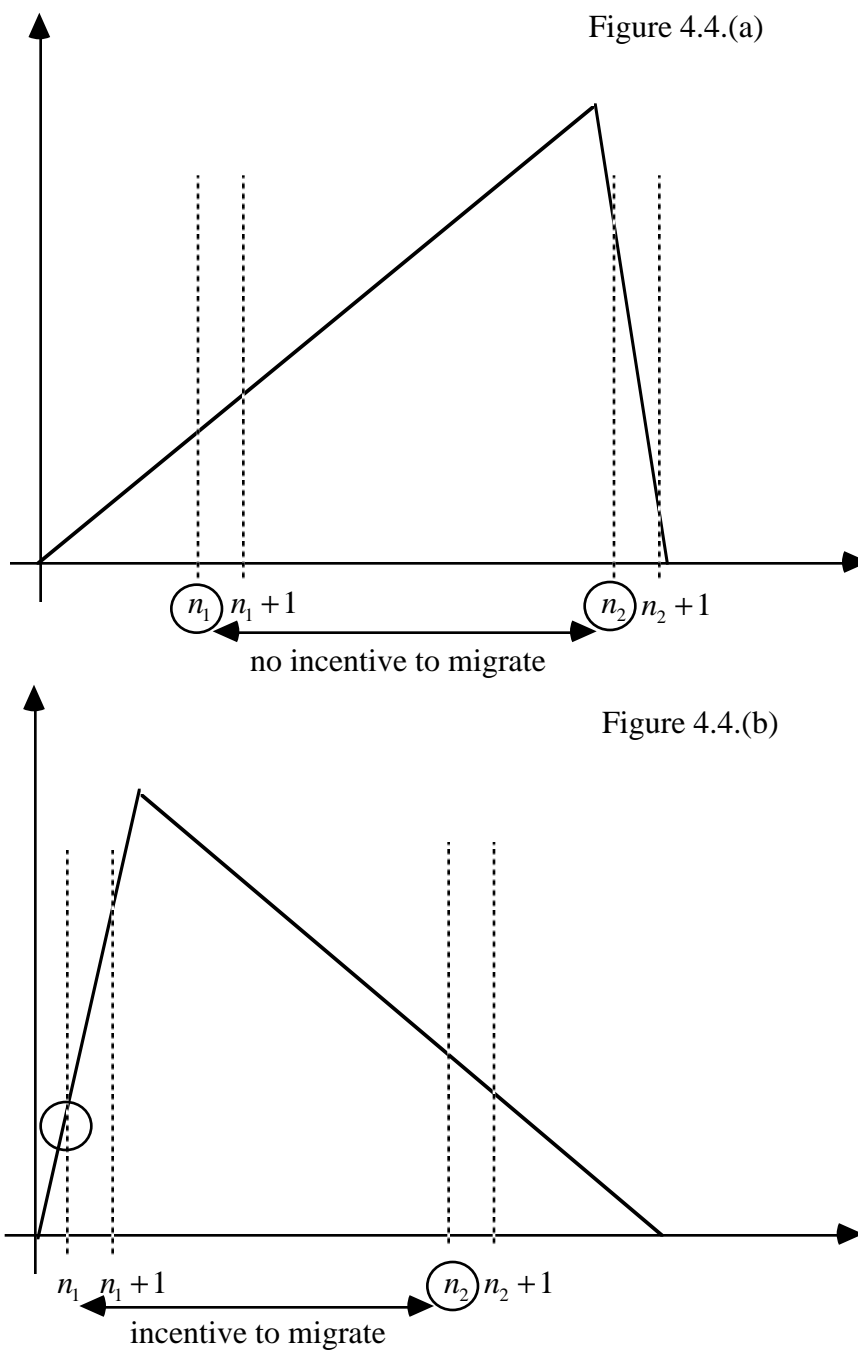n_1 $n_1 + 1$ n_2 $n_2 + 1$

incentive to migrate

Figure 4.4.:   Two uniquely maximizing fitness functions. (a) supports type III equilibria, (b) does not. See explanation in text.

Figure 4.4. shows two similar simple fitness functions illustrating the above given condition. One of them is able to support type III equilibria, the other is not. In order to see that assume that an equilibrium with a subsized group of size n_1 is given. The supersized group of size n_2 in that situation has to provide larger fitness than the group of size n_1, because otherwise migration from the supersized to the subsized group will happen. It is now clear that in case (a) migration will not occur, since in either case the migrating individual is worse off after migration than before. In case (b), however, there is either for an individual of the supersized group or for the individual of the subsized group (maybe for both) an incentive to migrate.

Discussion. If migration is costly, individuals will migrate to another group only if the gain in fitness compensates them for the migrational cost. Thus, if migrational cost is high, every situation might be an equilibrium. Cost of migration acts, therefore, as a conservative force that tends to preserve given situations. Introducing cost of migration into the model gives rise to equilibrium situations that are not of types I,II or III. Since in real life animals reproduce, it is expected that if accumulations are possible then they will continue to grow to stable accumulations of unconditional migration supporting sizes (assuming that there is a cost of migration). Reproduction, therefore, counteracts the preservation of smaller accumulations.

One way to introduce a cost of migration is to allow migration only from an accumulation into solitude and from solitude into an accumulation, but no migration between accumulations. This would yield any situation consisting of accumulations of conditional migration supporting sizes to be an equilibrium.

It is assumed in the model that an individual is able to determine before migrating how high the its fitness within its accumulation is compared to those of individuals in another accumulation. In a more realistic setting accumulations might meet each other

randomly. Individuals of meeting accumulations can compare the fitness of their own accumulation to the fitness of the other one by comparing an observable index of 'well being' of the individuals of the other accumulations with their own. If those individuals are significantly better off than the ones of their own accumulation, an incentive to migrate is established. Again a counterforce to migration in this case might be given by a social structure which excludes intruders. Also individuals who enjoy high social rank should be more reluctant to migrate than those with a low rank, since previously acquired privileges might be lost.

One factor of accumulation growth in actual biological species is reproduction. Accumulations are in general also mating communities, and their size will grow over time by generating offspring.

Once the accumulation size grows above a size which keeps fitness above solitary fitness, individuals will have an incentive to leave the accumulation. They will either go into solitude or migrate together with others. The migration of several individuals simulataneously can be described by letting a first individual migrate into solitude and the others successively join this first one forming another accumulation. This process will continue as long as the fitness in the new accumulation is larger than in the old one after migration of an individual.

In general, then, we conclude that individuals should accumulate beyond an optimal accumulation size, even in more sophisticated models. Accumulations where individuals have lower competitiveness give their members higher fitness and will attract more individuals. If a distributable metabolic sink and a distributable metabolic source are such that the effect of the metabolic sink outweighs the effect of the metabolic source for small accumulation sizes, evolution will support tolerance and the formation of accumulations. This makes the identification of distributable metabolic sinks and sources an essential biological - and also sociological - task. We have to

identify, analyze and possibly implement them for their potential to cause and maintain accumulations within populations of individuals.

Chapter 5.   Increase in Genetic Variation and Not-Merely Local
Optimization as a possible Consequence of   Accumulation

One essential problem in contemporary evolutionary biology is that the process of evolution driven by selection and mutation is only a "locally maximizing machine" (seeElster (1979)).   Under selection and mutation individuals of a species will eventually bear traits which optimize their fitness under this selective regime. It is, however, very unlikely that this optimal fitness is indeed the globally optimal one. It more likely is a merely local optimum and it might be actually the lowest of those. In order for the species to reach a higher optimum at least part of the population has to survive and reproduce by lowering their individual fitness. Only then at least a part of species can, via reproduction, 'leave the achieved local optimum and travel through a valley of lower fitness to reach another peak'. This is of course not possible under the survival-of-the-fittest notion. Any individual of lower fitness is selected against and the reaching of another fitness optimum than the currently occupied one is very unlikely. Once a local fitness optimum is reached the species has to remain there as long as there is now external change of the selective regime. In traditional evolutionary biology there is no possibility for an *internal* change of the selective regime other than adaptation.

In this chapter I will show that the ability to form accumulations can change the selective regime from within the species. It can provide the species with the possibility to leave a local optimum, and reach a higher, or even a global, one. I will show that accumulation of individuals can balance mutation and selection with respect to a certain trait so that individuals of originally lower fitness can be maintained within the population. This gives the population the potential to leave, at least partially, the currently occupied optimum. With this, however, the probability of having to remain at this optimum might become significantly less than 1 and a new optimum might be

achieved - either by single individuals or by the whole population (if the new optimum proves to be of significantly higher fitness than the old one).

5.1. The raising and dampening of fitness by the receptance under a metabolic sink

I am confining this investigation to the case of a metabolic sink with $m^\Gamma = 1$ and one realization. Recall that in chapter 4 the standard receptance under one realization of Γ and $m^\Gamma = 1$ was defined by

$$\overline{\rho}^\Gamma_{\{\alpha\}:S} = \frac{\eta^\Gamma_S \cdot \rho^\Gamma}{|S|}$$

and the standard escapability as

$$\overline{\xi}^\Gamma_{\{\alpha\}:S} = 1 - \overline{\rho}^\Gamma_{\{\alpha\}:S}$$

Also recall that the individual escapability ξ^Γ is defined as $\xi^\Gamma = 1 - \rho^\Gamma$. The overall format of escapability then becomes

$$\overline{\xi}^\Gamma_{\{\alpha\}:S} = 1 - \frac{1 - \xi^\Gamma}{n} \cdot \eta^\Gamma_S$$

where η^Γ_S is again assumed to be only dependent on the number of accumulations. Then $\overline{\xi}^\Gamma_{\{\alpha\}:S}$ can be rewritten as

$$\overline{\xi}^\Gamma_{\{\alpha\}:S} = 1 - \frac{1 - \xi^\Gamma}{n} \cdot \eta^\Gamma_S = 1 - \frac{\eta^\Gamma_S}{n} + \frac{\xi^\Gamma}{n} \cdot \eta^\Gamma_S = \left(1 - \frac{\eta^\Gamma_S}{n}\right) + \frac{\eta^\Gamma_S}{n} \cdot \xi^\Gamma \qquad (1)$$

In chapter 4 I assumed all individual escapabilites to be identical. I will now drop this assumption. Equation (1) then becomes

$$\overline{\xi}^{\Gamma}_{\{\alpha\}:S} = \left(1 - \frac{\eta^{\Gamma}_S}{n}\right) + \frac{\eta^{\Gamma}_S}{n} \cdot \xi^{\Gamma}_{\alpha} \tag{2}$$

$\overline{\xi}^{\Gamma}_{\{\alpha\}:S}$ is therefore a function of ξ^{Γ}_{α}. The additive term $\frac{\eta^{\Gamma}_S}{n} \cdot \xi^{\Gamma}_{\alpha}$ in equation (2) means that $\overline{\xi}^{\Gamma}_{\{\alpha\}:S}$ is a compressed version of ξ^{Γ}_{α}, because $1 - \frac{\eta^{\Gamma}_S}{n}$ is not dependent on ξ^{Γ}_{α}. Since $|\frac{\eta^{\Gamma}_S}{n} \cdot \xi^{\Gamma}_{\alpha} - \frac{\eta^{\Gamma}_S}{n} \cdot \xi^{\Gamma}_{\beta}| < |\xi^{\Gamma}_{\alpha} - \xi^{\Gamma}_{\beta}|$ for all $n \le \eta^{\Gamma}_S \le 1$ and $n > 1$ the term $\frac{\eta^{\Gamma}_S}{n}$ is called the *dampening term* of equation (2).The term $1 - \frac{\eta^{\Gamma}_S}{n}$ on the other hand raises the graph of $\frac{\eta^{\Gamma}_S}{n} \cdot \xi^{\Gamma}_{\alpha}$. $1 - \frac{\eta^{\Gamma}_S}{n}$ is increasing as n increases, so for larger n raising will be higher than for lower ones. The term $1 - \frac{\eta^{\Gamma}_S}{n}$ is therefore called the *raising term* of equation (2). The two essential inequalities which describe the raising and dampening of ξ^{Γ}_{α} under $\overline{\xi}^{\Gamma}_{\{\alpha\}:S}$ are:

The dampening inequality: Let $S \subseteq \mathscr{T}$ be an accumulation in $\mathscr{T}$. Let $|S| > 1$. Then:

$$\forall \alpha, \beta \in S : |\overline{\xi}^{\Gamma}_{\{\alpha\}:S} - \overline{\xi}^{\Gamma}_{\{\beta\}:S}| < |\xi^{\Gamma}_{\alpha} - \xi^{\Gamma}_{\beta}| \tag{3}$$

and

The raising inequality: Let $T, S \subseteq \mathscr{T}$ be accumulations in $\mathscr{T}$. Let $|S| > |T|$. Then:

$$\forall \alpha \in S \cap T : \overline{\xi}^{\Gamma}_{\{\alpha\}:S} > \overline{\xi}^{\Gamma}_{\{\alpha\}:T} \tag{4}$$

The escapabiltiy under a distributable metabolic sink is a measure of fitness. In chapter 4 we have already discovered that under a distributable metabolic sink an individual has a higher fitness in a larger accumulation than in a smaller one. This is expressed by the raising inequality. The dampening inequality gives more insight into how the fitness is raised: Accumulation raises the fitness of individuals differently. Individuals of higher fitness benefit less than individuals of lower fitness. Figure 5.1 illustrates this. The fitness of the solitary weaker individual approaches the fitness of the solitary stronger individual as accumulation size increases.
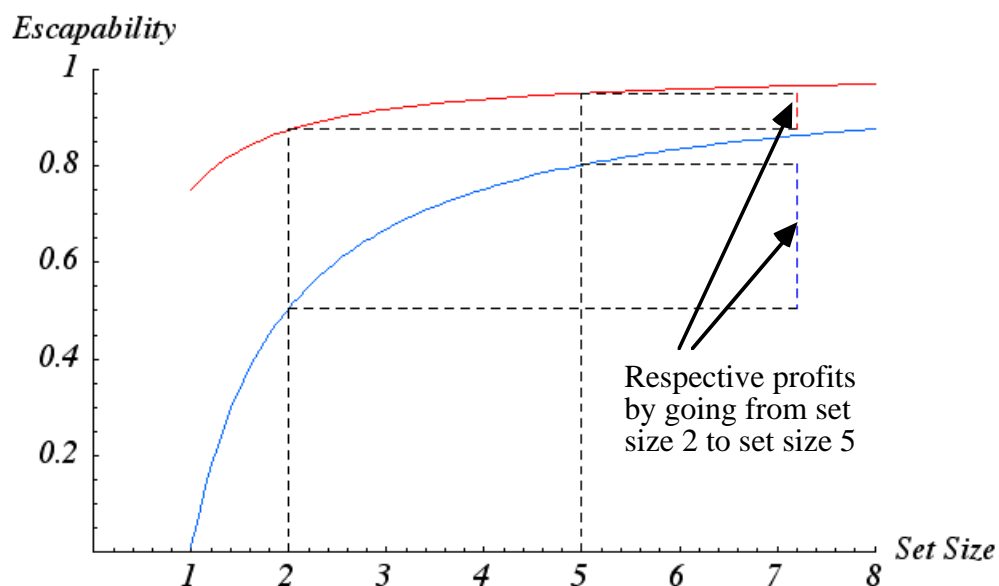

Figure 5.1.: Two graphs for escapability for solitarian escapability of .01 and .75 respectively. Going from set size 2 to set size 5 shows that the solitary weaker individual profits significantly more than the solitary stronger one. The raising property increases both individuals escapability, the dampening property decreases their distances from each other.

As the accumulation size of S increases $\overline{\xi}^{\Gamma}_{\{\alpha\}:S} \rightarrow 1$ for all individuals α. This means that forming accumulations is a strategy for a species to eliminate the selective regime imposed by a distributable metabolic sink. If the accumulation size is large

enough, then individuals of lower solitary fitness - or with lower individual escapability - are maintained in the population. The dampening of the selective regime will result in an increased genetic variation in the species. The species will start to genetically "bleed out" around its attained local fitness maximum. If this bleeding out is intense enough such that the species reaches genetically the attractive region of another higher maximum then, if this maximum under accumulation is high enough, selection will again happen, and the species will evolve towards the new maximum.

For this mechanism to work it has to be assumed that selection is not "strict". That means that an individual within a certain ε environment of the maximal fitness need not have a lower fitness than an individual with the maximal fitness. This can be justified by introducing some randomness into the selective process. Such an assumption will make the model more realistic.

5.2.   Graphical representations

In the following I illustrate dampening and raising of escapability in accumulations. For the graphical representation I will introduce some conditions which are rather restrictive. These conditions do, however, apply only to the graphical representation, and will not change the fundamental ideas discussed in chapter 5.1.

First, I assume a species for which small changes in genetics will result in small changes of fitness.

Second, I assume that there are "layers of equal fitness". Individuals within one layer are not selected against other individuals in that layer, although their escapability is lower. This is a simplification of the randomness assumption stated at the end of the previous paragraph.
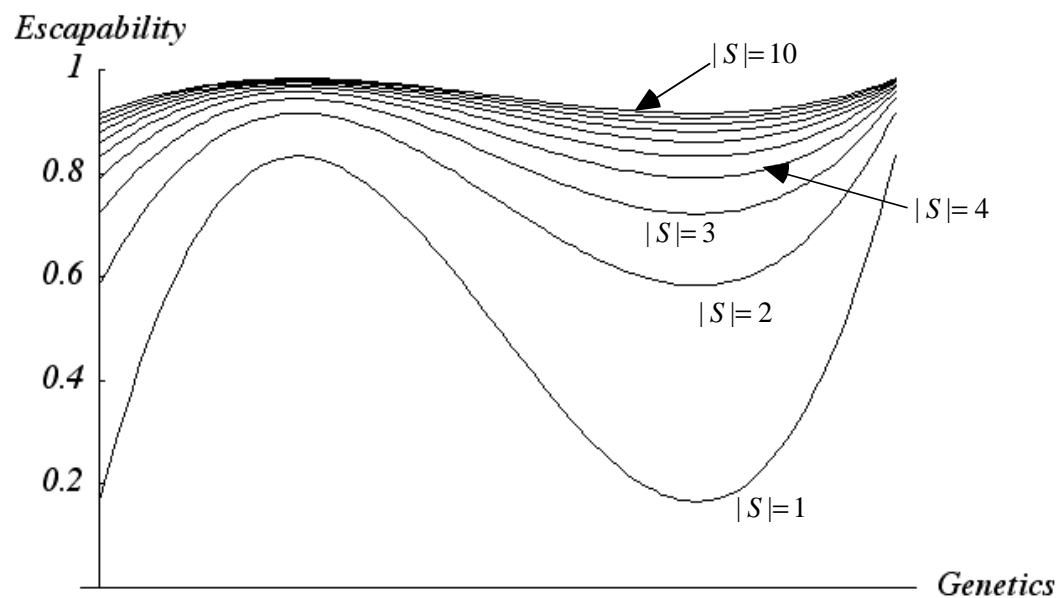
Figure 5.2.: Graphs for escapability are given for different values of $|S|$. The rise of escapability is of towards 0 decreasing return, with the most significant increase when going from solitarity to sets of pairs. We also note that weak individuals benefit more from pairing up than strong ones.

Figure 5.3 shows graphs of escapabilities with levels of equal fitness to illustrate the increase of genetic variation under accumulation.
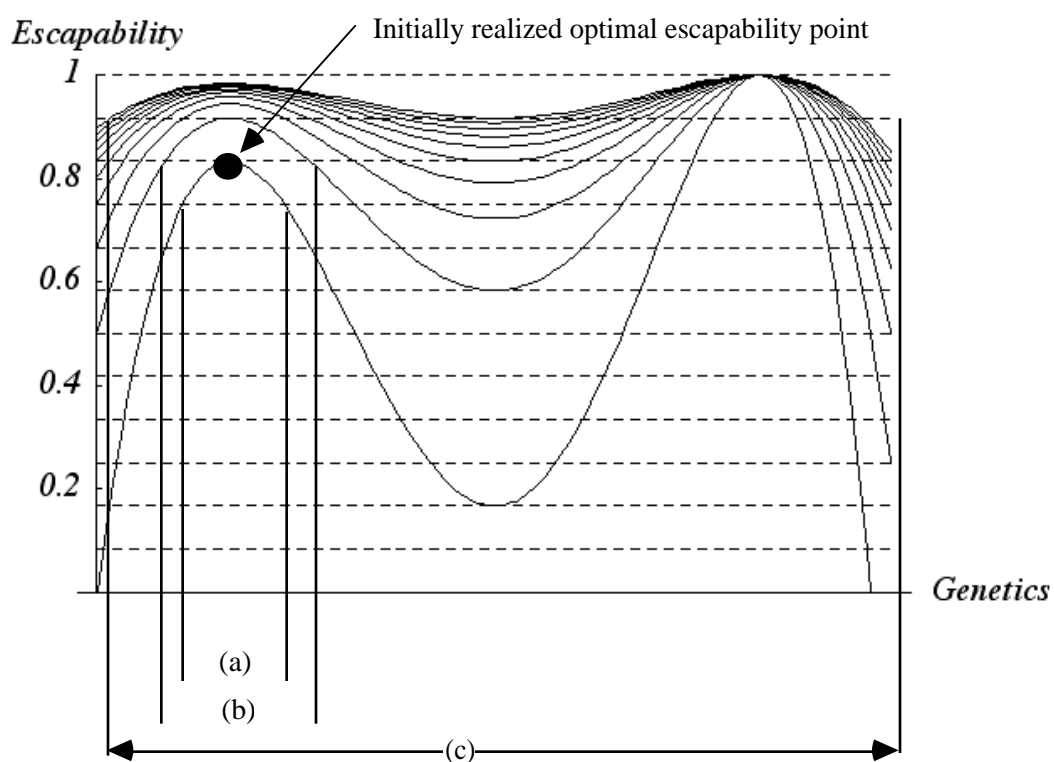
Figure 5.3.: Increasing genetic variation with accumulation size.

Figure 5.4 shows an example where the genetics emerging under accumulation is of greater fitness than the one evolved under the original solitary regime. Remaining solitary means remaining trapped in the local genetic optimum. First, accumulation yields an increase in variation and, once the attractive region of the higher optimum is reached, selection will favor those closer to that optimum. In this example each individual will eventually be of higher solitary fitness than any individual under the initial regime.
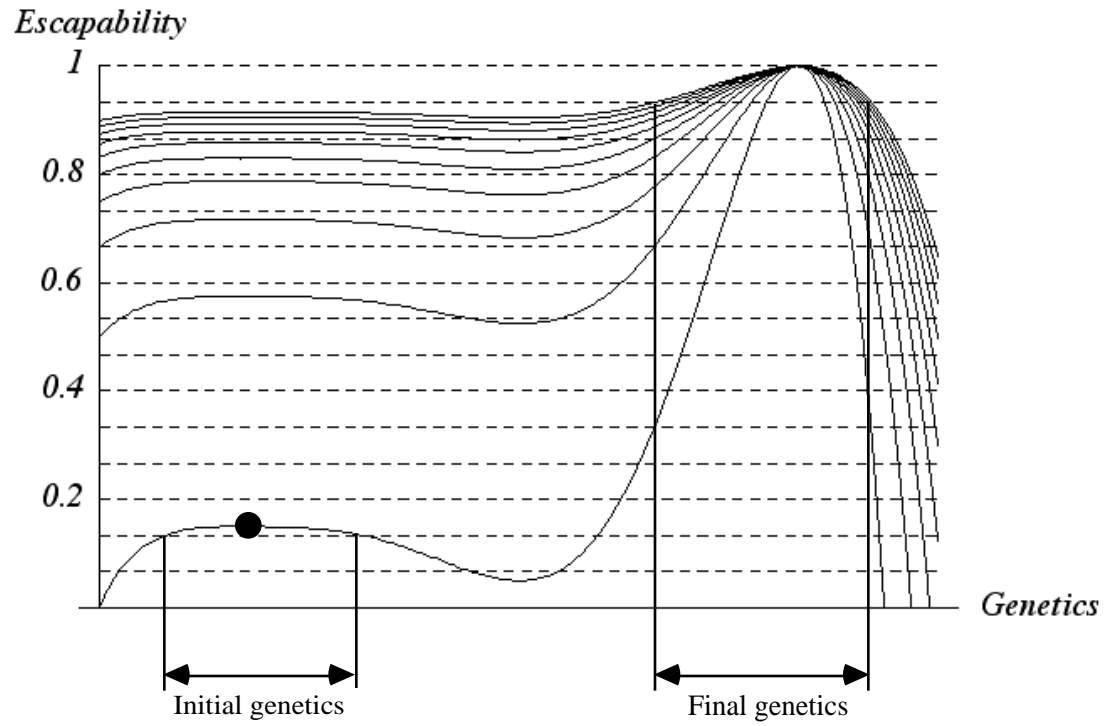
Figure 5.4.: An example of a solitarian escapability which under accumulation yields an overall higher solitarian fitness than the original one.

Chapter 6.   Conclusion

In this chapter I will summarize the ideas and results of the thesis, and indicate directions of further research.

The axiomatic approach. One problem in theoretical population biology today is the lack of a unified approach like the one in theoretical physics (See Meyen (1987) for more on the discussion on the structure of theoretical biology). To each biological problem there are many possible approaches, and even in simple models (e.g. predator-prey systems) there is no theoretical consensus which mathematical terms to use to model certain features of the system (e.g. capture rate of prey by predator). This lack of consensus makes the axiomatic approach essential. At least two advantages have to be mentioned. First, the assumptions are clearly listed and force the researcher to derive all theoretical conclusions from those axioms alone. Second, different axiomatic systems can be compared and a difference in approach becomes more apparent. That makes it more likely for some consistent theory to emerge. By successively adding axioms to an axiomatic system we can model more and more complex situations.

In my thesis I have introduced a basic axiomatic system which attempts to capture the essence of the situation of a metabolic individual - an individual who will only continue to exist if it is able to maintain a certain level of metabolic energy. This is the basic dilemma in which all living beings find themselves, and the complexities of life emerge as a consequence of the different approaches taken to resolve this dilemma.

Metabolic space and time. The specific problem I address with my approach is the emergence of cooperation in individuals originally unable to cooperate. In order for cooperation to emerge in a biological setting, individuals have to acquire the ability to

live closely to each other.   If the objective of cooperation is to defend against a common metabolic sink individuals have to communicate with each other (forming an accumulation and moving simultaneously requires communication) and possibly attack simultaneously. This requires initial closeness between individuals. This initial closeness cannot be assumed if those individuals compete over metabolic resources which are distributed in the same space.

The axioms of FundAx are set theoretic axioms that describe the relation between individuals and their metabolic sources and sinks (see chapter 2). FundAx gives rise to the uniqueness of the set of total encounter associated with an encounter event, and the concepts of cluster, accumulation and solitary individual can be derived (see chapter 3). Note that those concepts imply some "spatial quality", without space being explicitly introduced. Many approaches in theoretical biology ignore space as a component because there is no consensus how to account for it. Introducing space would, hence, lead to unforeseeable complications. For instance, in the area of population genetics equations are in general derived under the assumption that mating is completely random. However, it is apparent that an individual will more likely mate with another individual who lives "close by". Analogous to the concepts of 'metabolic source' and 'metabolic sink' a concept like 'mating range' can be introduced which defines individuals who are members of a 'mating cluster', a 'mating accumulation', or are 'mating solitaries'. Mating will, then, happen within mating clusters.   These ideas can be defined in the conceptual framework proposed in my thesis.   Such extensions will have to be worked out more explicitly in future research.

The concept of the 'set of total encounter' gives therefore rise to a biological – here, purely metabolic - notion of space. Biological individuals evolve in a physical Euclidean space. To base behavioral investigations on the Euclidean notions of space (e.g. Euclidean distance, speed, volume etc.) appears, however, to complicate issues,

since different species of individuals "use" space as well as time differently. This different use of space and time should be acknowledged and captured as early as possible in order to obtain a clear understanding of the 'meaning' which spatial and temporal notions have for individuals. Those meanings are captured by probabilities of encounter. If such a probability is small, then the metabolic distance is large, and vice versa. A derivation of a metabolic distance concept is given in appendix 4.

The following thought experiment will illustrate the idea of a metabolic notion of space further. Assume a rabbit, a turtle, and a (hungry) fox are locked in a room without any possibility to hide. The rabbit will try to be saved from the fox by attempting to increase the Euclidean distance between itself and the fox. Assume now the fox has cornered the rabbit in a fashion which does not allow the rabbit to escape anymore. In that case Euclidean distance has no biological meaning for either the rabbit or the fox: no matter what that Euclidean distance will be the rabbit will be captured. The metabolic distance between rabbit and fox is in that case 0 (for possibly infinitely many Euclidean distances), since the probability of capture is 1. The turtle, on the other hand, will not even attempt to increase its Euclidean distance from the fox when approached. As soon as the fox approaches, the turtle will retreat into its protective shell. It has not changed the Euclidean distance between itself and the fox, but rather by retreating into its shell it has changed the *meaning* of the Euclidean distance. Regardless of how close the fox is in Euclidean space, the turtle can increase the metabolic distance between itself and the fox to infinity at any time without even having to relocate in Euclidean space. On the other hand, the turtle is a vegetarian, and the food it depends on does not require it to engage in fast movements. The turtle has, therefore, attained an evolutionary state that is close to perfect: Completely removed from its metabolic sinks and always exposed to its metabolic sources. While the rabbit has adapted to its predators, the turtle has removed itself from them. The concept of

space that will describe the escape strategies of a rabbit from a fox is certainly much more complicated than the concept of space necessary to do the same for a turtle. In the case of the turtle space with regard to its predators and its food sources is nearly eliminated. More precisely, the turtle still needs to pay attention when approached by a predator and estimate distances in order to decide when to retreat. And it needs to move in order to obtain food. However, this is no comparison to the spatial and temporal tasks a rabbit is facing when hunted by one of its predators.

For an individual who is completely removed from its metabolic sinks (which means that the probability of reception of a representation of those metabolic sinks is 0 at any time point), and who is in permanent contact with its metabolic sources (which means that the probability of reception of a representation of those sources is 1 at any time point), concepts of space and time cannot have any biological relevance. For such an individual space and time will have ceased to exist and will have no meaning. Consequently the individual will cease to engage in any form of movement, of transformation of space and time. Examples of such individuals are most plants. Since individuals with lower reception of metabolic sinks and higher reception of metabolic sources are selected for, the general tendency of a species evolution will be towards an elimination of space and time. How far that elimination can be realized depends on the correlation between metabolic distances from sinks and sources. As long as this correlation is positive - the smaller the distance from a metabolic source the smaller the distance from a metabolic sink – the elimination of time and space is not possible. Positive correlation is given in the case of the rabbit-fox example: The rabbit is forced to leave its burrow in order to forage. By doing so it decreases its distance to food as well as its distance to predators. The turtle-fox example, on the other hand, shows no strong positive correlation between distances from metabolic sources and metabolic sinks, since the turtle is in the lucky position of carrying its "burrow" around.

Therefore, a turtle always has roughly the same probability of being captured by a predator, whether foraging or not. For most species there is, however, a positive correlation of the distances, and adaptation is one way to make that correlation less positive over time. Yet, adaptation can never result in the correlation being not-positive. Any mechanism which 'uncorrelates' the distance between metabolic sources and metabolic sinks will be selected for and finding and investigating those mechanisms is essential for evolutionary research. During the evolution of a species we can observe how this correlation of distances between individuals and metabolic sources and sinks changes.

In biological settings the Euclidean space is often the "null-space" in the sense that 'closer' in Euclidean terms means also 'closer' in the terms given by any metabolic source or sink. This does not mean that a cluster or an accumulation under one metabolic source or sink will also be a cluster or accumulation under another one, but rather that if two individuals are closer to each other under one metabolic source or sink, then this will also hold for any other metabolic source or sink. This statement, however, does not follow from the axioms used in this thesis. A new axiom declaring the Euclidean space as the null-space for a list of metabolic sources and sinks under consideration has to be introduced to pursue this idea further. An objective of cooperation that requires closeness of individuals in the Euclidean sense can only be pursued by individuals if those have already evolved a way of living close to each other in the Euclidean sense. Appendix 4 discusses the concept of *metabolic distance* that shows how the concepts of cluster and accumulation can be used to define a concept of distance and, therefore, a concept of space.

The idea of a metabolic concept of space has an analogy in Physics. Due to Einstein's Theory of relativity space and time are deformed from their ideal Euclidean state due to the gravitation of bodies within this space. Around different physical

bodies space and time are in different states of contraction. Analogously, the meaning of space and time for a biological individual depends on how it relates to its metabolic sources and sinks.

One strategy to increase the distance to a metabolic sink is the formation of accumulations under that metabolic sink as described in this thesis.   But this, in general, will also increase the distance to any metabolic source. A change in the individuals might increase the distance to the metabolic sink even further without increasing the distance to the metabolic sources (e.g. the lion-confusion-supporting surface patterns of zebras). This, however, gives rise to the idea that there might be changes in the individuals that decrease the distance to the metabolic sources without decreasing the distance to the metabolic sink. These changes can be behavioral like e.g. reduction of competition and aggression, the ability to share, division of labor, etc. Those strategies of cooperation will be selected for if they increase the distance to metabolic sinks, and decrease the distance to metabolic sources. If formation of accumulations is advantageous, then a degradation of competition over food will happen over time. The ability to share will emerge from a degeneration of interest in defending food. This might be advantageous if food items are to large to be ingested at once, or if the variation in encountering those food items is large - which means that the probability of encountering no food item before starvation is high. In both cases the expected number of encounters has to be high enough to sustain the accumulation.

Equilibrium accumulation sizes. In chapter 4 I have showed that under a distributable metabolic sink individuals have an incentive to form accumulations, under a distributable metabolic source they have an incentive to disperse. If no metabolic source is present, then individuals will form arbitrary large accumulations under a metabolic sink. If a metabolic source is added, then competition will limit the optimal

accumulation size. Furthermore, the optimal accumulation size is not, in general, the one to emerge as equilibrium if individuals are allowed to join accumulations as long as they individually benefit from joining. As long as there are solitary individuals the equilibrium accumulation size will result in a fitness that is not significantly larger than or equal to the fitness of solitary individuals. Nevertheless accumulation will happen and the equilibrium accumulation size is an evolutionary stable and approachable equilibrium. This was already pointed out by Sibly (1983). In chapter 4 of this thesis I derived several possible equilibria that yield fitness that is in general higher than the solitary one under the simplifying assumption that there is no cost of migration and no explicit spatial relationship between accumulations. Also, the possibility of reproduction is omitted. Reproduction will give rise to larger accumulation sizes with individual fitness being lower than solitary fitness. This will result in individuals migrating into solitude, or in subsets of individuals splitting off as accumulations from the original accumulation.

Different levels of selection. Interesting to note is that reproduction in individuals leads under these ideas to reproduction of accumulations. Individuals as well as accumulations are entities under distributable metabolic sources and sinks. Therefore, distributable metabolic sources and sinks link at least two levels of complexity on which selection can occur. Indeed, as soon as we introduce the concept of reproduction in accumulations, we can think about selection on accumulations as well. The faster an accumulation can reproduce, the higher the accumulation's fitness. The speed of an accumulation's reproduction is, however, directly proportional to the speed of reproduction in individuals. The speed of individual reproduction depends, in turn, on individual fitness. This presents a very interesting problem: If we postulate that there is some selection on accumulations, then this selective force will drive the equilibrium

size of accumulations towards the size optimizing individual fitness and away from the original suboptimal equilibrium. Therefore, selection on accumulations is expected to give rise to a higher intolerance among individuals in supersized accumulations, and higher tolerance among individuals in subsized accumulations. The new equilibrium group size(s) will be closer to the fitness optimizing group size. This means that the fitness function will be skewed to the right (as in figure 4.4.(a)). This, again, is a research that still has to be done. By developing those thoughts explicitly I hope to provide an example on how a selection at two different levels of evolution can actually happen, and how a selection on individuals can imply selection on groups of individuals. In Keller's book (1999, p.11) Reeve and Keller address this question in the following form:

> ... What attractive evolutionary forces bind low-level vehicles (...),
> like physical stretches of DNA (...), chromosomes, and cells, into
> intermediate vehicles, like multicellular organisms? Under what
> conditions do these attractive forces exceed the repulsive ... forces
> and under what conditions do they not?
> ... Similarly (...), what attractive evolutionary forces bind
> intermediate-level vehicles, such as organisms, into higher-level
> vehicles, such as social groups or individuals? Under what conditions
> do these attractive forces exceed the repulsive ... forces?

Using individual fitness functions dependent on accumulation sizes promises some clarification on these issues.

Increase in genetic variability. In chapter 5 of this thesis I have shown that

accumulation under a distributable metabolic sink will result in an increase of genetic variation in the accumulating species. This increase of genetic variation is the basis for individuals to be able to "degenerate" within accumulations. This holds under an assumption that exposure is constant with regard to changes in accumulation size. Genetic variation can then increase due to the dampening of the original solitary selective regime under accumulation that decreases the difference in fitness between individuals. This gives rise to greater genetic flexibility. Individuals of lower solitary fitness are not necessarily selected against and new fitness optima can possibly be reached. Due to its increased genetic variation a species consisting of accumulations is expected to react more flexibly to changes of the environment than a species consisting of solitary individuals.

If we allow sexual reproduction in the individuals then there is the possibility that genetic variation in accumulations will decrease due to inbreeding (if there is no sufficient influx of new genetic material due to migration). This will happen when e.g. accumulations are stationary and will not encounter and mingle with each other. When there is extensive inbreeding there will still be an increase in fitness due to accumulation that will, in turn, lower the selective pressure and lead to a degeneration of the species. This degeneration can be observed in eusocial species as termites, ants, and honey bees, as well as in the naked mole rat (see Sherman, Jarvis, Alexander (1991)) all of them forming colonies of extreme inbreeding. The degeneration of individuals in those species makes them unable to return to a life in solitude. They are dependent on being embedded in the social structure of their accumulation and will die if removed from it. At this stage of individual degeneration - when migration into solitude is no longer a survivable option - accumulations are more like organisms, and individuals are more like organs or cells than independent entities. At this point selection does not unconditionally favor an individual who pursues exclusively its own

benefit without taking the benefit of the accumulation into account as well. By damaging the accumulation the individual might damage itself, because it cannot leave that accumulation anymore. Again, further research has to be done to address these ideas properly.

Division of labor. A phenomenon which is widely observed in strongly inbreeding colony types of accumulations is 'division of labor'. Division of labor often depends on age like in honey bees. Young workers will be responsible for cleaning, older ones for foraging, and the oldest ones for taking care of the brood and the queen. Again, a degenerative mechanism can be suspected behind this phenomenon. First, it is required that the overall task (taking care of the colony) is distributable in the sense that it separates into sub tasks (e.g., cleaning, foraging, defending, brood care, reproduction) that can be performed independently of each other. Second, there should be an automatic mechanism that successively "switches" those tasks on as the individual ages. How to develop a model that can capture evolutionary mechanisms leading to a realization of the division of labor is yet another topic for future research.

APPENDICES

Appendix 1: Axioms

1. Fundamental Axiomatic System (FundAx)

A) **Existential Axiom:**

FundAx 1:

There exist the following three types of objects: individuals, metabolic sources, and metabolic sinks.

B) **Relational Axioms:**

Let $\mathscr{I}$ be the finite set of all individuals. Let Γ be a metabolic source or sink with regard to each individual of the set $\mathscr{I}$.

FundAx 2 (Existence of encounter events):

Let $S \subseteq \mathscr{I}$ and $S \neq \varnothing$. There is a non empty set E_S^Γ of events called *encounter between S and* Γ. Formally: $\forall S \subseteq \mathscr{I} : S \neq \varnothing \Leftrightarrow \mathrm{E}_S^\Gamma \neq \varnothing$

FundAx 3 (Superset closure of encounter events):

Let $S, W \subseteq \mathscr{I}$ and $S, W \neq \varnothing$. Then: $S \subset W \Rightarrow \mathrm{E}_S^\Gamma \subset \mathrm{E}_W^\Gamma$.

FundAx 4 (Existence of focus events):

Let $S \subseteq \mathscr{I}$, and $S \neq \varnothing$. There is a set Φ_S^Γ of events called *focus between S and* Γ. Formally: $\forall S \subseteq \mathscr{I} : S \neq \varnothing \Leftrightarrow \Phi_S^\Gamma \neq \varnothing$

FundAx 5 (Subset Closure of focus events):

Let $S, W \subseteq \mathscr{I}$, and $S, W \neq \varnothing$. Then, $S \subset W \Rightarrow \Phi_S^\Gamma \supset \Phi_W^\Gamma$.

FundAx 6 (Existence of reception events):

Let $S \neq \varnothing$. There exists a set P_S^Γ of events called *reception of Γ by*

S. Formally: $\forall S \subseteq \mathscr{I} : S \neq \varnothing \Leftrightarrow \Phi_S^\Gamma \neq \varnothing$

FundAx 7 (Subset closure of reception events):

Let $S, W \subseteq \mathscr{I}$, and $S, W \neq \varnothing$. Then, $S \subset W \Rightarrow P_S^\Gamma \supset P_W^\Gamma$.

FundAx 8 (Existence of a resignation event):

There exists an event $\omega_{\mathscr{I}}^\Gamma$ called the *resignation between $\mathscr{I}$ and Γ*.

2.   Axiomatic System for Accumulations (AccumAx)

Let $\mathscr{I}$ be the finite set of all individuals. Let Γ be a metabolic source or sink with regard to each individual of the set $\mathscr{I}$. Then,

AccumAx consists of FundAx and the following axiom:

AccumAx 1 (Existence of stories):

There exists a non empty set $\Sigma_{\mathscr{I}}^\Gamma$ of stories concerning $\mathscr{I}$ and Γ. This set is complete, i.e., if $[\sigma]$ is a story concerning $\mathscr{I}$ and Γ according to the definition of the concept 'story', then $[\sigma] \in \Sigma_{\mathscr{I}}^\Gamma$.

Appendix 2: Metabolic payoff function

Definition (Metabolic payoff function): Let $S_1, S_2, S_3 \subseteq \mathscr{I}$. Let S_1 be an accumulation or a solitary individual. Let $S_1 \supseteq S_2 \supseteq S_3$. Let $\alpha \in \mathscr{I}$. Let Γ be a metabolic source or sink for all individuals in $\mathscr{I}$. Let a number b_α^Γ be given such that $b_\alpha^\Gamma > 0$ if Γ is a metabolic source for α and $b_\alpha^\Gamma < 0$ if Γ is a metabolic sink for α. Let $u_\alpha^\Gamma : \Sigma_{\mathscr{I}}^\Gamma \to \{n \cdot b_\alpha \mid n \in \mathbb{N}_0\}$ be a function such that

i)   if $e \in \mathrm{E}_{S_1}^\Gamma$, then: $u_\alpha^\Gamma([e \to \omega_{\mathscr{I}}^\Gamma]) = 0$.

ii)   if $e \in \mathrm{E}_{S_1}^\Gamma$ and $f \in \Phi_{S_2}^\Gamma$, then: $u_\alpha^\Gamma([e \to f \to \omega_{\mathscr{I}}^\Gamma]) = 0$.

iii)   if $e \in \mathrm{E}_{S_1}^\Gamma$ $f \in \Phi_{S_2}^\Gamma$, and $r \in \mathrm{P}_{S_3}^\Gamma$. Then:

$$\text{If } \alpha \notin S_3 : u_\alpha^\Gamma([e \to f \to r]) = 0$$

$$\text{If } \alpha \in S_3 : u_\alpha^\Gamma([e \to f \to r]) = b_\alpha^\Gamma$$

iv)   if $[\sigma_1] \in \Sigma_{\mathscr{I}}^\Gamma$ and $[\sigma_2] \in \Sigma_{\mathscr{I}}^\Gamma$, then $u_\alpha^\Gamma([\sigma_1 \to \sigma_2]) = u_\alpha^\Gamma([\sigma_1]) + u_\alpha^\Gamma([\sigma_2])$

Then u_α^Γ is called a *metabolic payoff function for α under Γ*.   ▲

For each $\sigma \in \Sigma_{\mathscr{I}}^\Gamma$ the function u_α is a homomorphism. The metabolic payoff will be negative if Γ is a metabolic sink, and positive if Γ is a metabolic source.

Appendix 3: A predator-prey model

The following model illustrates that aggregation under a distributable threat is a globally attractive ESS, that, however, eventually the aggregated individuals do not have higher fitness than the solitary ones. This example also includes a change of accumulation encounter probability dependent on the number of accumulations present. In that case accumulations can emerge in which individuals have fitness lower than solitary.

The model is given by the following conditions:

(1)   Given is a predator.

(2)   Given are m prey individuals, m is the population size of the prey.

(3)   Given are N fields. Each field is able to contain an arbitrary number k of prey individuals, $k \leq m$, and can be encountered by the predator.

(4)   The predator encounters at discrete time points $t \in \mathbb{N}_0$ fields; one at a time. The encounters are uniformly random and independent.

(5)   Condition for the searching predator: The predator keeps searching as long as he does not encounter a populated field.

(6)   Once the predator has encountered a populated field, he randomly focuses on exactly one of the prey individuals inhabiting that field.

We call any given distribution of the *m* prey individuals over the N fields a *situation*. The set of individuals in one field is called a *group*.

Let there be $l \leq m$ fields be populated by the *m* prey individuals. The *j*-th of these *l* fields contains i_j individuals. Thus $m = i_1 + i_2 + ... + i_l$. Especially if $l = m$ then $i_j = 1$ for $j = 1, 2, ..., m$, which describes a situation in which all individuals are solitary. Denote with α one of the *m* prey individuals. The question I try to answer is:

Given a certain situation, what is the probability of the predator to focus on individual α?

Since the predator is assumed to be searching the probability that he will encounter a populated field is 1. The probability of the predator encountering the field inhabited by α is $\frac{1}{l}$. The probability of focussing on α if its field is encountered is $\frac{1}{i^\alpha}$, where i^α is the number of individuals in α's field. The probability of focussing on α is therefore $\frac{1}{l \cdot i^\alpha}$.

For $l = m$, which is the case where all individuals live solitarily, we have a probability of focussing on *x* of $\frac{1}{m}$. For $l = 1$, which is the case that all individuals live within a herd inhabiting a single field, the probability of focussing on α is $\frac{1}{m}$ as well. Assuming therefore the same solitary capture rate γ for each prey individual there is no gain in survival probability for an individual by going from the complete solitary to the completely aaccumulated case under a searching predator.

It proves however to be interesting to investigate this model more closely. Figure A3.1 shows the case of five prey individuals accumulating. We can see that although the survival probability in the end of accumulation is the same as in the beginning, the intermediate states offer always at least one individual to increase its own survival probability by joining with another group. It will by doing this always damage the

group which it leaves and profit the group it joins, leaving members of groups other than these two unconcerned if it is not the last one of its group leaving. If it is the last one in its group, then with leaving solitude it damages all members of groups which it does not join, profits the members of the group it will join only during the first half of the aggregation, while damaging them by joining during the second half. Itself will always profit therefore will always have the incentive to surrender its solitude. We extend therefore the model by another two rules:

(6)   Individuals have the opportunity to leave their fields joining others in theirs.

(7)   Maximally one individual changes fields during one time unit.

Figure A3.1 gives one special history of accumulation. I will prove in the following that the totally accumulated situation is an ESS, and furthermore that this ESS is globally attracting, which means that individuals will always fully accumulate.

The fitness of all individuals within one group is the same, assuming their potential to escape the predator once focussed is the same, means that the solitary capture rate γ has for all prey individuals the same value. Denote by $\varphi_i(n_1, n_2, ..., n_k)$ the fitness of an individual within the i-th group of the population partition $(n_1, n_2, ..., n_k)$. Then $\varphi_i(n_1, n_2, ..., n_k) = 1 - \dfrac{\gamma}{k \cdot n_i}$. Note that the average fitness is always the same, and therefore independent of the decomposition of the population into groups, which is obtained by calculating

$$
\begin{aligned}
\frac{1}{m} \sum_{i=1}^{k} n_i \cdot \varphi_i(n_1, n_2, ..., n_k) &= \frac{1}{m} \sum_{i=1}^{k} n_i \cdot \left(1 - \frac{\gamma}{k \cdot n_i}\right) \\
&= \frac{1}{m} \sum_{i=1}^{k} \left(n_i - \frac{\gamma}{k}\right) \\
&= \frac{1}{m} \sum_{i=1}^{k} n_i - \frac{1}{m} \sum_{i=1}^{k} \frac{\gamma}{k} \\
&= 1 - \frac{\gamma}{m}
\end{aligned}
$$
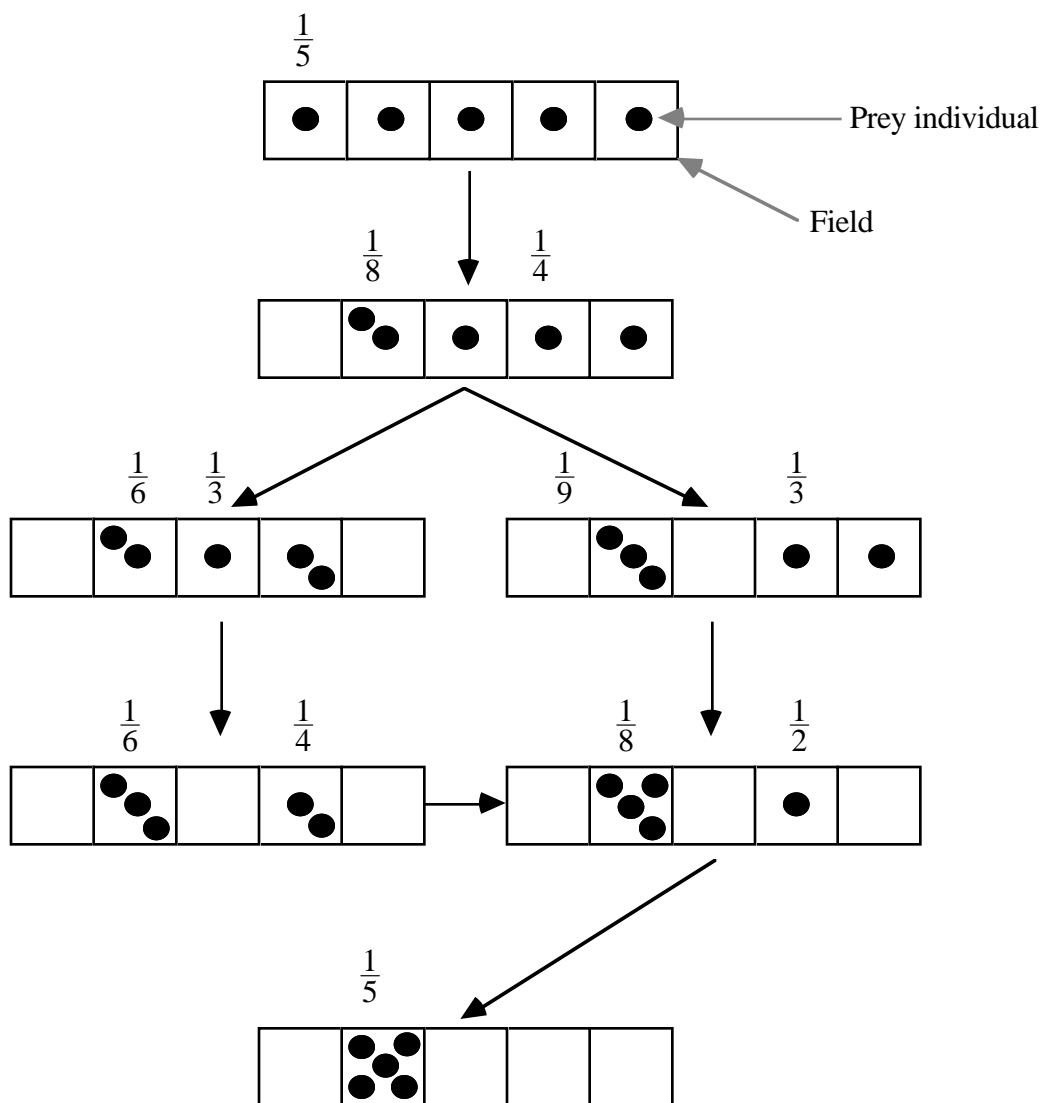
FigureA3.1: Only 5 fields for 5 individuals are shown since the searching
predator will encounter with probability 1 a populated field.
The fractions above the fields show the focus probabilities for
an individual in that field. In the purely solitary as in the
completely aaccumulated case the focus probability is the same.
There is however for the cases in between always for at least one
individual an incentive to join another group than the one it already
belongs to in order to increase its fitness. Starting, therefore, with
any situation the system will end up in the completely accumulated
state after finitely many steps. The actual capture rate is the focus
probability times the solitary capture rate γ

Lets introduce new notation. Let $n_j, k \in \mathbb{N}_0$ be so that $\sum_{j=1}^{k} n_j = m$ and $n_j \le n_{j+1}$ for $j = 1, 2, ..., k$. Then the tupel of group sizes $(n_1, n_2, ..., n_k)$ is called a *situation scheme*. Given two situation schemes $A = (a_1, a_2, ..., a_{k_A})$ and $B = (b_1, b_2, ..., b_{k_B})$ we say that a migration by at most one individual transforming A into B has happened if and only if one of the following conditions are satisfied:

(1)

(No migration or migration from a group to a group of size one less)

(2)   and ⊞⊟⊠⊡. Then there are two cases.

    a)   At the first index i with $a_i \ne b_i$ we have $a_i > b_i$ (which means that there was a migration from a group to a group at least that large.) Then there is exactly one index $j > i$ such that $a_j < b_j$, and for all other indeces $l \ne i, j$ it holds that $a_l = b_l$.

    b)   At the first index i with $a_i \ne b_i$ we have $a_i < b_i$ (which means that there was a migration from a group to a smaller group.) Then there is exactly one index $j > i$ such that $a_j > b_j$, and for all other indeces $l \ne i, j$ it holds that $a_l = b_l$.

(3) $k_A \ne k_B$. Then there are two cases.

    a) $k_A < k_B$. Then there is one index $i > 1$ such that $a_{i-1} > b_i$, and the number of 1's in B is one larger than the number of 1's in A. (Migration into solitude)

    b) $k_A > k_B$. Then there is one index $i > 1$ such that $a_i < b_{i-1}$, and the number of 1's in A is one larger than the number of 1's in B. (Migration from solitude into an accumulation)

A sequence of situationschemes obtained by successive migration of at most one

individual is called a *(migration) history scheme*.

In the following I prove that the fully aggregated state is a globally attractive ESS. The lemma below states that no individual will migrate to a group of smaller size than the one it emerged from.

Lemma: Assume an individual migrates from group i to group j with $n_i \leq n_j$. Then $(n_1, n_2, ..., n_k)$ becomes $(n_1^{\#}, n_2^{\#}, ..., n_{k^{\#}}^{\#})$, where $k^{\#} \leq k$, and $n_j^{\#} = n_j + 1$, $n_i^{\#} = n_i - 1$, and $n_l^{\#} = n_l$ for $l \neq i, j$. Then:

$$\varphi_j\left(n_1^{\#}, n_2^{\#}, ..., n_{k^{\#}}^{\#}\right) > \varphi_i\left(n_1, n_2, ..., n_k\right).$$

Proof: To prove this claim this we have to consider the two cases: $k^{\#} = k$ (which means $n_i > 1$), and $k^{\#} < k$ (which means $n_i = 1$, and $k^{\#} = k - 1$).

1. if $k^{\#} = k$, then:

$$
\begin{aligned}
\varphi_j\left(n_1^{\#}, n_2^{\#}, ..., n_{k^{\#}}^{\#}\right) &= 1 - \frac{\gamma}{k^{\#} \cdot n_j^{\#}} \\
&= 1 - \frac{\gamma}{k \cdot (n_j + 1)} \\
&> 1 - \frac{\gamma}{k \cdot n_j} \quad , \\
&\geq 1 - \frac{\gamma}{k \cdot n_i} \\
&= \varphi_i\left(n_1, n_2, ..., n_k\right)
\end{aligned}
$$

because $n_i \leq n_j$.

2. if $k^{\#} = k - 1 \geq 1$, then $n_i = 1$. Thus $n_j \geq 1$. Therefore $n_j \cdot (k - 1) \geq 1$, which implies that $(n_j + 1) \cdot (k - 1) \geq (k - 1) + 1$, and therefore $(n_j + 1) \cdot (k - 1) \geq k$. This means, with $n_i = 1$, that $(k - 1) \cdot (n_j + 1) \geq k \cdot n_i$. Thus:

$$\varphi_j\left(n_1^{\#},n_2^{\#},...,n_{k^{\#}}^{\#}\right) \quad = \quad 1 - \frac{\gamma}{k^{\#}\cdot n_j^{\#}}$$

$$= \quad 1 - \frac{\gamma}{(k-1)\cdot(n_j+1)}$$

$$\geq \quad 1 - \frac{\gamma}{k\cdot n_i}$$

$$= \quad \varphi_i\left(n_1,n_2,...,n_k\right)$$

This proves the lemma. We see here also that for the case $m = 2$ it makes no difference whether to aggregate under a searching predator or not. ❑

The above lemma shows that there is always an incentive for an individual to join another group at least as large as the one it is in right now. Therefore (m) is the unique approachable ESS of the model.

We summarize this result in a theorem:

Theorem. Given a fitness function $\varphi(n,k) := 1 - \frac{\gamma}{k \cdot n}$, with $0 < \gamma \leq 1$. Then independent of the total number of individuals involved the fully accumulated state is always a globally attractive ESS.

Summary. It is here of interest that the fitness of a certain given individual in the complete solitary and the complete accumulated case is the same, while fluctuating with the advance of the migration process from solitude to full accumulation. This is therefore an example where an ESS does not optimize survival for all members of the population. This motivates the suspicion that there can be models constructed for which the fully aggregated case is slightly deleterious to the individual and still a globally attractive ESS. This can be accomplished by introducing competitiveness among individuals. A simple example can be constructed by assuming that a fitness function is

defined by $\varphi(n,k) := \left(1 - \dfrac{\gamma}{k \cdot n}\right) \cdot \vartheta(n)$, where $\vartheta(n)$ is the fitness disadvantage due to competitiveness in an accumulation of size n. $\vartheta(n)$ is increasing in n. A necessary and sufficient condition for full accumulation is then given by

$$
\begin{aligned}
x < y \quad &\Longleftrightarrow \\
\forall k \geq 2 \quad : \quad &\left(1 - \frac{\gamma}{k \cdot x}\right) \cdot \vartheta(x) < \left(1 - \frac{\gamma}{k \cdot (y+1)}\right) \cdot \vartheta(y+1) \\
&\wedge \quad \left(1 - \frac{\gamma}{k}\right) \cdot \vartheta(1) < \left(1 - \frac{\gamma}{(k-1) \cdot (y+1)}\right) \cdot \vartheta(y+1)
\end{aligned}
$$

Appendix 4: Metabolic distance

In this appendix I show that a concept of distance between individuals and distance between an individual and a metabolic source or sink can be defined using encounter probabilities.

Given is a finite set $\mathscr{I}$ of individuals. Let $T^{\Gamma}_{\alpha_1,\ldots,\alpha_n}$ be the event that $\alpha_1,\ldots,\alpha_n$ are all elements of a randomly drawn set of total encounter under Γ. The event $T^{\Gamma}_{\alpha_1,\ldots,\alpha_n}$ is represented by the set of all sets of total encounter containing $\alpha_1,\ldots,\alpha_n$, thus $T^{\Gamma}_{\alpha_1,\ldots,\alpha_n} := \left\{ S \mid \{\alpha_1,\ldots,\alpha_n\} \subseteq S \wedge \exists e \in \mathrm{E}^{\Gamma} : \hat{e} = S \right\}$. If $n > 1$ then: $\{\alpha_1,\ldots,\alpha_n\}$ is a cluster under Γ if and only if $T^{\Gamma}_{\alpha_1,\ldots,\alpha_n} \neq \varnothing$. Let $\hat{\eta}^{\Gamma}$ be a probability measure on the set of all sets of total encounter. Denote with $P[T^{\Gamma}_{\alpha_1,\ldots,\alpha_n}]$ the probability that event $T^{\Gamma}_{\alpha_1,\ldots,\alpha_n}$ happens. If $P[T^{\Gamma}_{\alpha_1,\ldots,\alpha_n}] \neq 0$ and $n > 1$ then $T^{\Gamma}_{\alpha_1,\ldots,\alpha_n} \neq \varnothing$ which in turn implies that $\{\alpha_1,\ldots,\alpha_n\}$ is a cluster under Γ. The converse is true as well since it is assumed that $\mathscr{I}$ is a finite set: If $\{\alpha_1,\ldots,\alpha_n\}$ is a cluster under Γ, then $P[T^{\Gamma}_{\alpha_1,\ldots,\alpha_n}] \neq 0$. On the other hand, $P[T^{\Gamma}_{\alpha}] \neq 0$ does not imply that α is a solitary individual. $P[T^{\Gamma}_{\alpha}] \neq 0$ means that the probability of α being within a set of total encounter is positive. If this is true for all individuals, then there are no individuals which are "hidden" from Γ.

The distance concept between two individuals. Denote $p^{\Gamma}_{\alpha|\beta} := \dfrac{P[T^{\Gamma}_{\alpha,\beta}]}{P[T^{\Gamma}_{\beta}]}$. Then $p^{\Gamma}_{\alpha|\beta}$ is the probability that α will be an element of a randomly drawn set of total encounter under Γ under the condition that β is an element of the set. The following statements are obvious:

1. $p^{\Gamma}_{\alpha|\alpha} = 1$.

2. If $\{\alpha,\beta\}$ is not a cluster under Γ then and only then $p^{\Gamma}_{\alpha|\beta} = p^{\Gamma}_{\beta|\alpha} = 0$.

3. In general $p^{\Gamma}_{\alpha|\beta} \neq p^{\Gamma}_{\beta|\alpha}$.

If $p_{\alpha|\gamma}^{\Gamma} > p_{\alpha|\beta}^{\Gamma}$, then the probability of encountering α when encountering γ is larger than the probability of encountering α when encountering β. That can be interpreted as α being closer to γ than to β. On the other hand, if $p_{\gamma|\alpha}^{\Gamma} > p_{\beta|\alpha}^{\Gamma}$ then the probability of encountering γ when encountering α is larger than the probability of encountering β when encountering α, which would also imply that α is closer to γ than to β. This motivates the following definition:

Definition (closer to): α is said to be closer to γ than to β under $\hat{\eta}^{\Gamma}$ if and only if

$$p_{\alpha|\gamma}^{\Gamma} > p_{\alpha|\beta}^{\Gamma} \text{ and } p_{\gamma|\alpha}^{\Gamma} > p_{\beta|\alpha}^{\Gamma} \qquad \blacktriangle$$

The question is now whether how these two inequalities relate to each other.

$p_{\gamma|\alpha}^{\Gamma} > p_{\beta|\alpha}^{\Gamma}$, if and only if $P[T_{\alpha,\gamma}^{\Gamma}] > P[T_{\alpha,\beta}^{\Gamma}]$ and $p_{\alpha|\gamma}^{\Gamma} > p_{\alpha|\beta}^{\Gamma}$ if and only if $\dfrac{P[T_{\alpha,\gamma}^{\Gamma}]}{P[T_{\gamma}^{\Gamma}]} > \dfrac{P[T_{\alpha,\beta}^{\Gamma}]}{P[T_{\beta}^{\Gamma}]}$. Therefore:

$$\text{If } P[T_{\gamma}^{\Gamma}] \geq P[T_{\beta}^{\Gamma}], \text{ then: } p_{\alpha|\gamma}^{\Gamma} > p_{\alpha|\beta}^{\Gamma} \Rightarrow p_{\gamma|\alpha}^{\Gamma} > p_{\beta|\alpha}^{\Gamma}.$$
$$\text{If } P[T_{\gamma}^{\Gamma}] \leq P[T_{\beta}^{\Gamma}], \text{ then: } p_{\gamma|\alpha}^{\Gamma} > p_{\beta|\alpha}^{\Gamma} \Rightarrow p_{\alpha|\gamma}^{\Gamma} > p_{\alpha|\beta}^{\Gamma}.$$

Therefore: If $P[T_{\gamma}^{\Gamma}] = P[T_{\beta}^{\Gamma}]$, then: $p_{\gamma|\alpha}^{\Gamma} > p_{\beta|\alpha}^{\Gamma} \Leftrightarrow p_{\alpha|\gamma}^{\Gamma} > p_{\alpha|\beta}^{\Gamma}$. This gives rise to the following concept:

Definition (the strong principle of spatial uniformity of encounter (SPSUE)):
We say that *the strong principle of spatial uniformity of encounter (SPSUE) holds* if and only if

$$\exists 0 < q \le 1 \forall \alpha \in \mathscr{T} : P[T_\alpha^\Gamma] = q. \qquad \blacktriangle$$

In general the SPSUE does not to hold! The very nature of the approach makes it possible to talk about closeness between individuals only if those are members of the same cluster, and therefore the same accumualtion. A weaker version of the principle stated above is therefore possible without loosing the equivalence of the two approaches to describing closeness.

Definition (the weak principle of spatial uniformity of encounter (WPSUE)): We say that *the weak principle of spatial uniformity of encounter (WPSUE) holds* if and only if

$$\forall S = \langle S \rangle_{accum} \exists 0 < q_S \le 1 \forall \alpha \in S : P[T_\alpha^\Gamma] = q_S \qquad \blacktriangle$$

It is apparent that whenever SPSUE holds, then also WPSUE: SPSUE $\Rightarrow$ WPSUE. If $p_{\alpha|\beta}^\Gamma = 1$ then $P[T_{\alpha,\beta}^\Gamma] = P[T_\beta^\Gamma]$. From $T_{\alpha,\beta}^\Gamma \subseteq T_\beta^\Gamma$ it follows that $P[T_\beta^\Gamma \setminus T_{\alpha,\beta}^\Gamma] = 0$. that means that there is no cluster in $T_\beta^\Gamma \setminus T_{\alpha,\beta}^\Gamma$. Since T_β^Γ and $T_{\alpha,\beta}^\Gamma$ are, however, sets of clusters, we conclude that $T_\beta^\Gamma \setminus T_{\alpha,\beta}^\Gamma = \varnothing$, and therefore $T_{\alpha,\beta}^\Gamma = T_\beta^\Gamma$. This means that β is indistinguishable from α under $\hat{\eta}^\Gamma$, which means that there is set of total encounter containing β which does not as well contain α. If β is indistinguishable from α it does, therefore, not follow necessarily that α is indistinguishable from β. There might be sets of total encounter which do contain α but not β. Clearly, if the WPSUE holdes, then whenever β is indistinguishable from α then α is also indistinguishable from β. In this cased we say shortly: α and β are indistinguishable. It can not be concluded that if α and β are indistinguishable that both are the same individual.

However, α is always indistinguishable from itself.

The larger $p_{\alpha|\beta}^{\Gamma}$ the closer α and β (in the sense of the definition of 'closer to' given before). This enables us to give general approach how to use those conditional probabilities to define a 'distance' between two individuals.

Definition (cluster distance from one individual to another): Any function $\Delta(\alpha,\beta)$ with the following property is called a *cluster distance under Γ from α to β*:

$$\exists f:[0,1]\to \mathbb{R}_0^+ \quad : \qquad \Delta(\alpha,\beta)=f(p_{\alpha|\beta}^{\Gamma})$$
$$\wedge \quad f \text{ is strictly increasing} \qquad \blacktriangle$$
$$\wedge \qquad f(1)=0$$

Note that $\{\alpha,\beta\}$ does not have to be a cluster in order for the cluster distance to be defined. Let Δ be a cluster distance under Γ. Then clearly $\Delta(\alpha,\alpha)=0$. If β is indistinguishable from α then $\Delta(\alpha,\beta)=0$. In general $\Delta(\alpha,\beta)\neq\Delta(\beta,\alpha)$. However, if WPSUE holds, then $\Delta(\alpha,\beta)=\Delta(\beta,\alpha)$ whenever $\{\alpha,\beta\}$ is a cluster. If $\{\alpha,\beta\}$ is not a cluster, then $\Delta(\alpha,\beta)=f(0)$ which is the maximal cluster distance, and of course also $\Delta(\alpha,\beta)=\Delta(\beta,\alpha)$. The concept of cluster distance can be refined to the concept of accumulation distance due to the relation between clusters and accumulations.

Definition (accumulation distance from one individual to another): Any cluster distance $\Delta(\alpha,\beta)$ with the following property is called an *accumulation distance under Γ from α to β*:

$$\Delta(\alpha,\beta)=Min\left\{f(0),\sum_{i=1}^{n}\Delta(\alpha_i,\alpha_{i+1})\mid n\in\mathbb{N}\wedge\alpha_1=\alpha\wedge\alpha_n=\beta\right\} \qquad \blacktriangle$$

Although the concept of 'accumulation' does not explicitly appear in the definition of

'accumulation distance', the definition implies that if α and β are both within an accumulation then all the α_i's necessary to calculate the distance from α to β have to be within the accumulation as well. Again, if WPSUE holds, then $\Delta(\alpha,\beta) = \Delta(\beta,\alpha)$. If α and β are in two different accumulations, then $\Delta(\alpha,\beta) = \Delta(\beta,\alpha) = f(0)$.

The definition of an accumulation distance Δ implies that the triangle inequality holds:

$$\forall \alpha,\beta,\gamma \in \mathcal{T} : \Delta(\alpha,\beta) + \Delta(\beta,\gamma) \geq \Delta(\alpha,\gamma)$$

The triangle inequality holds even if the WPSUE does not. If the WPSUE holds, then $\mathcal{T}$ forms together with an accumulation distance function Δ a metric space.

Theorem: Let Δ be an accumulation distance. Assume that the WPSUE holds. Then $\mathcal{T}$ associated with Δ forms a metric space.

Proof: We have to show that Δ satisfies the axioms of a metric.

1) Δ is non-negative: This is true by the definition of a cluster distance.

2) $\Delta(\alpha,\alpha) = 0$: This is true, because $p_{\alpha|\alpha}^{\Gamma} = 1$ and $f(1) = 0$.
       (Property 2 follows also from properties 3 and 5)

3)   It is true that $\Delta(\alpha,\beta) = 0$ whenever α and β are indistinguishable.

4) Δ is symmetric.

5)   It was already stated that the triangle inrequality holds.   ❑

GLOSSARY

$\mathscr{I}$ The finite set of individuals

Let $S, K, H \subseteq \mathscr{I}$. Let Γ be a metabolic source or sink.

$P\{S\}$ The powerset of S. $P\{S\} := \{H \mid H \subseteq S\}$

E_S^Γ The set of encounter events between S and Γ.

$\hat{\mathrm{E}}_S^\Gamma$ The set of encounter events between S and Γ where S is the set of total encounter.

Φ_K^Γ The set of focus events between K and Γ.

$\hat{\Phi}_K^\Gamma$ The set of focus events between K and Γ where K is the set of total focus.

P_H^Γ The set of reception events of Γ by H.

$\hat{\mathrm{P}}_H^\Gamma$ The set of reception events of Γ by H where H is the set of total reception.

$\Sigma_{\mathscr{S}}^{\Gamma}$ The set of stories concerning $\mathscr{S}$ and Γ

η_S^{Γ} *exposure of S to* Γ The probability that an encounter event is between S and Γ.

$\hat{\eta}_S^{\Gamma}$ *total exposure of S to* Γ The probability that an encounter event is between at least S and Γ. This means that S is the set of total encounter of this event.

φ_H^{Γ} *acceptance of* Γ *by H*   The probability that a focus event is between H and Γ.

$\hat{\varphi}_H^{\Gamma}$ *total acceptance of* Γ *by H*   The probability that a focus event is between at most H and Γ. This means that H is the set of total focus of this event.

ρ_K^{Γ} *receptance of* Γ *by K*   The probability that a reception event is between K and Γ.

$\hat{\rho}_K^{\Gamma}$ *total receptance of* Γ *by K*   The probability that a reception event is between at most K and Γ. This means that K is the set of total reception of this event.

| | total receptance of ⊙ by ⊃ after total focus between | The probability of H being the set of total reception under the condition that K is K *and* Γ the preceeding set of total focus under Γ. |

$\hat{\rho}^{\Gamma}_{H:S}$ *total receptance of Γ by H through accumulation S*   The probability of reception of Γ by H where $H \subseteq S$, and S is an accumulation.

$\rho^{\Gamma}_{\{\alpha\}|K}$ *receptance of Γ by α after total focus between K and Γ*   The probability that a reception event of Γ by at least α occurs under the condition that K is the preceeding set of total focus under Γ.

$\hat{\xi}^{\Gamma}_{\{\alpha\}:S}$ *escapability of α from Γ through S*   Probability of avoiding metabolic change after an encounter between Γ and the accumulation S has happened.

REFERENCES

Axelrod, R. 1984. *The evolution of cooperation*. BasicBooks

Baird, R. N., Dill, L. M. 1996. *Ecological and social determinants of group size in transientKiller whales*. Behavioral Ecology 7: 408 - 416

Barta, Z., Flynn, R., Giraldeau, L.-A. 1997. *Geometry for a selfish foraging group: a genetic algorithm approach.* Proc. R. Soc. Lond. B 264: 1233 - 1238

Bauer, H. 1990. *Maß- und Integrationstheorie.* Walter DeGruyter Berlin New York

Bendor, J., Swistak, P. 1997. *The evolutionary stability of cooperation.* American Political Science Review, vol. 91, No. 2

Dawkins, R. 1976. *The selfish gene*. Oxford University Press

Dawkins, R. 1989. *The selfish gene*. Oxford University Press

Dugatkin, L. A. 1997. *Cooperation among animals.* Oxford Universtiy Press

Elster, J. 1979. *Ulysses and the sirens - Studies in rationality and irrationality.* Cambridge University Press

Giraldeau, L.-A., Gillis, D. 1984. *Optimal group size can be stable: A reply to Sibly.*
    Animal Behavior 33: 666 - 667

Giraldeau, L.-A., Caraco, T. 2000. *Social foraging theory*. Princeton University Press

Hamilton, W. D. 1964. *The genetical evolution of social behavior.* I,II.
    J. Theor. Biol. 7: 1 - 52

Hamilton, W. D. 1971. *Geometry for the selfish herd.* J. Theor. Biol. 31: 295 - 311

Hamilton, W. D. 1972. *Altruism and related phenomena, mainly in social insects*. Am.
    Rev. Ecol. Syst. 3: 192 - 232

Hedrick, P. W., Parker, J. D. 1997. *Evolutionary genetics and genetic variation of
    haplodiploids and X-linked genes.* Annu. Rev. Ecol. Syst. 28: 55 - 83

Hines, W. G. S. 1987. *Evolutionary stable strategies: A review of basic theory*. Theoretical
    Population Biology 31: 195 - 272

Keller, L. (Ed.) 1999. *Levels of selection in evolution.* Princeton University press

Mesterton-Gibbons, M., Dugatkin, L. A. 1992: *Cooperation among unrelated individuals:
    Evolutionary factors.* The Quarterly Review of Biology, vol. 67, no. 3: 276 - 281

Meyen, Sregei V. 1987. *On the structure of theoretical biology.*
Lectures in Theoretical Biology (K. Kull, T. Tiivel, eds.) Estonian Naturalists
Society, Tallinn "Valgus"

Novak, M. A., Sigmund, K. 1998. *What two legs can learn from four legs.*
Nature, vol. 395, 22 October 1998.

Packer, C., Ruttan, L.1987. *The evolution of cooperative hunting.*
The American Naturalist, vol. 132, no. 2: 159 - 198

Schmid-Hempel, P. 1994. *Infection and colony variability in social insects.*
Phil. Trans. R. Soc. Lond. B 346: 313 - 321

Sibly, R. M. 1983. *Optimal group size is unstable.* Animal Behavior 31: 947 - 948

Sherman, P. W., Jarvis, J. U. M., Alexander, R. D. 1991. *The biology of the naked
mole-rat.* Princeton University Press

Shykoff, J. A., Schmid-Hempel, P. 1991. *Parasites and the advantage of genetic variability
within social insect colonies.* Proc. R. Soc. Lond. B 243: 55 - 58

Smith , M. 1993. *The theory of evolution.* Canto edition, Cambridge University Press

Stadler, B. M. R., Stadler, P. F., Wagner, G. P., Fontana, W. 2001. *The topology of the
possible: Formal spaces underlying patterns of evolutionary change.* J. Theor.
Biol. 213: 241 - 274

Trivers, R., Hare, H. 1976. *Haplodiploidy and the evolution of the social insects.* Science, vol. 191, number 4224: 249 - 263

Trivers, R. 1971. *The evolution of reciprocal altruism.* The Quarterly Review of Biology, vol. 46: 35 - 57

Takada, T., Kigami, J. 1991. *The dynamical attainability of ESS in evolutionary games.* J. Math. Biol. 29: 513 - 529

Weibull, J. W. 1998. *What have we learned form evolutionary game theory so far?* Scandinavian Working Papers in Economics