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2 Timescales, Symmetry, and Uncertainty Reduction in the Origins of Hierarchy in Biological Systems

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Introduction

An outstanding question in biology is why life has evolved to be hierarchically organized. From genomes, to cells, tissues, individuals, societies, and eco-systems, evolution generates structures with nested spatial and temporal levels (e.g., Feldman & Eshel, 1982; Buss, 1987; Campbell, 1990; Maynard Smith & Szathmary, 1995, Valentine & May, 1996, Jablonski, 2000; Michod, 2000, Gould, 2002; Frank, 2003; Jablonka & Lamb, 2005, Frank, 2009). Typically, with each new structural level comes new functionality—a new feature with positive payoff consequences. This new functionality can be in the form of a new behavioral output such as a feeding response to a previously inaccessible resource. Or, it can arise when coarse-grained information encapsulated at the new level through some mechanism feeds back to lower levels, changing the accessibility of strategies for components and allowing the space of functions that components can perform to increase. An example is the protein kinases, which have been repeatedly recruited into many different functional pathways over the course of their evolutionary history (e.g., Manning et al., 2002).

In this chapter we present a novel approach to the origin of levels problem. We suggest that a primary driver of evolutionary change is the reduction of environmental uncertainty through the construction of dynamical processes with a range of characteristic time constants, or nested slow variables. Slow variables arise from mechanisms that naturally integrate over fast, microscopic dynamics. Proteins, for example, have a long half-life relative to RNA transcripts, and can be thought of as the summed output of translation. Cells have a long half-life relative to proteins, and are a function of the summed output of arrays of spatially structured proteins. Both proteins and cells represent some average measure of the noisier activity of their constituents and processes of formation. Slow variables, then, can be thought of as coarse-grained variables encoding statistics that are informative about the state of the system. Hence a median protein density is often thought to be informative about the rate of gene expression and RNA translation. Further examples include the steady state density of

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cells in multicellular organisms, and, as we will discuss in this chapter, power structures and related stable interaction networks in societies of individuals, and properties of environmental architecture built by organisms such as leafcutter ants and corals.

As a consequence of integrating over abundant microscopic processes, features that can serve as slow variables provide better predictors of the local future configuration of a system than the states of the fluctuating microscopic components. We propose that *when detectable by the system or its components*, slow variables can reduce environmental uncertainty and, by increasing predictability, promote accelerated rates of microscopic adaptation. The reduced uncertainty facilitates adaptation in two ways: It allows components to fine-tune their behavior and it frees components to search at low cost a larger space of strategies for extracting resources. This phenomenon has been studied extensively in relation to neutral networks in RNA folding. Many different sequences can fold into the same secondary structure. This implies that over time, structure changes more slowly than sequence, thereby freeing sequences to explore many configurations under normalizing selection (Schuster & Fontana, 1998).

The preliminary data analysis and theory that we discuss in this chapter suggest that slow variables *arise* through the accumulation of physically instantiated (e.g., through cementation processes or nest building, which result in physical structures, or through changes to neural circuits) memory[1] of asymmetric, and typically competitive, outcomes.[2] At some threshold, this asymmetry is reinforced though feedback to the lower levels from the integrated output of higher levels amplifying the asymmetry. We use the term "consolidation of slow variables" to capture the insight that as this history of competitive outcomes builds up, the coarse-grained representations of these dynamics become more robust predictors of the system's future state.

As we shall discuss, one obvious danger of slow variables is lock-in. If a process changes very slowly relative to some underlying microscopic dynamic, it can cease to be good predictor over short time frames, and will lag behind critical shifts at the microscopic level. We propose that hierarchy is a solution to the dual problem of informational noise and informational inertia. Our thesis is that *evolution has led to systems that operate over multiple timescales to balance the trade-off between robustness and adaptability.* Slow variables serve as reliable referents for decision making. Faster variables track changes at the microscopic level, providing a mechanism through which information can percolate up through levels to facilitate trajectory correction when environments change. If this thesis is correct, evolution will have had to fine-tune the timescales of adaptive dynamics (for examples with respect to mutation, see Ishii et al., 1989; Baer, Miyamoto & Denver, 2007).

The origins of the theory of slow variables can be found in a variety of fields within the evolutionary literature. We briefly review these fields to show how the theory builds on existing ideas. We then ground the thesis of slow variables in two case studies. Providing a formal, mathematical framework for the theory of slow variables

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is beyond the scope of this chapter; but, in the section entitled "Slow Variable Features, Function, and Detection," we discuss two mathematical concepts—the concept of the macrostate and the concept of symmetry breaking—that we believe are required to formalize the theory.

Brief Review of Related Ideas in Evolutionary Theory

Since the late 1980s, interest in the origins of hierarchy has grown within the evolutionary biology community. This can be attributed to developments in four areas of research: the mechanisms of inheritance; the levels of selection; the evolution of development; and the theory of niche construction.

From the empirical perspective, interest in the origins of hierarchy has grown out of the observation that several times in the history of life, highly integrated and coordinated aggregations arose out of collections of self-replicating, autonomous components with only partially aligned interests (e.g., Feldman & Eshel, 1982; Buss, 1987; Maynard Smith & Szathmary, 1995; Frank, 2003; Jablonka & Lamb, 2005; Frank, 2009).

These transitions have been called the major transitions in evolution (Maynard Smith & Szathmary, 1995) and in some cases are thought to reflect transitions to new levels of individuality (Buss, 1987; Michod, 2000, 2007). Much of the work in this area has focused on the role of novel mechanisms of inheritance and transmission mechanisms, including the evolution of epigenetic, learning, and symbolic transmission mechanisms (see also Feldman & Eshel, 1982; Jablonka & Lamb, 2005). The transition from unicellular to multicellular organisms, for example, has been hypothesized to have been made possible by the evolution of a germ line, whereas the transition from loose, homogeneous aggregates of organisms to integrated, differentiated societies is thought to have been facilitated by the evolution of an elaborate combinatorial symbol system—natural language.

Unfortunately, principled, information-theoretic definitions of individuality remain elusive,[3] and so there is substantial controversy and misunderstanding with respect to what constitutes evidence for a new type of individual (see Santelices, 2008; Krakauer & Zanotto, 2009), as well as controversy over what constitutes a major transition. In addition, there have been very few studies of the dynamical process (e.g., models of phase transitions or symmetry breaking) underlying the origins of new levels outside the pattern formation literature with obvious bearing on the evolution of development (e.g., Palmer, 2004).[4]

Within the multilevel selection community, interest in the origins of hierarchy is readily appreciated in relation to a decades-long debate on the preferred level at which selection operates (as illustrated by the reception of the recent paper by Nowak, Tarnita & Wilson, 2010). Traditional multilevel selection theory is based largely on equilibrium solutions operating on aggregate variables. Often the variables are assumed to

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be fundamental when in fact they are only nominal (Krakauer & Flack, 2010). As an example, consider the Hamilton kin-selection framework. The aggregate variables in kin-selection models correspond to benefit, cost, and relatedness. Because these variables are not typically derived through modeling of microscopic interactions, it can be unclear what in nature they correspond to, or how they should best be measured (see supplement in Nowak, Tarnita & Wilson, 2010).

Consensus is slowly building that to justify the sound choice of macroscopic or aggregate variables as a principled representation of some coarse-grained microscopic processes, we are better off starting with observations at the microscopic level. Hence, within the community of researchers working on the multilevel selection theory, there is a push to model mechanisms that give rise to different degrees of assortative mixing[5]—correlation among individuals in space or time (e.g., Roussett, 2004; supplement in Nowak, Tarnita & Wilson, 2010), and restricting kin selection to those mechanisms that can be grounded only in genetic assortativity.

Another area of evolutionary theory in which hierarchy is a theme might broadly be called "construction dynamics." Areas of research that fall under construction dynamics are those that are explicitly concerned with understanding processes giving rise to ordered phenotypic states. The most rigorous empirical work in biology of this kind includes studies of developmental biology and, in particular, studies connecting cellular differentiation to the gene regulatory architecture underlying aspects of development (e.g., Davidson et al., 2002; Davidson & Levine, 2008). One goal of this work to give a principled computational account—describe the logic of gene activation in terms of Boolean operations—of the emergence of morphological features from gene-gene and gene-protein interactions. And an ultimate goal is to determine whether aspects (e.g., subcircuits) of this process have been conserved over evolutionary time (Erwin & Davidson, 2009; Davidson, 2009).

A fourth area—which perhaps also falls under the rubric of construction dynamics—of evolutionary theory that is concerned with understanding how increasingly inclusive states arise is niche construction (Lewontin, 1982; Dawkins, 1982; Odling-Smee, Laland & Feldman, 2003, Laland & Sterelny, 2006). Niche construction, which finds its origins at the interface of ecology and evolution, posits that organisms, by modifying variables in their ecological and social[6] environments (Laland, Odling-Smee & Feldman, 2003; Borenstein, Kendal & Feldman, 2006; Flack et al., 2006; Flack & Krakauer, 2009, Boehm & Flack, 2010), can partially control the selection pressures to which they are subject. Another way to put this is that by controlling the rate of change or trajectory of environmental variables, organisms are better able to predict their environments (Boehm & Flack, 2010).

The observation that organisms modify environmental processes suggests that the environmental and organismal timescales cannot easily be separated, as is assumed to be true in a typical adiabatic treatment of evolutionary ecology (for a discussion of

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the adiabatic assumption in evolutionary dynamics, see Krakauer, Page & Erwin, 2009). The majority of niche construction studies have focused on the consequences of niche construction on processes of adaptation (e.g., Odling-Smee, Laland & Feldmann, 2003; Kylafis & Loreau, 2008). Many basic questions remain. Among them are how coupling comes about and what factors promote persistence of coupling.

Answering these questions requires an understanding of the precise procedures organisms use to adaptively modify the environment, and how these procedures and their associated outputs or behaviors are encoded. When modification is a collective process with multiple individuals and species contributing, the problem becomes one of collective social integration. When posed this way, this problem has much in common with central issues in the evolution of development, pattern formation, and collective animal behavior. Within the niche construction literature, such issues have been somewhat marginal, showing up largely in work on social niche construction (Flack, Krakuaer & de Waal, 2005; Flack et al. 2006; Flack & Krakauer, 2006; Flack & de Waal, 2007; Flack & Krakauer, 2009; Boehm & Flack, 2010) where the integration of the population cannot be taken for granted.

Two Case Studies of Distributed Slow Variables

As the examples at the start of this chapter were designed to allow, slow variables can include environmental features that can be described in terms of mass, volume, chemical, and energetic observables, as well as social features that are better described in terms of information or relational coordinates from node degree in a network, to interaction frequency, through more sophisticated measures of conflict, coordination, or cooperation.

We review in detail two case studies for which the ideas of multiple timescales, and adaptive slow variables, are informative. In the first example, from social evolution, the slow variable—statistical features of a power distribution—reduces uncertainty about the behavioral strategies of group members. This is achieved by increasing the predictability of the cost of social interactions. Power structure arises from social interactions, and, hence, can be thought of as a *fully constructed* slow variable. In the second example, from paleoecology, the slow variable—the mass and volume of a reef—reduces organismal uncertainty about ecological features including ocean currents and resource availability. The reef arises from the interaction of organisms with one another and with properties of the physical environment. Hence we call it a *partially constructed* or *modified* slow variable. Each of these studies is associated with a biological time series:[7] one on the order of years and the other on the order of millennia. We have chosen these two examples because they evolve along fundamentally different time and space scales and represent aggregations of fundamentally different kinds of components. This allows us to gauge the generality of the framework.

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Readers not interested in details of the case studies can skip to the section entitled "General Features of the Case Studies," which provides a summary of the important points.

A Case Study from Social Evolution: The Consolidation of Power Structures

Within the social evolution and animal behavior communities, studies of the emergence[8] of structure have centered on spatial pattern formation in flocking, schooling, and swarming species (e.g., Couzin, 2009). Equally impressive are collective social phenomena—the arrangement of individuals in relation to one another in a social coordinate space, typically defined in terms of networks of conflict, cooperation, and coordination. Observation and experiment in primates suggest that slowly changing social networks arise from and feed down to influence individual behavior and interaction patterns by changing the cost of interaction (Flack et al., 2006; Flack & Krakauer, 2006; Flack, Krakauer & de Waal, 2005, Boehm & Flack, 2010). We review how these kinds of slowly changing social structures arise and introduce predictability into individual interactions. We explore these issues in the specific context of the consolidation of power structures in macaque societies, providing enough empirical detail to make the case study comprehensible to a nonspecialist.[9] We begin with some background on the concept of power.

We operationally define an individual's power as the degree of consensus among group members that it can use force successfully during agonistic interactions (Bierstedt, 1950; Flack & Krakauer, 2006). We have suggested in previous work (Flack & Krakauer, 2006; Boehm & Flack, 2010; Brush, Krakauer & Flack, in prep.) that there are four critical properties of power: perception—individuals in the given system are said to have power if others in that system perceive them as capable of using force; consensus—if power is to be useful in the social domain, it is the collective perception of group members that matters; temporal stability—the perception that an individual is powerful needs to be stable over time if power is to be predictive and therefore useful for decision making; and computability—individuals must be able to assess their relative power, and this estimate must be correlated in the face of error with their inherent fighting ability, if the resulting power structure is to be stable and predictive.

An individual's estimate of its power can predict—when the estimate is a good one—the cost it will pay if a fight erupts, thereby changing the probability and predictability of social strategy use (Flack, Krakauer & de Waal, 2005; Flack, de Waal & Krakauer, 2005; Flack et al., 2006, Flack & Krakauer, 2006). A positively skewed distribution of power with a long tail (e.g., a power law tail) describes a society in which members of a nonvanishing minority of individuals are collectively perceived as disproportionately powerful. The power structure in our study group is best described by this kind of heavy-tailed distribution (Flack & Krakauer, 2006). Our data suggest that

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these power structures can support the implementation of novel, beneficial conflict regulatory mechanisms, such as policing (Flack, de Waal & Krakauer, 2005), in which individuals intervene in and impartially break up fights among group members. For any individual to adopt this policing role, it must be able to estimate with relatively low error the cost it will pay for intervening, and that cost must be low. We have found (Flack, de Waal & Krakauer 2005) that in our study group this cost is negligible for the individuals in the tail of the power distribution.

A behavioral knockout experiment (Flack, Krakauer & de Waal, 2005; Flack et al., 2006), in which the policing mechanism was temporarily disabled, showed that regulatory mechanisms like policing are critical contributors to social robustness. Knockout resulted in a destabilization of the groups' social networks: The cost of social interaction increased; investment in social capital acquisition, like alliance partners, decreased; and the cliquishness and assortative structure of the group's social networks increased. Data from this experiment and related studies suggest that the predictive utility of power for estimating the cost of social interaction depends on the extent of the coupling between the power distribution and the underlying conflict and signaling networks from which it arises. Although the power structure must change slowly to be useful as a predictor of interaction cost, it cannot change too slowly because it needs to approximately represent the underlying distribution of asymmetries in fighting ability, and this changes over time (Boehm & Flack, 2010).

Information about power in pigtailed macaque societies is encoded in a status signaling network. Power structure arises from a collective process in which each individual integrates over the status signals it has received to estimate how it is perceived by the group (Flack & Krakauer, 2006; Brush, Krakauer & Flack, in prep.). This signaling network arises in turn from an underlying aggression network, which in turn arises out of a social interaction network (see fig. 2.1). We sketch below the process generating each network and, ultimately, the power structure.

Individuals interact. An interaction is any event in which there is an opportunity for immediate contact or in which a signal has been exchanged. Interaction patterns vary in time, such that at any given moment some fraction of group members is in contact, proximity, or signaling from afar. Sampling these interactions at a regular interval gives a time series in which the successive "events" can be represented as interaction networks. The nodes in these networks correspond to individuals, and the presence of an (undirected) edge between two nodes indicates an interaction was observed. These time-sampled networks are sparsely connected. If we collapse these temporally resolved network data into a single static network, we can calculate the overall probability of individual i interacting with individual j. A simple measure, for example, of i's probability of interacting with j is the number of times i interacts (the weight of the ij edge) with j divided by the total number of times i interacts with all of its partners (i's degree).[10]

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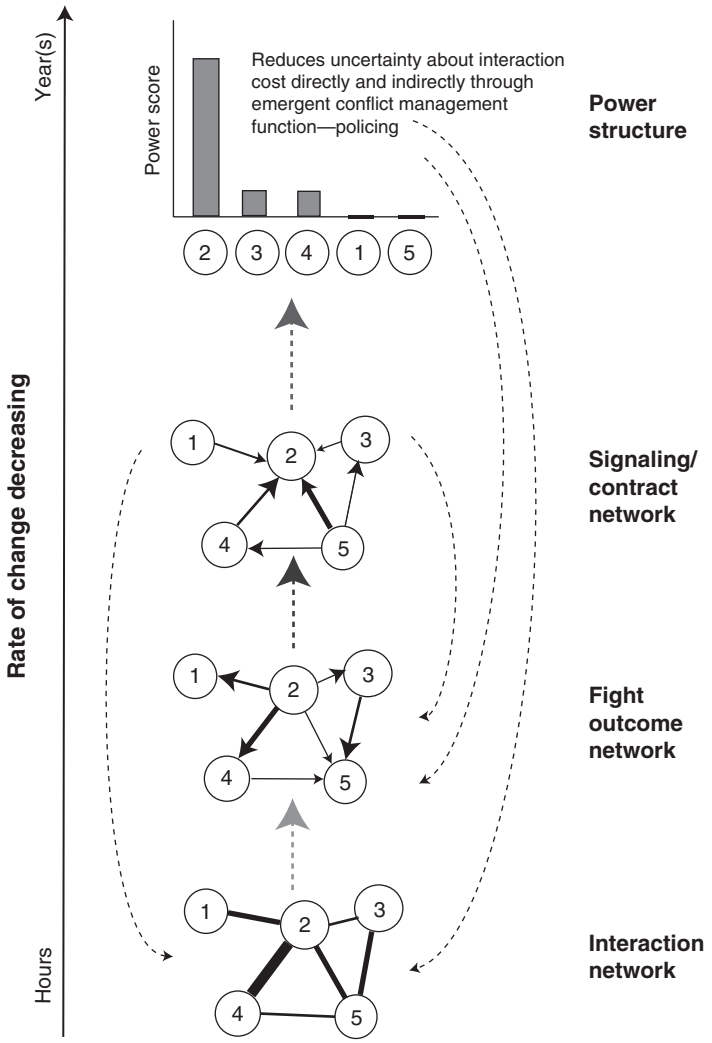

Figure 2.1
Schematic illustrating the dynamics and proliferation of temporal scales underlying the consolidation of power structure and the emergence of a new conflict management function through the buildup and amplification of asymmetries resulting from competitive interactions among individuals. See text for details.

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Macaques fight for dominance and other resources. Whether individuals win or lose fights depends on temporally stable factors, including body size, fighting experience, and size of alliance networks. Contextual factors, including fatigue, variation in priorities, leverage, the presence of coalition partners, and immediate past successes or failures in fights (reviewed in Boehm & Flack, 2010), are also important insofar as they generate stochasticity in fight outcomes. The average probability of winning can be defined as some function of the ability of the opponents to perceive asymmetries in fighting ability due to body size, experience, size of alliance network, and so on, and to correctly estimate the implications of these asymmetries weighted by information obtained from a past history of fighting (see also Preuschoft & van Schaik, 2000).

In the absence of any prior information, each individual starts with a 50–50 chance of winning. This symmetry will be broken once a fight history has accumulated through direct experience or observations confirming any perceived differences in body size or fighting ability have been informative.[11] Presumably symmetry will be broken faster (e.g., it will take fewer fights to verify) the larger the inherent asymmetry.[12]

This process results in a fight outcome network. The nodes in this network correspond to individuals. The presence of an edge means that a fight occurred between node *i* and node *j*. The edge flows toward the individual who lost the fight. If the fight was a draw, the edge is undirected. The edge can be annotated with a vector containing elements that are updated with respect to the sampling interval, with the first element giving the number of fights, and the second element giving the number of fights won by individual *i*. Because we are interested in the rate at which fight outcomes reverse, the time evolution of the network must be tracked. Hence the aggregated network is computed from many network snapshots collected (for example, on an hour timescale) over the course of the study.

Once a pattern of losing exceeds a certain threshold, an expressed (as opposed to an inherent) asymmetry is established. In our study group, the individual perceiving itself as likely to lose signals this recognition using what is called a subordination signal (de Waal, 1982, 1986; Preuschoft & van Schaik, 2000; Flack & de Waal, 2007). In pigtailed macaques the signal is a peaceful variant of the silent bared-teeth display (Flack & de Waal, 2007). Subordination signals are unidirectional, meaning only the animal perceiving itself as the subordinate emits them (de Waal, 1986; de Waal & Luttrell, 1985; Flack & de Waal, 2007). Our analyses suggest that subordination signals communicate agreement to a primitive social contract in which the signaler agrees for some time period to the subordinate role, and thus to yield when a conflict arises in the future (Flack & de Waal, 2007). The contract, which is cost-free (Bergstrom & Lachmann, 1998), is upheld as long as two conditions are satisfied: The signaler must yield during periods of scarce resources or when the receiver expresses an interest in a resource, and the underlying asymmetry must continue to be perceived by the subordinate as large. The advantage of the contract is that it establishes a new conditional

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symmetry, in which the sender and receiver are free to interact with a reduced concern that a fight will erupt—a form of context-specific equality (Flack & de Waal, 2007).

These signaling interactions generate the slowly changing status-signaling network, by which we mean that edges in the signaling network are deleted, added, and reversed relatively slowly compared to the rate at which fights erupt or individuals interact. As with the fight outcome network one level down, the nodes in this network correspond to individuals. The presence of an edge indicates that a signaling event occurred between node *i* and node *j*. The edge flows to the receiver of the signal and is weighted by the number of signals exchanged.[13,14] Because we are interested in the rate at which contracts change and the number of signals emitted by the subordinate under a given contract, the time evolution of the network must be tracked. Hence the aggregated network is computed from many network snapshots collected (on, for example, the hour timescale) over the course of the study.

Our data suggest that it takes several reversals of edges in the fight network before the signal is withheld, and many more before signal sender and receiver reverse their contract (de Waal, 1982; de Waal & Luttrell, 1985; de Waal, 1986). This means that statistical features—for example, the rate of edge flipping and network level statistics, such as mean weighted in-degree—of the signaling network should be relatively impervious to fluctuations in fight outcomes (Boehm & Flack, 2010).

Encoded in the signaling network is information about the degree of consensus among group members that any individual is capable of successfully using force (Flack & Krakauer, 2006; Brush, Krakauer & Flack, in prep.). We have shown that individuals, by taking into account how many signals they receive in total from their population of signalers weighted by an estimate of the diversity of the signaling population, can estimate (using an appropriate heuristic) how much power others collectively perceive them to have. They also seem to be capable of roughly estimating the population distribution of power in the group (Flack, de Waal & Krakauer, 2005; Flack & Krakauer, 2006).

Three factors appear to conspire to generate power structures with slowly changing statistical features (e.g., mean, variance, kurtosis, rank order of individuals in the distribution). First, many fight reversals have to "build up" to reverse each subordination contract. Second, multiple pairs of individuals need to change whether they have a contract or change the "direction" of that contract. And, finally, the probability of a reversal occurring is reduced by virtue of the fact that the contracts reduce the number of agonistic interactions, which slows the rate at which a history can accumulate that supports the inverse pattern of asymmetry (Flack & de Waal, 2007).

Hence we have three, hierarchically organized networks—an interaction network, a fight outcome network, and a status signaling, or social contract, network—and a power distribution that is read off the signaling network.

Our data suggest that the advantage to building multiple networks is that their variable rates of change can be used to maximize objectives that would be at odds

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if there were only a single timescale (Flack & de Waal, 2007; Boehm & Flack, 2010). Individuals, by temporarily agreeing to a contract, can reference the contract for strategic decisions concerning the receiver (or dominant partner) rather than the rapidly changing and potentially misleading fluctuations in fight outcomes with that individual. Individuals can use information about their relative power encoded in the signaling network to make decisions about how to behave during polyadic conflicts, as described at the beginning of this case study. Allowing a low level of fighting to continue even after contracts and a stable power structure have been established is advantageous because it allows learning to continue and so provides a mechanism by which the social contract can be reversed (and relative power can change) when new asymmetries have been established.

In summary, the value of a social slow variable such as power lies in the fact it reduces uncertainty about the cost of social interactions. In doing so, it allows for more efficient social, and presumably ecological, resource extraction, thereby facilitating the implementation of conflict management mechanisms that amplify these effects.

A Case Study from Paleoecology: Reefs as Ecological Aggregates

Ecological assemblages in the fossil record display greater long-term persistence than would be expected from the apparently transitory nature of many ecological communities. Such patterns of persistence can range from thousands to even several million years, despite ongoing environmental disturbances and species invasions (DiMichele et al., 2004; Brett & Baird, 1995; Miller, 1997). The interpretation of the data supporting this argument has been controversial, with some proponents favoring a high degree of species coevolution so that the assemblage acts as a superorganism (a Clemensian view) while others view the pattern as reflecting overlapping environmental requirements (a Gleasonian view) or an epiphenomenon of poor data analysis. The relationship between stability and diversity has long been controversial within ecology (Ives & Carpenter, 2007), and our intent here is not to review this debate. The paleoecological record, however, supports four factors that may explain the prolonged persistence and biodiversity of ecological communities (DiMichele et al., 2004): (1) coadapted ecological relationships and mutualisms that constrain the number of interacting species; (2) coexistence of species with strongly overlapping environmental requirement networks, so that species co-occur even in the absence of coevolved relationships; (3) biogeographic control of the regional species pool, so that abundant species are likely, simply on a statistical basis, to co-occur in ecological assemblages; and (4) the law of large numbers (Hubbell, 2001) that may produce patterns of apparent stability through the neutral model of biodiversity.

The hypothesis advanced in this chapter provides a different perspective on long-term ecological persistence, which we illustrate with a discussion of reefs. The concept

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of slow variables introduces another explanation for the persistence of ecological communities over evolutionary timescales: it may reflect the generation of ecological structures that respond to environmental changes over much longer timescales than individual organisms, and thus provide a degree of ecological stability. In other words, ecological structures such as reefs and forests, while they persist, influence the environment sufficiently to reduce environmental uncertainty and allow a variety of species to coexist. This results in an increase in biodiversity (fig. 2.2).

Although today reefs are commonly viewed as wave-resistant structures dominated by scleractinian corals and found in sunny, tropical climes, reefs have been produced for at least 2 billion years, far longer than scleractinian corals have been around. Throughout the history of life, reefs have been built by a variety of organisms, including microbial assemblages, sponges, a variety of corals, bryozoans, and bivalves, among other groups. In almost all cases reefs are spatially confined structures built by sessile organisms (and thus composed of carbonate) and are wave-resistant structures that stand above the surrounding sediment and consequently influence current patterns. Depending on the organisms that construct the reef, they often produce a complex three-dimensional structure with a host of diverse environments for other organisms (Wood, 1999). Thus reefs act as ecosystem engineers (Jones, Lawton & Shachak, 1997; Wright & Jones, 2006) to modify the environment of other species and enhance overall biodiversity. Both modern (e.g., the Great Barrier Reef, Australia; Belize) and fossil reefs are some of the largest biogenic structures on Earth, and can have an influence over thousands of square kilometers. Moreover, these structures can persist for thousands to tens of thousands of years. Remarkably, Pleistocene reef communities have remained stable across substantial glacially induced drops in sea level (Pandolfi, 1996). In addition, throughout the Phanerozoic (542 million years ago to today), reef communities have displayed ecological persistence on evolutionary timescales (Kiessling, 2005, 2009).

Initiation of a reef involves interaction between reef-constructing organisms and the substrate. For microbes, this may involve trapping and binding sediment or secreting carbonate to form a microbially bound structure. For many reef-forming animals such as corals, however, the critical interaction involves larval settling, often on hard substrate. The dominant ecological force thought to be shaping this process and coral recruitment more generally is competition among larva and juvenile coral on one hand, and macroalgae on the other (Dubinksy & Stambler, 2011). Many different mechanisms of competition have been reported, including preemption of space, basal encroachment, and shading (see papers in Dubinksy & Stambler, 2011).

As the reef develops, it attracts a variety of other organisms, many of which are preferentially associated with reef ecosystems and may be virtually absent in nonreef environments. This produces a trophic network. As reefs grow in size, they increasingly modify the surrounding environment, including wave and current activity, sedimentation

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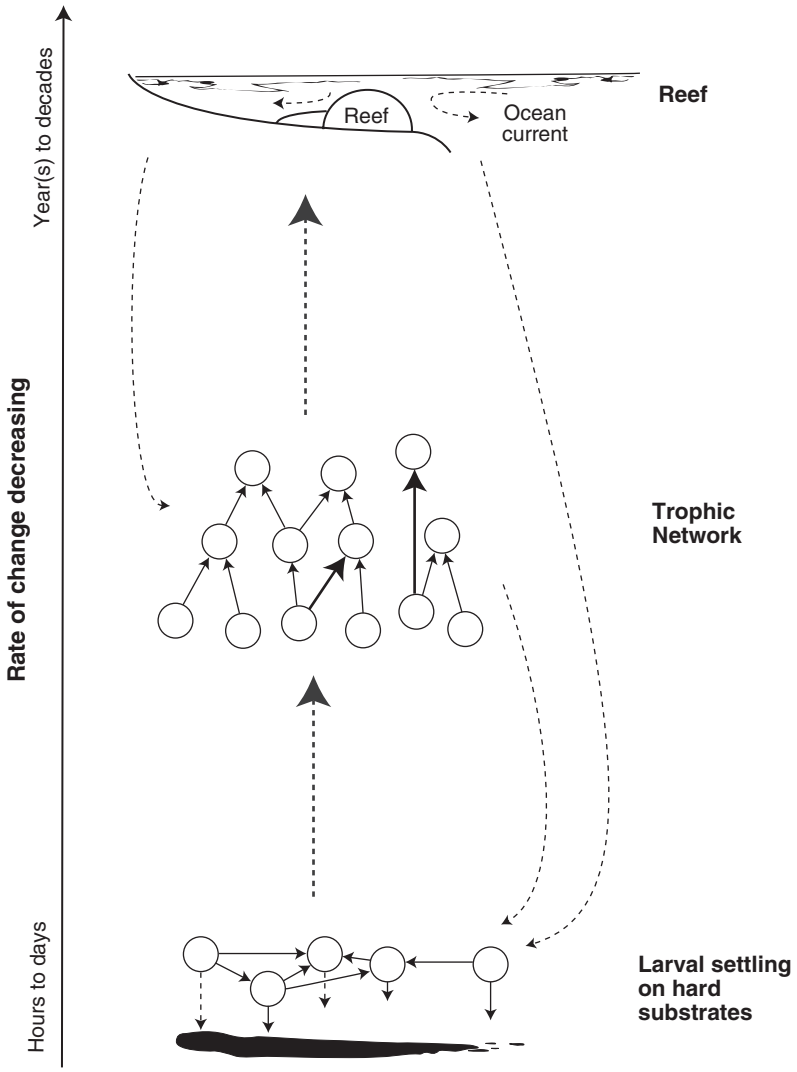

Figure 2.2
A schematic illustrating the dynamics by which reefs arise from density-dependent interactions among reef organisms. See text for details.

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patterns, and so on. For example, the scleractinian corals that construct most modern reefs often produce a relatively open, almost fractal structure with many cavities. This increases the number of environments available for occupation by reef-dwelling species.

The formation of a reef crest has similar consequences. The reef crest absorbs the energy of incoming waves and is populated by organisms that can adapt to high-energy environments. This eventually creates back reef environments that may have cavities conducive to more delicate forms. Here, the environment provides a signal through wave energy, light, and nutrient flows, allowing other types of organisms to thrive. As the reef expands, the heterogeneity of reef environments grows and a greater variety of organisms can be supported.

At a more regional level, a single reef is often a small part of a more extensive platform of numerous other reefs that may entirely surround an oceanic island, or may cover hundreds to thousands of square kilometers.

Interactions among reef-constructing organisms represent the first and fastest network of interactions. Any asymmetry in competitive settling ability is then reinforced through sedimentation, which amplifies any latent competitive asymmetries and generates a new network of largely within-lineage interactions. Growth of the reef by modifying the flow wave and light energy through slowly changing structures leads to further divergence in population densities, but also supports a greater variety of species and new forms of trophic network. Hence the reduction in the uncertainty of the physical environment leads to a greater range of interactions in the community and eventually to a greater diversity of niches.

General Features of the Case Studies

The general features of the case studies are summarized in tables 2.1 and 2.2. In the power structure case study, multiple nested temporal variables are associated with two processes. At the pair-wise level, the existence of a contract between two individuals, which can be represented as a binary variable that is either "on" or "off," changes slowly relative to the underlying fight dynamics, only changing to on if it becomes apparent to the opponents that there is a clear asymmetry between them. At the group level, moments of the distribution of power, such as its mean, variance, and kurtosis,[15] as well as where an individual sits in that distribution, change slowly relative to both the timescale on which fight outcomes fluctuate and the timescale on which the contracts reverse.

In the reef case study, the hierarchical levels of reef ecosystems represent different networks of interaction: between substrate and larvae; among the species within a food web; between an individual reef and the surrounding environment, and beyond that, among individual reefs across a larger reef tract as they exchange larvae and collectively affect currents and other environmental variables (see fig. 2.2). As with the social networks, the reef interaction networks change over progressively slower

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Table 2.1
Summary of the slow and fast variables for the power and reef case studies.

	Social Dynamics	Ecological Dynamics
Fast Variable	Fight outcomes	Ecological interactions (e.g. competition and cementation)
Slow Variable(s)	Contract and power distribution	Reef architecture and mass
Uncertainty Reduction	Interaction cost	Hydrodynamic energy

Table 2.2
Summary of the process by which symmetry is broken and the slow variable consolidated, shown for the power and reef case studies.

Symmetry Breaking	Social Dynamics	Ecological Dynamics	Summary
Stage 1:	Fights/time	Species abundance/time	Rapid rate of individual interactions, with randomly distributed competitive abilities
Stage 2:	Signal/time	Cementation/time	Individuals signal or secrete into environment as a function of outcome of stage 1.
Stage 3:	Power/time	Volume/time	Stochastic fluctuations fixed in stage 2 accumulate slowly in the form of social power or material mass, consolidating initial variation and amplifying competitive asymmetry through feedback to stages 1 and 2.

timescales. Larval settling happens on timescales of hours to days, albeit generally at certain times of the year. Individual trophic interactions occur on a timescale of days to weeks, although the resulting food webs may persist for years, depending on the changing composition of species and their relative abundances.

The macroscopic, physical structure of the reef can endure on a timescale of years or decades. Indeed, since many of the effects of the reef are a consequence of its size and mass, these effects would persist even if all organisms disappeared, until the reef slowly eroded. The volume or mass of a reef is thus a candidate slow variable, and the broader reef tract is an even slower variable on a larger spatial and temporal scale.

In both case studies, the construction of the slow variables reduces uncertainty about environmental states: in the power case, by increasing the predictability of social interaction cost, and in the reef case, by increasing predictability of wave energy and the hydrodynamic environment.

In both cases, the slow variables arise as asymmetries are established as competitive interactions grow. In the power example, the asymmetry builds up through memory of past outcomes of competitive interactions. Once it becomes clear that one individual

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in a pair is more likely to lose a fight (e.g., a threshold is crossed), the individual that perceives itself to be the likely loser signals. The signal can then be said to feed down to consolidate the history and reify the asymmetry. In the reef example, the asymmetry builds up through larval settling and cementation resulting from a complex competition dynamic between macroalgae and larvae and juvenile coral.[16]

Slow Variable Features, Functions, and Detection

Slow Variables as Macroscopic Variables

The simplest examples of macroscopic properties illustrative of the kinds of dynamical process generating slow variables come from the study of physical macroscopic variables like temperature, pressure, and entropy. These variables are averages over abundant fast variables, which correspond to many microstates and constitute macroscopic properties of a system (Callen, 1985). Temperature, for example, is an average over the microscopic motions of single particles. Technically it is related to an average over the energy in each degree of freedom of the particles (say, translational and rotational motion). The value of this average is that it allows us to think of temperature as an effective variable, which describes how heat is transferred via conduction, convection, and radiation. These are all statistical mechanisms constructed at the scale of the "effective" variable. For example, Fourier's law of heat conduction predicts how heat is transferred from high-temperature to low-temperature material without describing the individual particles. This represents a statistical law expressed through an equality that predicts the average behavior of a system—an effective degree of freedom—without attending to the microscopic degrees of freedom of the system. When we consider a number of macroscopic properties together, sufficient to explain the behavior of our system, they constitute a macrostate of our system.

Just as with physical systems, we can identify macroscopic variables in biological systems. Consider a social or ecological system with a given number of individuals or species. We can coarse-grain the variables (e.g., individuals can be grouped according to age, sex, and fighting ability, and species can be grouped into genera). We can then calculate suitable averages that form candidate macroscopic properties of our adaptive system. Collections of these properties that are predictive of future states of our system constitute candidate macrostates. For example, it might be that knowledge of the sex ratio, the population size, and the average age constitutes a very useful macrostate for predicting resistance to disease.

One problem is that in systems with numerous parts and properties, many different macroscopic functions can be calculated. As observers of the system, we may find many or all of these macroscopic functions to be of interest. However, only some of these properties will be useful coarse-grainings from the system's (or its components') perspective. In the case of biological and social systems, the macroscopic variables of

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interest are those against which system components can tune their strategies, either in evolutionary or ontogenetic time.

Slow variables are macroscopic states that (1) change slowly with respect to the underlying dynamics generating the state, (2) are associated with specific biological or behavioral updating mechanisms,[17] and (3) have features that change on a scale that can be *detected*, directly or through a proxy, by components in the system. For example, variability of glacial cycles over 10,000+ years is too long to be useful for adaptation for even the longest-lived organisms. Hence *slow variables can be understood as macroscopic variables with properties that allow for the evolution of parameters governing microstate behavior.*[18] In the power case, moments of the distribution of power, including its mean, variance, and kurtosis, change more slowly than changes in fight outcomes and the formation and dissolution of subordination contracts. In the case of reefs, reef properties such as mass change more slowly than the cementation processes that produce these features.

Uncertainty Reduction

As averages, macroscopic variables provide information about the future state of the system. Detection of these variables, or their proxies, by an adaptive system produces a reduction in uncertainty.[19] By detection, we simply mean that the variables can affect components in the system. Detection is required for adaptation, as illustrated with the above example on variability of glacial cycles, whether in evolutionary or ontogenetic time.

When the components in a system produce slowly changing features like reefs or power structures with detectable features, they essentially produce a regular, predictable environment. Hence the reef reduces variability in ocean currents, making them more predictable. It also ensures a diversity of niches and high biodiversity, compared with, say, the range of organisms that might be found in the open ocean. Power structure in monkey societies predicts the cost of social interaction and consequently can modulate the frequency and diversity of affiliative interactions.

Slow variables can serve as *reference states* (Flack & de Waal, 2007; Boehm & Flack, 2010): states that are insensitive to fluctuations at lower levels or in the environment and so serve as a good "data points" to use in decision making and adaptation. Ants navigate according to pheromone trails cumulatively deposited by other ants, and not by following single ants or invariant features of the environment. Monkeys use social contracts consolidated through status signal exchange, rather than fight outcomes, to decide how to interact. And corals and other reef organisms, by contributing to reef mass through cementation processes, create a predictable, resource-rich environment against which they can adapt.

It is our hypothesis that evolution produces temporal hierarchies (adaptive macrostates) because these provide economical, sufficient predictors of environmental states

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for organisms, thereby reducing uncertainty and facilitating adaptation. Hence collections of cells or individuals emerge as more efficient means of responding to environmental fluctuations.[20]

Whereas temperature and pressure are our way of efficiently describing and responding to changing environments, aggregates in biology are nature's way of doing so. This stands in contrast to the conventional view in evolutionary theory that—because aggregates typically reduce the reproductive output of lower levels—the origin of aggregation is a problem to be explained. If the above hypothesis is correct, aggregation under certain conditions is a *solution* to uncertainty.

Detecting Slow Variables

Can slow variables be optimized by the components building them? And, can the components evolve or learn better means for detecting properties of slow variables with the greatest predictive utility?

Consider the case of power. Studies of the consolidation of power structure, as well as studies of timescales in other systems (e.g., Fairhall et al., 2001; Honey et al., 2007; Kim et al., 2010; Shirvalkar, Rapp & Shapiro, 2010), suggest that an advantage to building multiple networks with multiple timescales is that their variable rates of change can be used to maximize objectives that would be at odds if there were only a single timescale (Flack & de Waal, 2007; Boehm & Flack, 2010). In the case of power, individuals, by temporarily agreeing to a contract, can reference the contract for strategic decisions concerning the receiver (or dominant partner) rather than the rapidly changing and potentially misleading fluctuations in fight outcomes with that individual. Individuals can use information about their relative power encoded in the signaling network to make decisions about how to behave during polyadic conflicts (see below). Of course maintaining a low level of fighting even after the contracts and power structure are established is useful because it allows learning to continue and so provides a mechanism by which the coupling between the power structure and fight distribution can be tuned.

We can summarize this process in more general terms. The process by which slow variables are constructed is collective: the slow variables arise over time through the joint behavior of multiple individuals or components acting strategicially. The consolidated variable reduces social uncertainty by feeding down to direct component behavior along certain trajectories. This facilitates adaptation through learning dynamics or genetic inheritance. Ongoing variation in fast competitive processes percolates up to the slow processes, allowing for error-correction through either analog or digital mechanisms, so that slow variables continue to be useful predictors of the underlying distribution of traits or abilities, or environmental features as these underlying distributions shift in time or with changes to context.[21] In a concrete sense, the system is computing with multiple timescales.

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The extent to which a slow variable is a good predictor of the average fast dynamics depends on how quickly changes at the microscopic level can percolate up. Hence we do not want too much timescale separation. On the other hand, reduced coupling between the aggregate properties of the system and the microscopic dynamics—which occurs as the aggregate variables change more and more slowly—can result in lock-in to a constructed environment that is suboptimal. The problem for the system then is to find the adaptive degree of coupling between the higher and lower levels (see also Fairhall et al., 2001).

This brings us to our second question: Can the coupling can be modulated through collective dynamics? To answer this question, we need to understand how components can evolve or learn better means for detecting slow variables. *The only slow variables that matter are those that the system can use*. Since the system is both using and constructing slow variables, we might call the process of finding the right slow variables a process of *endogenous coarse-graining*.[22]

In the case of power, individuals, after learning they are likely to lose, emit a signal that communicates agreement to a subordination contract. They then use the contract—through memory of the signaling event—to make decisions about how to interact, rather than using the most recent fight outcome, or recalling their perception of the entire history of wins and losses each time a decision needs to be made. In this case, it appears that making decisions using knowledge of the slow variable that summarizes the history of fights—the contract—is cognitively less demanding than remembering the entire history of events. However, the data suggest that stabilizing these contracts required the evolution of a signal that could effectively stand in for the fight history—more generally, the evolution of a mechanism by which the average could be updated once a critical threshold was passed. We do not yet understand how difficult it is to evolve such signals and mechanisms. The fact that in the existing data[23] these signals are not widespread among social primates with nonegalitarian structures suggests that this problem is nontrivial.

In addition to evolving mechanisms for communicating agreement to social contracts, individuals need means for estimating their power. Without some capacity to estimate power, information about power cannot be used to make social decisions. Before we can determine how individuals might make such an estimate, we need a principled statistical description of the distribution of power so that we know what it is they are trying to estimate. Recall that in systems with many parts and properties, many different macroscopic functions can be calculated. To test the utility of a coarse-graining, or in some cases, an average, we rely on the property of *statistical sufficiency* (Fisher, 1922).

A garden-variety statistic is simply a function of a sample where the function itself is independent of the sample's distribution. A sufficient statistic takes this idea further and is a statistic that is just as informative about some statistical parameter as any

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other statistic, and as informative as the complete sample from which the statistic was calculated. In the case of power we would like to determine whether some property of its distribution is a sufficient statistic for other variables of social importance. Once we identify a potential sufficient statistic, we can ask if the individuals in the system, given their information-processing capabilities, can estimate the statistic using a heuristic (e.g., Kahneman, Slovic & Tversky, 1982; Pearl, 1984) and local information, which serves as input to the computation.

Although many technical and conceptual issues are raised by framing detection of slow variables as a computational problem, the basic idea that individuals can use heuristics to estimate summary statistics is not problematic in the case of power or in social systems in which learning plays an important role.[24] It is less clear how computational ideas might help us understand adaptation to slow variables in systems such as reefs, in which strategy updating occurs in evolutionary time rather than ontogenetic time.

Reef organisms are unlikely to be making estimates of reef mass to determine the likely impact of ocean currents when making decisions about where to forage, take shelter, or mate. However, the genotype encodes the history of environmental states the organism experienced in evolutionary time. It can consequently be thought of as a hypothesis about the likely environmental state the organism will encounter (Krakauer & Zanotto, 2009), with the phenotype serving as the experiment to test a selective hypothesis. In this sense, information about slow variables such as reef mass can be said to be encoded in the genotype insofar as adaptations that arose in the context of large reefs are more useful on large reefs than small ones or in the open ocean. The extent to which this process is formally similar to the slow variable feature estimation in systems with learning is one of the many open questions that remain for future work.

The Consolidation of Slow Variables and Emergence of New Functionality through Symmetry-Breaking

For our purposes, symmetry is an invariance under a specified group of changes, which can be orientations, actions, or other properties. For example, competitive ability might be invariant on average assuming a change in identity.

The breaking of symmetry is often associated with the occurrence of some new phenomenon and an increase in effective complexity (Nicolis & Progogine, 1989). In physics, for example, superconductivity is thought to be critical to the emergence of new physical properties of a system (Tinkham, 2004). In the competitive example, if a small fluctuation in outcome meant that resources could be acquired by excluding others, thereby promoting an increase in competitive ability, this would represent a broken symmetry. It would also represent an increase in effective complexity and a decrease in Shannon entropy, as we will have transitioned from a state of maximum

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ignorance (a uniform distribution over abilities) to a state of minimum ignorance, where one competitor wins.

Spontaneous symmetry-breaking occurs when the laws or equations of a system are symmetrical but specific solutions do not respect the same symmetry. For example, in a superconductor, the symmetry possessed by free electrons in a material is broken at low temperatures because the lowest energy solution is one in which the electrons pair up. *Spontaneous* here simply means endogenous to the dynamics of the system and not catalyzed by some exogenous input. Explicit symmetry-breaking occurs when the rules governing a system are not manifestly invariant under the symmetry group considered. Over a century ago the geneticist Bateson suggested that as symmetry is broken, more information is expressed by an organism, and greater structure is observed. This is consistent with the idea from physics that symmetry-breaking is accompanied by a transition to a less probable but more structured state. In this process, fluctuations from mean behavior are important and can give rise to unexpected behavior that biases the equilibrium state of a system. In other words, asymmetry in a macrostate can emerge from the collective actions of local or transient symmetry-breaking in the microscopic degrees of freedom. Noisy outcomes of competition can lead to long-lasting inequalities. Perhaps the best-known example of this process in biology comes from the study of spontaneous symmetry-breaking during developmental pattern formation, introduced by Turing (1951).

We are currently exploring whether we can model the emergence of power structure as a symmetry-breaking process. The intuition is as follows. The initial condition is one of equivalence: two individuals who are unfamiliar with each other's fighting abilities think they are equally likely to lose a fight if a fight were to erupt between them. As a history of fighting and a corresponding memory for the outcomes build up, the individuals learn who in the pair is likely to lose. It is an open question whether the learning is the result of small fluctuations in fight outcomes and hence can be characterized as a process of spontaneous symmetry-breaking, or whether individuals are learning about inherent underlying asymmetries they did not initially perceive. In that case, the symmetry-breaking would be explicit.

Once an individual learns that it is likely to lose, symmetry is broken, and the relationship shows increased structure. Now there are two possible states (dominant and subordinate) instead of just one (adversarial). This new state is consolidated through the exchange of the signal, which changes slowly and so serves as a good reference state for decision making. Without it, there is only the memory for outcomes distributed over multiple brains, and so any state change that results from the buildup of the memory is not verifiable. As the network of subordination signals builds up, encoding a power structure, asymmetry is consolidated through feedback to the two lower levels. The power structure amplifies the asymmetries by changing the cost of social interactions. Although this increases the mean rate of interaction, the effect is more pronounced for higher-power animals, allowing them to pick up more signals.

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Thus the statistics of the power structure, derived from the signals, stabilize around values that change on a much slower timescale than the underlying fight dynamics and rate at which contracts are reversed.

In the case study of the reef, the intuition goes as follows. In an unbroken soft substrate, reef initiation is dependent on a piece of shell, or a similar hard substrate on which coral larvae can settle. That hard substrate and the resulting larval settlement breaks the environmental symmetry, inducing a positive feedback process that may result in the formation of a larger structure and which can be amplified by the buildup in competitive asymmetries between larvae, juvenile coral and macroalgae. As the reef-builders construct a larger structure, they generate a variety of subenvironments, in effect progressively breaking the environmental symmetries. These new subenvironments contain information about environmental conditions, which influence either the morphology of the organisms that grow there (if they are phenotypically plastic, as many corals are) or their probability of persistence. This has the effect of consolidating the environmental signals through feedback to the trophic interactions and larval settling patterns. As in the social example (albeit on far longer timescales), this has the effect of stabilizing the reef architecture around structures that change on much slower timescales relative to the underlying ecological dynamics. In table 2.1 we summarize the slow and fast variables in the case studies. In table 2.2 we compare the symmetry-breaking processes in the two case studies.

Conclusions

We have hypothesized that the construction of slow variables, which increase the predictability of environmental variables, represents the first step in the evolution of hierarchical biological organization. Slow variables are macroscopic products of a system capable of feeding back to constrain the behavior of individual components. Slow variables arise through a process of symmetry-breaking, whereby either small fluctuations in competitive ability at the individual level are amplified through memory, generating long-lived asymmetries in competitive ability, or individuals come to learn underlying differences in fighting ability. The slow variables serve to increase the predictive ability of the system components by serving as aggregate reference states for behavior or strategy choice.

Identifying reliable macroscopic properties in most living systems is a nontrivial problem for both observers and the system itself. The system might not have the search capacity or computational power to identify predictive features. In the case of power, if individuals do not interact frequently enough to build up a long enough history of fights, symmetry-breaking might not occur and the slow variable social contract never arises. These kinds of problems raise various empirical and theoretical questions. For example, a sizable data set is required to validate that a posited slow

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variable is actually a good predictor. These data are almost never available to observers and are almost certainly not available to components of the system itself. Hence we must develop concepts that reflect both mathematical rigor and biological parsimony: We need to take into account the largest data set that can be recorded and processed by any component of the system given its cognitive capacity.

The formal challenge presented by the theory of slow variables is therefore fourfold. First, the time constants of posited slow variables must be measured quantitatively and their associated statistics must be shown empirically to constitute informative macroscopic variables. By this we mean that they are computable or estimable by individuals (or perhaps species) so that they can be used for decision making or to inform strategy choice in either evolutionary or ontogenetic time. Second, formal models for competitive symmetry-breaking in biological and social systems are required in order to develop a mechanistically grounded theory for slow variable evolution. Finally, the mechanistic theory should predict time constants for the slow variables given factors like the degree of environmental uncertainty, life span of individuals in a population, and the complexity of their perceptual systems. Hence the kinds of issues that need to be addressed in future work include (i) development of good measures for decomposing networks and time formally describing the role of spontaneous symmetry-breaking in hierarchy origination, (ii) evaluating the formal relation between slow variables and adaptive order parameters describing adaptive macrostates, (iii) exploring the adaptive benefits of reducing environmental uncertainty through suitable averaging processes, and (iv) given trade-offs between robustness and evolvability, predicting how much timescale separation across the emerging hierarchy of levels is adaptive in the long term.

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Notes

1. An adaptive system can be said to have memory any time there is a mechanism by which pattern can be extracted from a time series or network, encoded and stored, such that the representation of the pattern changes slowly compared to the time series or network itself.

2. We consider a behavior or process to be competitive if it reduces the density of another type of individual, organism, or species.

3. For a discussion of individuality as it relates to autonomy, see Bertschinger, Olbrich, and Ay (2008).

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4. The pattern formation work in development is not conventionally considered to address the levels question, but to us it seems quite relevant.

5. Family, group, species, and clade reflect different degrees of assortative mixing in space and time.

6. Social niche construction describes the process whereby individuals through their interactions with one another coconstruct their social environments, building social structures and changing the social selection pressures to which they are subject.

7. A time series is a sequence of data points measured at successive times, ideally at uniform intervals if the data are sampled. If the data comprise a complete or nearly complete representation of the events that occurred over a given observation period, the spacing between data points reflects the spacing between the events that the time series describes, as perceived by the data collector. A high-dimensional time series is one in which each time step is associated with a vector, which captures multiple features of the event, rather than a single data point.

8. An emergent property has the following characteristics: (1) the process generating it involves compression or coarse-graining of lower-level dynamics and (2) the coarse-graining is associated with some surprise value (e.g., a new function). It remains under debate whether a phase transition is required or consolidation of a slow variable is sufficient.

9. This sketch of what is presently understood about how power structures emerge in macaque societies is based on a series of studies by Flack, Krakauer, and collaborators on agonistic interactions, status signaling, social networks, and conflict management in pigtailed macaques and what is generally understood about macaque dominance relations (see Thierry, Singh & Kaumanns, 2004).

10. These probabilities can be corrected for variability across individuals in interaction rate.

11. We discus symmetry breaking in the section entitled "The Consolidation of Slow Variables and the Emergence of New Functionality through Symmetry Breaking."

12. Inherent asymmetry means the actual difference in size, fighting ability (assessed using independent data), or alliance network, regardless of how this is perceived by either opponent.

13. The sampling procedure for collecting signals should be the same for all signalers.

14. Although the signals are given infrequently compared to the interaction rate, they are repeated. The number of signals given by the subordinate to the dominant appears to contain information about the perceived magnitude of the expressed asymmetry (Flack & Krakauer, 2006).

15. Kurtosis is the skewedness of a distribution.

16. It should be noted that the details of the role of this process in reef formation are less well understood than they are in the case of pigtailed macaque power structures. Hence the longer case study for power.

17. The subordination contracts have an additional feature worth noting. The contracts are not simply averages over the aggression dynamics that change continuously. They are more like digital

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place-holders, as they require a long history of fighting to be built up and a threshold-level of asymmetry to be established before a contract can be established or one can be substituted for another.

18. We discuss the issue of detection in greater detail in the section entitled "Detecting Slow Variables."

19. For a similar view on the role of uncertainty reduction in the evolution of collective behavior, see Bettencourt (2009).

20. Biological systems also have spatial scales. Whether a similar logic can account for spatial hierarchies is an open question.

21. For a similar explanation for the range of timescales associated with neural codes, see Fairhall et al. (2001).

22. "Endogenous coarsegraining" is a term also used by Fontana and colleagues in their search for a natural representation of molecular dynamics (Feret et al., 2009). Crutchfield (1994) has referred to this process as "intrinsic emergence."

23. A caveat: Researchers look for submission/subordination signals almost exclusively in the context of aggression. Our studies (Flack & de Waal, 2007) suggest that submission signals take on the meaning of subordination when used outside the context of aggression and that researchers should also be looking for such signals in peaceful contexts.

24. We are currently exploring how well individuals can estimate their power using heuristics, as well as how robust the predictive utility of the power structure is to estimation errors. In other words, how "off" can an individual's estimate be before the estimate is no longer informative about its power or predictive of its cost during social interactions?

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