Conserving Coherence Under Constraint

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Abstract

Organisms often respond to energy constraints, time pressure, or imminent threat by limiting behavioral options, lowering metabolic demands, and increasing their level of coordinated action. Although these responses can be viewed as an impairment, we propose that they can be adaptive responses which occur as the costs of coordinating complexity exceed an organism's capabilities at any given time. Accordingly, selection favors mechanisms that conserve the coherence of function by reducing the number of control inputs and reorganizing coupling among the components that remain. We propose that these transitions share a diagnostic signature that encompasses reduced degrees of freedom, reorganized coupling, stabilization of protected variables, and retained re-expansion capacity. We formalize this as a capacity–demand framework and articulate four named, testable hypotheses that specify when and how simplification and recovery should occur across biological scales. This perspective generates testable predictions about threshold-driven emergency modes, asymmetric recovery from emergency modes, and anthropogenic disturbance driving the simplification of function.

Keywords: adaptive simplification, coordination capacity, regime shift, dimensionality reduction, hysteresis, dormancy, collective behavior, coherence

Introduction

When constraints are low, flexibility can enhance fitness/performance. However, under constraints (e.g., food shortages, extreme environmental conditions and/or predation) many organisms will reduce complexity by adopting fixed behavioral patterns and/or becoming immobile (quiescent), or will become highly synchronized with one another (collective) (Geiser 2021; Roelofs 2017). New tracking and machine-learning tools now make these shifts measurable across scales (Pereira et al. 2022).

Historically, simplification has often been interpreted as dysfunction. However, across many biological systems, simplification in function can act as a regulated survival mechanism that allows organisms to remain viable near the boundaries of their functional capacities. The primary issue confronting an organism when functioning near the boundary of its functional capacity is maintaining coordination among components, not maximizing its operational complexity. Sampling the environment extensively when energy is very low can lead to starvation. Delaying response to an immediate threat can result in death. Therefore, the goal is to have enough coordination among the components of an organism to permit it to survive.

We refer to this pattern as the conservation of coherence (see Glossary). When coordination capacity is limited, selection should favor mechanisms to preserve coordinated function and thereby limit the degrees of freedom that need to be managed at one time (even at the expense of flexibility). This affords a simple evolutionary prediction which can be applied to all levels of biological organization and across all taxonomic groups. When demands exceed capacity, biological systems will tend to simplify to maintain coherent function because incoherence risks mortality.

Related frameworks and the novelty of conservation of coherence

There are several other theoretical frameworks which have explored how organisms maintain stability and act under uncertainty as demand increases. The emphasis of allostasis is on controlled adjustments to mediators or to set points. This type of response enables organisms to adapt to acute stressors and provides shorter term stability. Although the process may be successful for coping with acute stressors, prolonged activation can have cumulative costs (McEwen and Wingfield 2003; Word et al. 2022). An organism's robustness/resilience refers to its ability to withstand disturbances and recover from them. Typically, this involves several types of properties such as modularity and redundancy (Crespi et al. 2021; Kitano 2004). Critical Transition Theory studies how nonlinear systems provide insight into the abrupt transitions between different states in a system and the processes that result in these transitions along with the early warning signs of these transitions (Dakos et al. 2024; Scheffer et al. 2001; Scheffer et al. 2009). State-dependent decision theory models threshold-dependent behavioral switches as a function of resource state, risk, and expected fitness returns (Lima and Bednekoff 1999; Ydenberg and Dill 1986). Predictive Processing and the Free Energy Principle offer a complementary perspective that is computational in nature. These frameworks view both perception and action as forms of inference which are aimed at minimizing prediction errors, formally quantified as free energy (Friston 2010a; Friston et al. 2010; Hodson et al. 2024) within the constraints of time and energy. Conservation of coherence differs from all of the above frameworks in one key respect. It uniquely predicts that dimensionality reduction, coupling reorganization, protected variable stabilization, and retained re-expansion capacity co-occur at switching points. It is this joint signature that makes it possible to test whether an organism is actively conserving coherence or simply shutting down by way of a general stress response or behavioral suppression. Table 1 compares these frameworks with conservation of coherence and highlights its unique observable predictions.

Table 1. Related frameworks for stability and control under constraint

Framework	Key mechanisms	What it does not specify
Allostasis	Regulated shifts in mediators/set points to meet varying demands; repeated activation carries cumulative costs (allostatic load)	Pattern of coupling reorganization among system components at the transition
Resilience/Robustness	Buffering, redundancy, and modularity limit effects of perturbations	Why constrained systems converge on tighter coupling rather than maintaining modular independence
Critical Transition Theory	Nonlinear threshold-driven regime shifts with early warning signals and hysteresis	Whether the transition involves dimensionality compression, coupling tightening, or both
State-dependent Decision Theory	Threshold-dependent behavioral switches as a function of resource state, risk, and expected fitness returns	Restructuring of coordination architecture among remaining active components
Predictive Processing / Free Energy Principle	Perception and action as inference minimizing prediction error; constraints favor less exploratory policies	Coupling reorganization at organismal/group levels or hysteresis in recovery
Conservation of Coherence	Capacity–demand trigger for simplified, tightly coordinated regimes preserving core function	Uniquely predicts co-occurrence of dimensionality reduction, coupling reorganization, protected variable stabilization, and retained re-expansion capacity (joint signature) at switching points, it also predicts that recovery is asymmetric, with hysteresis proportional to the depth, duration, and severity of the triggering event

When demand exceeds capacity

We do not suggest that there is only one mechanism of preserving coherence - whether through physical processes, neural control, or simple interaction rules. These examples represent convergent functional solutions shaped by similar constraints and thus are not examples of mechanistic homologies. The framework would be challenged if systems routinely remained complex after coordination limits were exceeded without a rise in coordination failures, or if simplification occurred without a detectable drop in degrees of freedom and a reorganization of coupling that stabilizes key interactions while others are suppressed. Importantly, conservation of coherence does not predict that all stress responses involve simplification; systems with sufficient reserve capacity, redundant modules, or low coordination costs may buffer perturbations without reducing dimensionality. Furthermore, a mere reduction in activity level without restructuring of component interactions would not constitute evidence for this framework.

The framework is most applicable when a stable simplified regime exists to which the system can converge. In such instances, dimensionality compression, coupling reorganization, protected variable stabilization, and retained re-expansion capacity occur together. Stressors that are of a novel, severe, or poorly matched nature may instead produce disrupted non-equilibrium dynamics. These may involve stochastic responses, heterogeneous relaxation, the decoupling of processes, disorganized rather than coordinated changes in dimensionality, failure of protected variables, or impaired re-expansion capacity. Such disrupted dynamics might be expected, for instance, in microorganisms exposed to atypical sublethal stresses for which no coordinated response has evolved. In such situations, the system may become simpler only because of a failure of coordination, rather than a conservation of coherence. These cases are better termed stress-induced disruption, shutdown or collapse, which are outlined in the diagnostic matrix.

Table 2. Diagnostic matrix for distinguishing conservation of coherence from other responses to constraint

Pattern	**Dimensionality reduction**	**Coupling change/reorganization**	**Protected Variables Stabilized**	**Re-expansion capacity retained**	**Interpretation**
Conservation of Coherence	Yes	Yes, coordinated with compression	Yes	Yes	Adaptive Simplification
Stress/load response without simplification	No	Possible, but non-diagnostic	May be defended initially	Usually yes	Load response, not conservation of coherence
Behavioral suppression or shutdown	Yes/No	No coherent reorganization	Variable	Variable	Reduced activity without the full coherence-preserving signature
Stress-induced disruption/frustrated Dynamics	Variable or disorganized	Disorganized or lost	Variable	Variable	Novel or severe stress exceeding coordination capacity; full signature absent
Terminal Collapse	Yes or disorganized loss	Disorganized or lost	No	No	Pathology, failure, collapse
Indeterminate Case	Yes	Yes	Yes	Unknown	Requires recovery data to distinguish adaptive simplification from lock-in or collapse

The conservation of coherence framework adds a clear operational prediction to existing frameworks. Near switching points, adaptive simplification should show a joint temporal signature: a reduction in effective degrees of freedom (behavioral, physiological, interactional), reorganization of coupling (tightening coordination within the remaining active components while other degrees of freedom are down-regulated or decoupled), stabilization of key protected variables, and retained re-expansion capacity. Re-expansion capacity refers to the retained machinery that allows the system to detect improved conditions and rebuild coordination when constraints ease. This fourth component is what distinguishes adaptive simplification from terminal collapse: both may involve reduced activity or dimensionality. However, only adaptive simplification preserves the capacity for coordinated recovery. This can happen even if energy savings are minimal and coordination or information processing is the primary constraint.

The pattern of simplified, tightly coordinated behavior predicted by this framework can be seen in the collective escape behavior in starlings when under attack by peregrine falcons. Starlings will revert to a small number of coordinated escape modes (e.g., flash expansions, blackening, splits, waves). Whether these modes also involve moment-to-moment reductions in the dimensionality of individual trajectories remains an open and testable question (Storms et al. 2019). A direct means to test this would be to track individual bird movements in three dimensions before and during predator attacks. The question is whether the flock shifts to fewer independent movement patterns at the same moment that individual birds become more tightly coupled with one another.

Why coherence is important

We define coherence as the ability of functioning elements (e.g., cells, organs, behavioral components, or groups) to work together in real time in order to support continued function. Coherence is a function of timing and coupling between the various elements or parts of an organism; thus, it does not depend upon the performance of individual parts alone. Biological robustness relies on decoupling and modularity to buffer against perturbation (Kitano 2004). In contrast, coherence conservation entails a narrowing of active components paired with a strengthening of the coupling among the components that persist. For example, in a fish school, individuals coordinate their movement by interacting with their immediate neighbors, using local interaction rules (Herbert-Read et al. 2011). When faced with threat, each individual's range of independent movement narrows and the group's movement collapses to a few coordinated patterns. The empirical question of interest is not just whether individual activity is reduced, but whether the movements of individuals become more tightly coupled to those of their neighbors while a protected variable, such as group cohesion, is maintained.

Coherence is not directly measured in operational terms. It is inferred from the coordination state of the system which can be estimated from multivariate time-series data. Effective degrees of freedom can be estimated by posing the question: how many latent dimensions are required to describe behavior, physiology, or interaction patterns over a defined window of time (Bialek 2022)? For a single organism, this may involve principal component analysis (PCA) or other latent-variable analysis of posture, locomotor trajectories, or time-budget-states. In physiology, it could be estimating covariance structure of body temperature, heart rate, metabolic rate, and activity. In groups of organisms, it could mean measuring trajectory diversity, angular deviation, polarization, synchrony, or nearest-neighbor coupling. Coupling reorganization is evaluated by determining if the remaining active variables are more tightly coupled when other variables are suppressed or decoupled. This can be measured as time-varying correlation, covariance structure, synchrony or phase-locking among physiological signals, or in groups, as change in alignment, nearest neighbor distance, and the extent to which each individual's movement is dependent on the movements of its neighbors. Protected variables are variables that remain bounded during the regime shift while others change substantially. Some examples of protected variables include body temperature during torpor, maintenance of energy charge when metabolism is depressed, and group cohesion during collective escape.

When the coherence of a system changes, that change becomes visible in the number of effective degrees of freedom the system is operating with at any point in time. Degrees of freedom refer to how many ways a system can change independently of one another. Under constraint, effective degrees of freedom decrease as components become more tightly coupled. Higher degrees of freedom can afford more complex and flexible performance. However, they come at a cost. More sensors, more computation, and more control are needed to manage them (Bernstein 1967; Bialek 2022). The challenge of managing multiple independent variables has been formally recognized in motor coordination research, where it is known as the degrees of freedom problem (Morasso 2022). Biological systems routinely solve this problem by coupling their components together in ways that constrain the number of dimensions that need to be independently controlled. This allows them to achieve reliable performance under constraint (Latash 2024). These changes in dimensionality and coupling are measurable across behavioral, physiological, and interaction data (see Box 1).

Box 1: A diagnostic checklist for identifying coherence-preserving regime shifts

Dimensionality: determine the number of dimensions required to describe organisms' behaviors or physiological states within a particular time scale (e.g., principal component analysis of animal movement, covariance or factor structure of physiological states, order or dispersion of subjects in groups).

Coupling: examine if there is a reorganization of the coupling structure of a system undergoing a simplification regime shift (i.e., which links strengthen/weaken), including stronger coordination among elements of the active subset, and/or suppression/loosening of other linkages.

Variables protected during regime shift: determine which variables remain within a narrow range during a regime shift (i.e., body temperature maintains its range; position does not significantly move).

Coordination demand: estimate or experimentally manipulate the number, speed, interdependence, or uncertainty of the variables that must be coordinated. These can be set or quantified through the number of cues or neighbors, group density, noise level of sensory signals, volatility of the environment, or the time allowed to respond.

Thresholds/hysteresis: use change point methods or segmented regression to identify the thresholds where regime shift occurs and where there are different thresholds for entry vs exit from a given regime.

Inter-scale comparisons: Using the same measures to measure coherence at the individual level and group level to see whether simplification at the individual level enables coherence to emerge at the group level (e.g., individual freezing reduces an individual's degrees of freedom, and through this the group becomes more coordinated and therefore has greater polarization).

Re-expansion capacity: determine whether the simplified state retains mechanisms that support recovery. Possible measures include residual responsiveness to environmental cues, exit-trigger sensitivity, recovery rate after constraint removal, energetic reserve state, repair or stress-tolerance markers, arousal capacity in torpor, or persistence of social pathways that allow group coordination to re-form. This can be assessed by comparing stimulus-response latency before and during simplified states, testing whether the system responds to signals that conditions have improved, or tracking recovery trajectories after constraint removed.

When coherence is maintained by reducing complexity, effective dimensionality is reduced and the coupling structure reorganizes: coordination tightens within the remaining active components (often becoming more synchronized), while other processes are suppressed or decoupled. Animals may limit their movement to a few stereotyped patterns, reduce head and body motion, or they may use a limited number of habitual reflexes (Meier et al. 2022; Roelofs 2017; Taylor et al. 2023). Groups of animals can align in terms of speed and direction to facilitate group coordination (Storms et al. 2019). Such adjustments are typically temporary and reversible. However, if the cost of switching between states is high, recovery will be disproportionately expensive. This produces a form of asymmetry, as seen in the energetic cost of torpor arousal (Geiser et al. 2014) and hysteresis in ecosystem regime shifts (Scheffer et al. 2001).

What are the economic costs of coordination?

Maintaining coherence is governed by available resources. From cells to brains, metabolic supply constrains how much sensing, signaling, and computation can be sustained. The cost of neural signaling is significant as it requires a continued expenditure of ATP to maintain ion gradients, generate action potentials, and send synaptic signals (Padamsey and Rochefort 2023; Rae et al. 2024).

When resources are limited, animals alter movement, exploration, social coordination, and defensive responses. The energetic landscape framework shows that animals traveling with limited resources will either reduce how far they travel or utilize a form of locomotion that uses significantly less energy than other forms of locomotion (Cordes et al. 2025; Shepard et al. 2013; Wilson et al. 2012). For instance, birds that are soaring reduce the energetic cost of travel by gliding on rising air currents when possible. This saves energy that would otherwise be used for continuous beating of wings.

Time is another constraint. There is little time to compute flexible, context-sensitive responses when faced with imminent threat. Under imminent threat, defensive responses often shift toward fewer, tightly coordinated modes. Each stage prioritizes coherence of action/function to avoid catastrophic error (Mobbs et al. 2015; Roelofs and Dayan 2022).

Group coordination increases the costs associated with coordination and therefore favors the utilization of simpler rules of interaction in larger groups of animals. For instance, in fish schools or flocks of birds, instead of monitoring all members of a group, each member monitors only a few of its immediate neighbors, which decreases the amount of coordination each member must perform (Couzin 2009; Sumpter 2010). When the cost of flexible coordination of the group exceeds the benefits, groups may respond by aligning more tightly into cohesive, polarized movement or by dispersing when coordination costs are too high (Couzin 2009; Sumpter 2010). Both of these responses preserve coherence under coordination costs that would otherwise be unsustainable.

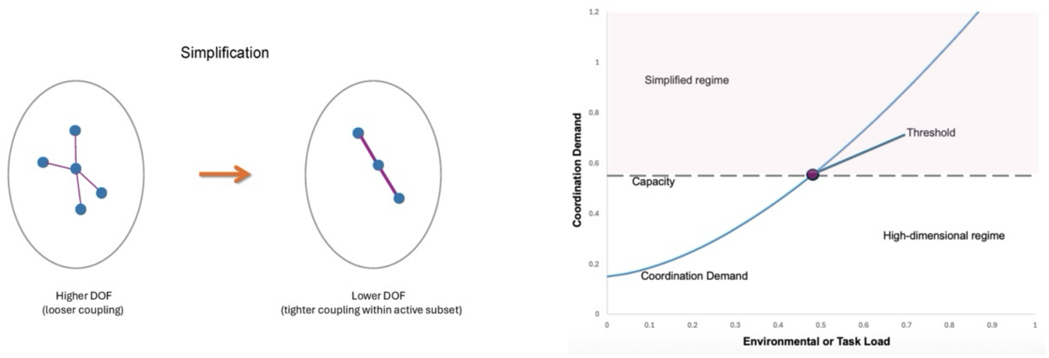
Simplification as a regime shift

A regime shift is a rapid switch in how an organism regulates its function. This occurs when coordination demand exceeds coordination capacity. In this new mode of operation, there will be fewer degrees of freedom and a reorganization of coupling that helps preserve important protected variables including body temperature or available oxygen (Figure 1). However, this often occurs at the expense of higher complexity behaviors like reproduction or exploration. Behavioral ecologists have documented numerous examples of state-dependent thresholds in the literature (Lima and Bednekoff 1999; Ydenberg and Dill 1986). The idea of coherence conservation adds a unique "signature" to this study area.

Figure 1. Capacity-demand mismatch leads to coherence-conserving simplification.
(A) Simplification is predicted to lead to a joint signature. Effective degrees of freedom will compress while the coupling among the remaining active components reorganizes and tightens. Other degrees of freedom are either suppressed or decoupled (H1). (B) Coordination demand increases as either environmental or task loads increase. When coordination demand exceeds coordination capacity, the system can then transition into a simplified regime (H2). (C) When switching regimes and rebuilding impose costs, the thresholds for entry and exit differ. This produces hysteresis - meaning recovery to a more complex regime requires more favorable conditions than the transition into the simplified regime (H3). (D) When individuals simplify, group level coherence can then emerge. Individual degrees of freedom will compress while group polarization and synchrony increase, illustrating cross level emergence (H4). DOF, degrees of freedom.

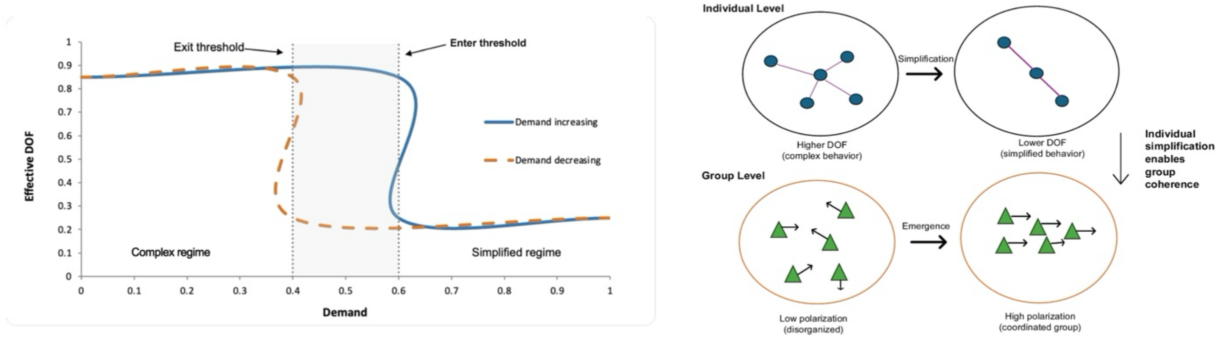
(A) H1: Coupling-compression signature

(B) H2: Coordination threshold



(C) H3: Hysteretic re-expansion

(D) H4: Cross-level Emergence



Simpler systems of organization do not equate to being passive systems. Freezing can allow for greater operational efficiency and preparation for an activity. Torpor states have active regulation through the use of neural circuitry. Dormant microorganisms retain the ability to maintain viable cell function at a reduced level of activity and continue to possess enough sensory capacity to activate an action when reactivated (Bradley 2025; Geiser 2021; Hrvatin et al. 2020; Roelofs 2017). These are simply alternative control methods, not malfunctions.

Additionally, regime shifts typically have recovery costs associated with them. Entering a simplified regime can have switching costs (lost time, missed opportunities, physiological reconfiguration), and exiting may require rebuilding capacity. Within a given episode, entry and exit thresholds can differ (e.g., hysteresis). Systems can enter the simplified mode at higher demand than the demand level at which they re-expand. Hysteresis can make a given state resistant to reversal, but it can also delay recovery after extended periods of disturbance (Dakos et al. 2024; Scheffer et al. 2001).

Common signatures across biological systems

The same pattern emerges across biological domains. Often systems will transition to lower cost and lower dimensional stable states for the most critical variables when their capacity limits are reached (see Table 2).

Table 2. How constrained regimes simplify

Biological Level	Common constraints	Coherence preserving regime	How the regime simplifies	Example Studies
Cells / Microbes	Starvation, antibiotics, oxidative stress	Dormant states, quiescent states, persister states	Biosynthetic activity and growth decrease; remaining metabolism consolidates around survival functions	Bradley 2025; Niu et al. 2024; McDonald et al. 2024
Plants / Invertebrates	Seasonal changes, desiccation or drought, decreased temperature, threat from predators	Seed dormancy, diapause, tonic immobility	Development and activity are arrested; resources directed to protective structures or states. Under threat, the range of behaviors will collapse to a single defensive state	Taylor et al. 2023; Baskin and Baskin 2014; Denlinger 2002; Sakai 2021
Endotherms	Food shortage, decreased temperature, energy deficit	Torpor, hibernation	Metabolic rate and body temperature reduced; thermoregulation narrows to a defended setpoint	Geiser 2021; Hrvatin et al. 2020; Shankar et al. 2023
Vertebrates	Immediate danger with limited time to respond	Freezing, tonic immobility	Range of behavioral options narrows to a few defensive responses; coordination tightens around threat monitoring	Roelofs 2017; Mobbs et al. 2015; Roelofs and Dayan 2022; Carli and Farabollini 2022
Animal groups	Predation, external disruption, social information overload	Alignment, clustering, reduction in task repertoire	Individual behavioral variability decreases; synchrony and polarization increase among group members	Couzin 2009; Sumpter 2010; Herbert-Read et al. 2011

Note: A coherence-preserving regime should also retain re-expansion capacity: some mechanism for detecting changed conditions and rebuilding higher-dimensional coordination.

The lower dimensional state can occur at many scales. Cells become dormant or persistent; plants, insects and other invertebrates cease development, and endotherms will decrease their metabolic activity by entering torpor or hibernation (Baskin and Baskin 2014; Bradley 2025; Denlinger 2002; Geiser 2021; Letten et al. 2024). Invertebrates also display defensive states such as tonic immobility (Sakai 2021; Taylor et al. 2023). Vertebrates defend against predators through freezing and tonic immobility (Carli and Farabollini 2022; Roelofs 2017; Roelofs and

Dayan 2022). In groups, all members adopt tighter rules of interaction. Each individual within the group will couple its movement more tightly with nearby neighbors, so that individuals' movements vary less independently and the group will subsequently cluster or polarize, as seen in starling flocks in response to a predator (Couzin 2009; Storms et al., 2019; Sumpter 2010). All of these states will share at least one common trait; that is reduced effective degrees of freedom with reorganization of coupling (tighter coordination within the active subset) (Table 2).

Evolutionary consequences

If conserving coherence is adaptive, selection should influence both entry into simplified states and recovery from them. Thus, the threshold for entering simplified states should vary with internal state (e.g., energy, health, developmental stage) and external conditions (e.g., threat level, temperature, group density). We predict that populations will evolve differences in when they simplify and how extreme those simplified states may become which should be based on how often demand exceeds capacity. This reframes behavioral flexibility as beneficial yet costly (Auld et al. 2010; Piersma and van Gils 2010). Organisms that are near their energetic limits may opt for quick entry into simple states (e.g., torpor or habitual behavior), while less constrained organisms will have sufficient energy resources to allow them to spend longer amounts of time learning or exploring.

The conservation of coherence framework also can predict why individuals within the same species differ in how they respond to the same type of constraint. The point at which an organism enters a simplified regime, and how quickly it makes that transition, are determined by two things: how much coordination capacity the organism has available and how much coordination demand is being placed on it. The various factors that can influence these include energetic reserves, environmental volatility, and individual differences in stress sensitivity and risk tolerance. These differences can be viewed as reflecting alternative strategies to manage coherence shaped by environmental variability, rather than being characterized as just noise (Biro and Stamps 2010; Dall et al. 2004; Sih et al. 2004).

Anthropogenic disturbances can interfere with the natural processes involved in the dynamics described above. Human disruption of the natural environment can force other species into states of heightened vigilance which can limit their ability to find food and reproduce (Rahman and Candolin 2022; Smith et al. 2021). While some studies have suggested that chronic anthropogenic disturbance can cause long-term changes in the behavior of some non-human species (Gaynor et al. 2019; Lee et al. 2024), direct empirical tests of hysteresis in behavioral dimensionality (where the threshold for entering a simplified regime differs from the threshold for re-expanding) are currently outstanding. Such tests would help identify when adaptive simplification becomes an ecological trap (Robertson and Hutto 2006; Schlaepfer et al. 2002).

Under chronic anthropogenic stress, recovery may become slower or fail altogether. Several plausible mechanisms could drive this. Accumulated allostatic load may degrade the physiological capacity to re-expand behavioral complexity (McEwen and Wingfield 2003). Persistent environmental cues may prevent organisms from detecting that conditions have improved. The chronic stress that drives prolonged simplification may simultaneously degrade the neural and social structures needed to re-expand (Girotti et al. 2024; Woo et al. 2021). As a result, systems may remain in low-flexibility states, which can have subsequent impacts on their mobility, learning, social interactions, and ultimately on the larger ecological dynamics (Gaynor et al. 2019; Lee et al. 2024; Sih et al. 2023; Uchida et al. 2024).

A concrete example illustrates the conservation implications. Ground-nesting shorebirds at beaches with high recreational disturbance spend more time in vigilance states and less time foraging and incubating (Burger 1994). The conservation of coherence framework predicts not simply that these birds are “more stressed” but that birds at high-disturbance sites should show measurably compressed behavioral dimensionality (fewer distinct behavioral modes in time budgets) and tighter coupling of remaining behaviors to disturbance cues compared to birds at well-protected sites. Critically, the framework also predicts that if disturbance is removed, recovery of normal behavioral repertoires should be asymmetric - requiring more favorable conditions than the initial compression. If confirmed, this hysteresis would mean that management closures need to account for behavioral recovery time, not just the removal of direct physical threats to nests and chicks.

Testing coherence conservation

Conservation of coherence yields four named, testable hypotheses:

H1 (Coupling–Compression Signature Hypothesis): As coordination demand approaches or exceeds coordination capacity, effective degrees of freedom should compress, coupling among the remaining active components should reorganize and tighten, and critical protected variables should remain stable. To differentiate adaptive simplification from collapse, the transition should also maintain re-expansion capacity: some remaining sensing, regulatory control, energetic reserve, repair process, or social structure that allows for re-expansion when constraints are eased. The aforementioned joint signature can be tested by combining latent-variable dimensionality estimates with time-varying coupling metrics in multivariate behavioral, physiological, or interaction datasets alongside measures of retained recovery infrastructure such as residual sensory responsiveness, regulatory control, or energetic reserves (Box 1).

H2 (Coordination Threshold Hypothesis): The stimulus to simplify is not any single stressor but rather an imbalance between what the system needs to coordinate and what it has the capacity to coordinate at that moment. Stress and energy shortages can be contributors to the imbalance, but they are not necessarily required. The critical trigger is that coordination demand exceeds what the system can manage. As such, increased demands on coordination should drive simplification even when there is only a small amount of energy savings. In contrast, added reserve capacity should enable the organism to maintain its original level of coordination longer. From an experimental point of view, one can distinguish between coordination demand and stress by using a concrete example. A predator cue can impose stress. However, the level of coordination demand can be varied independently without changing the intensity of the stressor. For example, while maintaining the same stressor intensity, the number of inputs that need to be integrated, the sensory noise that must be filtered, the density of the surrounding group, or the time that is available to respond can be varied. The framework predicts that at the same predator-cue intensity, systems facing higher coordination demand should simplify earlier and more deeply than those with lower demand. This will hold up to the point where demand exceeds the capacity for any viable coordinated response, beyond which the system will show disruption rather than adaptive simplification. Conversely, reducing the coordination demand or increasing the reserve capacity should delay the simplification even if the stressor is the same. The prediction is therefore not simply that more stress produces more simplification. Rather, simplification will take place when the demand that is created by the number, speed, or interdependence of variables to be coordinated grows beyond the capacity to coordinate them.

H3 (Hysteretic Re-expansion Hypothesis): There are costs associated with switching into a simplified regime and rebuilding coordination capacity after exiting said regime. When these costs are present, recovery from a simplified regime should require more favorable conditions than entry. The system simplifies at one threshold. It does not re-expand until conditions improve well beyond that point. Re-expansion should require more favorable conditions, greater energetic expenditure, or more time than the initial compression. The degree of asymmetry should scale with the depth and duration of simplification. This can be quantified by comparing entry versus recovery trajectories. We predict that events of simplification that are brief and shallow in nature (e.g., momentary freezing) should not display much evidence of hysteresis. On the other hand, long-duration events of significant simplification (e.g., extended torpor episodes or persistent reduction in behavioral complexity) are predicted to demonstrate considerable hysteresis. Hysteresis can also emerge from a different source. The triggering event itself may damage the system's coordination apparatus. This damage can be neurological, social, or physiological (Girotti et al. 2024; Woo et al. 2021). In such scenarios, the prolongation of asymmetry does not really depend on the duration of the simplified state. Even a brief episode is predicted to produce prolonged asymmetry if the infrastructure needed for re-expansion has been compromised.

H4 (Cross-level Emergence Hypothesis): The coherence signature does not need to be present at all scales at the same time. When one level of organization simplifies, another level may simultaneously show increased coherence. For example, individual animals may show reduced dimensionality while the group as a whole becomes more polarized or synchronized. Individual simplification can actually enable coherence to emerge at a higher level of organization. The failure to find the signature at one scale does not rule out its presence at another. Thus, testing this hypothesis would require analyzing the same metrics at both the individual and group scales concurrently (see Box 1), which would allow for evaluating independently-predicted coherence at each scale.

Pathways to formalization

The conservation of coherence framework is offered as a conceptual and empirical roadmap, rather than a complete quantitative model. There are a number of well-known mathematical traditions that formalize individual aspects of the framework's predictions, but none predict the co-occurrence of the four signature components as a coordinated transition under a capacity-demand imbalance. For example, in the case of synergetics, as developed by Haken, high-dimensional systems near transitions can be controlled by a small number of collective variables or order parameters, and many microscopic degrees of freedom become constrained by the emerging macroscopic pattern (Haken 1983). This offers a formal basis for H1, where the number of effective degrees of freedom decrease as a system transitions into a coherence-preserving regime. This logic is extended to biological coordination in Kelso's coordination dynamics and the Haken-Kelso-Bunz model, which demonstrate how stable coordination patterns emerge, lose stability, and switch between alternative states (Haken et al., 1985; Kelso

1995). These models are directly relevant to the predicted coupling reorganization that occurs near switching points.

Additional mathematical traditions address other components of the framework. Ashby's law of requisite variety states that the regulatory capacity of systems must match the variety of disturbances that a system must control (Ashby, 1956). This aligns with the capacity-demand logic of H2. When coordination demand exceeds what the system can regulate, successful regulation by the system entails either increasing capacity or reducing the effective variety being managed. The information bottleneck formalizes the trade-off between compressing inputs and preserving the information that is relevant to a target outcome (Tishby et al., 1999). This aligns with the framework's prediction that organisms compress their degrees of freedom while retaining the information that is necessary to stabilize protected variables. H3 could be formally described by slow-fast dynamical systems, which is grounded in geometric singular perturbation theory (Fenichel 1979), and which describes how systems in which entry and exit trajectories operate on different timescales, with recovery dynamics depending on the system's previous history. Metastable coordination dynamics describe how components, by way of a blend of integrative and segregative tendencies, can achieve transient coherence without actually requiring full synchronization (Tognoli and Kelso 2014). This gives formal grounding for H4, where individual level simplification can allow group level coherence to emerge.

Other candidate formalisms are also pertinent. Bifurcation analysis in coupled dynamical systems could derive H1-H3 from first principles. The emergence of group level synchrony predicted by H4 could be modeled by Kuramoto coupled oscillators (Kuramoto 1984). Optimal control under an explicit capacity constraint could formalize the threshold logic of H2. Cross-scale coupling reorganization could be captured by multilayer network approaches (Boccaletti et al. 2014).

The distinguishing feature of the conservation of coherence framework is that for living systems that are operating under bounded coordination capacity, the individual processes described by these formalisms do not operate independently. All are part of a single budgetary process. When demand exceeds capacity, the system must compress dimensionality, reorganize coupling, stabilize protected variables, and retain re-expansion machinery together. Not one of the components is sufficient to preserve function on its own. The formalization of the framework thus does not involve choosing any one of these mathematical traditions but rather integrating them under an explicit capacity constraint. The present paper sets out the biological signatures to be formalized. A companion empirical analysis is in preparation.

Worked example: applying H1–H4 to torpor

Torpor in small endotherms provides an ideal system for testing all four hypotheses. Continuous physiological monitoring is feasible in these animals. The transitions between active states and torpid states are both discrete and repeatable. This makes it possible to observe the same process multiple times within a single individual. Testing H1 (Coupling-Compression Signature) can be accomplished by collecting continuous, multivariate physiological data (heart rate, metabolic rate, body temperature, breathing rate, and activity) with implanted logger devices and then computing effective dimensionality (e.g., PCA or factor analysis) as the organism is transitioning into torpor. The prediction is as follows. When an animal enters torpor, the number of latent modes that are needed to represent the animals physiological state will decrease. The remaining active variables (metabolic rate, heart rate, and breathing) should become more tightly correlated, while body temperature is defended at a lower setpoint. The framework would be challenged if metabolic rate decreased without a concurrent decrease in multivariate dimensionality, without tighter coupling among remaining variables, or without body temperature being defended at a lower setpoint. Re-expansion capacity is maintained during torpor. Organisms retain the physiological machinery to arouse and successfully return to euthermy (Geiser 2021; Geiser et al. 2014).

In order to test H2 (Coordination Threshold), one would manipulate coordination demand independent of energy. Potential experiments include exposure of torpor-prone subjects to unpredictability in terms of environmental disturbances (intermittent noise/light), with ambient temperature and food levels maintained at a consistent level throughout the study. The framework predicts in this instance that coordination demand, not energy shortage, drives simplification. If this is correct, these disturbances should cause the animals to enter torpor sooner, despite no changes in their energy status. Barratt et al. (2025) showed that perceived predation risk alone increased torpor depth and duration in wild superb fairy-wrens. It remains to be tested whether this response reflects a form of compensation for reduced foraging intake or a direct response to increased coordination demand.

To test H3 (Hysteretic Re-expansion), one would compare the rate and energetic cost of physiological simplification during torpor entry against the rate and energetic cost of re-expansion during arousal using the same multivariate metrics. The prediction is that arousal should require more favorable conditions than entry into torpor. The degree of this asymmetry should increase as torpor bouts become longer or deeper. There are publicly available datasets that can provide an immediate opportunity to test this. For example, the Chmura et al. (2023) arctic ground squirrel body temperature archive contains 306 hibernation seasons from 199 individuals.

H4 (Cross-level Emergence) could be tested in colonial hibernators by measuring whether individual physiological simplification co-occurs with increased synchrony among colony members in torpor bout timing.

Evaluating support across biological scales

There is variation in the strength of evidence regarding the complete joint signature across biological scales. There is extensive documentation that global suppression of biosynthetic activity and priming for stress tolerance are associated with microbial persistence/dormancy (Bradley 2025; Hossain et al. 2023; Niu et al. 2024). The consolidation of metabolism around core survival functions in Persister cells is consistent with dimensionality reduction (McDonald et al. 2024). However, explicit multivariate analyses of coupling reorganization among physiological or molecular variables during the dormancy transition remain rare. Formal tests of hysteresis in the transition between active and dormant states are largely absent as well. This is a clear opportunity for applying the conservation of coherence framework to transcriptomic or metabolomic time series data.

In plant and invertebrate diapause and dormancy, development and activity arrest while resources are redirected to protective structures (Baskin and Baskin 2014; Denlinger 2002). Tonic immobility in invertebrates collapses the behavioral repertoire to a single defensive state (Sakai 2021; Taylor et al. 2023). These cases are consistent with dimensionality reduction, but coupling reorganization (tighter linkage among remaining active processes) has not been explicitly measured. Protected variable stabilization (structural integrity, metabolic viability) is implied but not formally quantified in most studies.

The most compelling evidence to support a common joint signature would be torpor and hibernation. Active regulation by identified neural circuits drives torpor entry (Hrvatin et al. 2020). During torpor, three main physiological parameters become tightly coupled (Geiser 2021). Geiser et al. (2014) compared torpor with pathological hypothermia in similar-sized mammals. Torpor displayed coordinated reduction in metabolic rate and body temperature with body temperature defended at a lowered set point. Hypothermia did not show this, despite similar reductions in both variables. This is consistent with the framework's prediction that coherent simplification produces a distinguishable signature. The same study showed that metabolic rate and body temperature follow different trajectories during entry versus arousal, consistent with recovery costs predicted by H3. Despite this evidence, relatively little research is available regarding whether the collapse in dimensionality of high-dimensional behavioral or physiological repertoires occurs at the same transition point. As a result, this leaves the full H1 signature partially tested.

During both tonic immobility and freezing in vertebrates, the range of defensive behaviors diminishes dramatically to include only a few coordinated defensive responses (Carli and Farabollini 2022; Roelofs and Dayan 2022). At the same time, autonomic functions become highly correlated and tightly linked around threat monitoring (Roelofs 2017; Roelofs and Dayan 2022). However, in order to confirm the full H1 signature, all four components must be shown to emerge together at the same transition point. This has not been formally tested. Evidence for hysteresis in recovery from freezing states also remains limited.

Collective behavior research has examined group responses to predator attacks. Research shows that when predators attack, groups consistently show increased synchronization in addition to increased group polarization (Couzin 2009; Herbert-Read et al. 2011; Sumpter 2010). Increased synchronization and group polarization are both consistent signs of increased or tighter coupling under the framework. However, Storms et al. (2019) identified several different escape patterns from starling flocks. These findings could be interpreted by some researchers as a maintained repertoire of escape behaviors instead of an example of dimensionality compression. This ambiguity further illustrates the importance of performing a dimensionality analysis on the trajectories of individual animals within a group, rather than measuring the degree of polarized behavior at the group level. Notably, diversity across escape motifs is compatible with the framework. The key consideration is what happens within any single motif. If the number of independent movement dimensions drops and the coordination between individuals tightens, then the joint signature is present. The number of different motifs the flock uses over the course of an encounter is not relevant. What really matters with respect to the joint signature is what actually occurs inside each one.

Evidence for re-expansion capacity exists across biological scales. Torpor is actively regulated by neural circuits that have been identified (Hrvatin, et al. 2020), indicating that regulatory control is maintained throughout the state of torpor rather than it being lost. Dormant microorganisms retain sensory capacity that is sufficient to detect when conditions improve and subsequently reactivate (Bradley 2025). Freezing vertebrates maintain sensory monitoring of the threat environment throughout the freezing episode (Roelofs 2017). However, when a system shifts to a low dimensional state where it loses the capacity to sense better conditions or restore its coordination, the state is more aptly described as collapse or pathology rather than conservation of coherence. Therefore, re-expansion capacity offers the temporal diagnostic that connects entry, maintenance, and recovery within the conservation of coherence framework.

What would falsify the framework

Two scenarios would falsify the framework. The first: organisms routinely exceed their coordination capacity with no increase in failure rates and no reduction in complexity. The second: the four components of the joint signature (dimensionality compression, coupling reorganization, protected variable stabilization, and retained re-expansion capacity) are consistently found to occur independently rather than occurring as a coordinated transition. On the other hand, the fact that an organism exhibits lower levels of activity, lower rates of metabolism, or lower levels of diversity in its behavior but has undergone no changes in coupling does not provide evidence for coherence conservation. Table 2 summarizes how to distinguish conservation of coherence from other patterns where constraint is present.

Discussion

We have suggested that "emergency modes" across biology may be viewed as coherence-preserving regime shifts. When an organism's ability to coordinate complex behavior is limited, it reduces the number of possible options for action and reorganizes coupling among the remaining options. This may explain why structurally similar emergency responses appear across such diverse biological systems, e.g., bacterial dormant states, freezing, torpor, habitual control, and flocking.

Considering emergency responses as regulated rather than pathological creates new considerations regarding when limits become too restrictive, when recovery occurs, and when repetitive activation of emergency responses could be detrimental. For conservation practitioners, this framework suggests that management strategies should aim to preserve recovery windows rather than simply minimizing disturbance intensity, because even moderate chronic stressors may prevent the re-expansion of complexity if they eliminate the time or energy required for recovery. Answering these questions will require an integration of ecological contexts into dimensionality assessments and cross-scale comparisons. Future work should attempt to clarify when hysteresis shifts from an adaptive buffer to an evolutionary constraint. It remains to be determined how selection distributes coherence across organizational levels during simplification. Furthermore, the variation in individual energy reserves and experience may shape both the initiation and recovery from a state of simplification, especially given novel anthropogenic stressors that may reduce or eliminate the windows of recovery on which these evolved mechanisms depend.

The presented work views emergency modes as shifts between regimes of function. Each regime shift carries a joint signature of coupling reorganization and compression of dimensionality (H1). Furthermore, entry into a new regime occurs when demands exceed current available capacity (a threshold that can be dissociated from energetic savings) (H2). Recovery can exhibit hysteresis by way of requiring more favorable conditions for exit from said regime than were needed for entry (H3). Additionally, individual simplification can enable coherence to emerge at higher organizational levels (H4). The major point of distinction is that all four (dimensionality compression, coupling reorganization, protected variable stabilization, and retained re-expansion capacity) must occur at a coordinated switching point. Together, H1 through H4 make testable predictions that can guide potential future comparisons and experimental design. The addition of re-expansion capacity creates a temporal diagnostic that can be used to distinguish between adaptive simplification and collapse in real data.

Glossary

Conservation of coherence: when demand on an organism exceeds its coordination capacity, the organism maintains coherent function by reducing its degrees of freedom, tightening coordination among the remaining active components, stabilizing critical protected variables, and retains re-expansion capacity.

Coordination Capacity: the energetic, information processing/neural, and temporal resources available to an organism for coordinating its behavior at any given point in time.

Coupling: The strength of the interaction between components of a system. An organism maintains its coherence by increasing the connection between active components and decreasing or eliminating the connection to other less important components; thus, changing their stability and interdependence.

Degrees of freedom: the number of independent ways a system can vary. Effective degrees of freedom decrease under constraint as components become more tightly coupled.

Hysteresis: an asymmetry between entry and exit conditions, such that the demand or capacity required to enter a regime differs from that required to leave it.

Protected variables: variables maintained within a narrow range during a regime shift (e.g., body temperature, oxygen delivery, spatial position), often at the expense of other degrees of freedom.

Regime shift: a rapid, nonlinear transition between distinct states of organization. This transition is triggered when a system crosses a critical threshold.

Re-expansion capacity: the capacity to sense, regulate, energize, structure, or socially coordinate that is retained by a simplified system that enables it to detect improved conditions and rebuild higher dimensional coordination when constraints are eased.

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References

Ashby, W.R. (1956) *An Introduction to Cybernetics.* Chapman & Hall.

Auld, J.R., Agrawal, A.A., and Relyea, R.A. (2010). Re-evaluating the costs and limits of adaptive phenotypic plasticity. *Proc. Biol. Sci.* 277, 503-511. doi: 10.1098/rspb.2009.1355

Barratt, A., Welbergen, J.A., Moore, B., and Turbill, C. (2025). Torpor use in response to predation risk in a small, free-living bird. Behav. Ecol. 36, araf069. doi: 10.1093/beheco/araf069

Baskin, C.C., and Baskin, J.M. (2014). *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination* 2nd edn. San Diego, CA: Academic Press. doi: 10.1016/C2013-0-00597-X

Bernstein, N. (1967). *The Coordination and Regulation of Movements*. Oxford: Pergamon Press.

Bialek, W. (2022). On the dimensionality of behavior. *Proc. Natl Acad. Sci. USA* 119, e2021860119. doi: 10.1073/pnas.2021860119

Biro, P.A., and Stamps, J.A. (2010). Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends Ecol. Evol.* 25, 653-659. doi: 10.1016/j.tree.2010.08.003

Boccaletti, S., Bianconi, G., Criado, R., del Genio, C.I., Gomez-Gardenes, J., Romance, M. et al. (2014). The structure and dynamics of multilayer networks. *Phys. Rep. 544, 1-122.* doi: 10.1016/j.physrep.2014.07.001.

Bradley, J.A. (2025). Microbial dormancy as an ecological and biogeochemical regulator on Earth. *Nat. Commun.* 16, 3909. doi: 10.1038/s41467-025-59167-6

Burger, J. (1994). The effect of human disturbance on foraging behavior and habitat use in piping plover (*Charadrius melodus*). *Estuaries* 17, 695-701. doi: 10.2307/1352398

Carli, G., and Farabollini, F. (2022). Tonic immobility as a survival, adaptive response and as a recovery mechanism. *Prog. Brain Res.* 271, 305-329. doi: 10.1016/bs.pbr.2022.05.001

Chmura, H.E., Duncan, C., Burrell, G., Barnes, B.M., Buck, C.L., and Williams, C.T. (2023). Climate change is altering the physiology and phenology of an arctic hibernator. Science 380, 846-850. doi: 10.1126/science.add6914

Cordes, L.S., Bishop, C.M., Börger, L., Nabe-Nielsen, J., and Harris, S.M. (2025). Optimal movement decisions in complex landscapes. *Trends Ecol. Evol.* 40, 960-969. doi: 10.1016/j.tree.2025.07.005

Couzin, I.D. (2009). Collective cognition in animal groups. *Trends Cogn. Sci.* 13, 36-43. doi: 10.1016/j.tics.2008.11.002

Crespi, E., Burnap, R., Chen, J., Das, M., Gassman, N., Rosa, E. et al. (2021). Resolving the rules of robustness and resilience in biology across scales. *Integr. Comp. Biol.* 61, 2163-2179. doi: 10.1093/icb/icab163

Dakos, V., Boulton, C.A., Buxton, J.E., Abrams, J.F., Arellano-Nava, B., Armstrong McKay, D.I. et al. (2024). Tipping point detection and early warnings in climate, ecological, and human systems. *Earth Syst. Dyn.* 15, 1117-1135. doi: 10.5194/esd-15-1117-2024

Dall, S.R.X., Houston, A.I., and McNamara, J.M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* 7, 734-739. doi: 10.1111/j.1461-0248.2004.00618.x

Denlinger, D.L. (2002). Regulation of diapause. *Annu. Rev. Entomol.* 47, 93-122. doi: 10.1146/annurev.ento.47.091201.145137

Fenichel, N. (1979) Geometric singular perturbation theory for ordinary differential equations. J. Differ. Equ. 31, 53-98. doi:10.1016/0022-0396(79)90152-9.

Friston, K. (2010a). The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* 11, 127-138. doi: 10.1038/nrn2787

Friston, K., Daunizeau, J., Kilner, J., and Kiebel, S.J. (2010). Action and behavior: a free-energy formulation. *Biol. Cybern.* 102, 227-260. doi: 10.1007/s00422-010-0364-z

Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E., and Brashares, J.S. (2019). Landscapes of fear: spatial patterns of risk perception and response. *Trends Ecol. Evol.* 34, 355-368. doi: 10.1016/j.tree.2019.01.004

Geiser, F. (2021). *Ecological Physiology of Daily Torpor and Hibernation*. Cham: Springer Nature Switzerland. doi: 10.1007/978-3-030-75525-6

Geiser, F., Currie, S.E., O'Shea, K.A., and Hiebert, S.M. (2014). Torpor and hypothermia: reversed hysteresis of metabolic rate and body temperature. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 307, R1324-R1329. doi: 10.1152/ajpregu.00214.2014

Girotti, M., Bulin, S.E., and Carreno, F.R. (2024). Effects of chronic stress on cognitive function - from neurobiology to intervention. *Neurobiol. Stress* 33, 100670. doi: 10.1016/j.ynstr.2024.100670

Haken, H. (1983) *Synergetics: An Introduction.* 3rd edn. Springer.

Haken, H., Kelso, J.A.S., Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biol. Cybern.* 51, 347-356. doi: 10.1007/BF00336922.

Herbert-Read, J.E., Perna, A., Mann, R.P., Schaerf, T.M., Sumpter, D.J.T., and Ward, A.J.W. (2011). Inferring the rules of interaction of shoaling fish. *Proc. Natl Acad. Sci. USA* 108, 18726-18731. doi: 10.1073/pnas.1109355108

Hodson, R., Mehta, M., and Smith, R. (2024). The empirical status of predictive coding and active inference. *Neurosci. Biobehav. Rev.* 157, 105473. doi: 10.1016/j.neubiorev.2023.105473

Hossain, T., Singh, A., and Butzin, N.C. (2023). *Escherichia coli* cells are primed for survival before lethal antibiotic stress. *Microbiol. Spectr.* 11, e01219-23. doi: 10.1128/spectrum.01219-23

Hrvatin, S., Sun, S., Wilcox, O.F., Yao, H., Lavin-Peter, A.J., Cicconet, M. et al. (2020). Neurons that regulate mouse torpor. *Nature* 583, 115-121. doi: 10.1038/s41586-020-2387-5

Kelso, J.A.S. (1995). *Dynamic Patterns: The Self-Organization of Brain and Behavior.* MIT Press.

Kitano, H. (2004). Biological robustness. *Nat. Rev. Genet.* 5, 826-837. doi: 10.1038/nrg1471

Kuramoto, Y. (1984). Chemical Oscillations, Waves, and Turbulence. Springer. doi: 10.1007/978-3-642-69689-3.

Latash, M.L. (2024). Terra incognita of the uncontrolled manifold. *J. Neurophysiol.* 132, 1729-1743. doi: 10.1152/jn.00350.2024

Lee, S.X.T., Amir, Z., Moore, J.H., Gaynor, K.M., and Luskin, M.S. (2024). Effects of human disturbances on wildlife behaviour and consequences for predator-prey overlap in Southeast Asia. *Nat. Commun.* 15, 1521. doi: 10.1038/s41467-024-45868-x

Letten, A.D., Yamamichi, M., Richardson, J.A., and Ke, P.-J. (2024). Microbial dormancy supports multi-species coexistence under resource fluctuations. Ecol. Lett. 27, e14507. doi: 10.1111/ele.14507

Lima, S.L., and Bednekoff, P.A. (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* 153, 649-659. doi: 10.1086/303202

McDonald, M.D., Owusu-Ansah, C., Ellenbogen, J.B., Malone, Z.D., Ricketts, M.P., Frolking, S.E. et al. (2024). What is microbial dormancy? *Trends Microbiol.* 32, 142-150. doi: 10.1016/j.tim.2023.08.006

McEwen, B.S., and Wingfield, J.C. (2003). The concept of allostasis in biology and biomedicine. *Horm. Behav.* 43, 2-15. doi: 10.1016/S0018-506X(02)00024-7

Meier, J.K., Staresina, B.P., and Schwabe, L. (2022). Stress diminishes outcome but enhances response representations during instrumental learning. *eLife* 11, e67517. doi: 10.7554/eLife.67517

Mobbs, D., Hagan, C.C., Dalgleish, T., Silston, B., and Prevost, C. (2015). The ecology of human fear: survival optimization and the nervous system. *Front. Neurosci.* 9, 55. doi: 10.3389/fnins.2015.00055

Morasso, P. (2022). A vexing question in motor control: the degrees of freedom problem. *Front. Bioeng. Biotechnol.* 9, 783501. doi: 10.3389/fbioe.2021.783501

Niu, H., Gu, J., and Zhang, Y. (2024). Bacterial persisters: molecular mechanisms and therapeutic development. *Signal Transduct. Target. Ther.* 9, 174. doi: 10.1038/s41392-024-01866-5

Padamsey, Z., and Rochefort, N.L. (2023). Paying the brain's energy bill. *Curr. Opin. Neurobiol.* 78, 102668. doi: 10.1016/j.conb.2022.102668

Pereira, T.D., Tabris, N., Matsliah, A., Turner, D.M., Li, J., Ravindranath, S. et al. (2022). SLEAP: a deep learning system for multi-animal pose tracking. *Nat. Methods* 19, 486-495. doi: 10.1038/s41592-022-01426-1

Piersma, T., and van Gils, J.A. (2010). *The Flexible Phenotype: A Body-Centred Integration of Ecology, Physiology, and Behaviour*. Oxford: Oxford University Press. doi: 10.1093/acprof:oso/9780199233991.001.0001

Rae, C.D., Baur, J.A., Borges, K., Dienel, G., Díaz-García, C.M., Douglass, S.R. et al. (2024). Brain energy metabolism: a roadmap for future research. *J. Neurochem.* 168, 910-954. doi: 10.1111/jnc.16032

Rahman, T., and Candolin, U. (2022). Linking animal behavior to ecosystem change in disturbed environments. *Front. Ecol. Evol.* 10, 893453. doi: 10.3389/fevo.2022.893453

Robertson, B.A., and Hutto, R.L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87, 1075-1085. doi: 10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2

Roelofs, K. (2017). Freeze for action: neurobiological mechanisms in animal and human freezing. *Philos. Trans. R. Soc. B. Biol. Sci.* 372, 20160206. doi: 10.1098/rstb.2016.0206

Roelofs, K., and Dayan, P. (2022). Freezing revisited: coordinated autonomic and central nervous system mechanisms. *Nat. Rev. Neurosci.* 23, 568-580. doi: 10.1038/s41583-022-00608-2

Sakai, M. (2021). *Death-Feigning in Insects: Mechanism and Function of Tonic Immobility*. Singapore: Springer. doi: 10.1007/978-981-33-6598-8

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature* 413, 591-596. doi: 10.1038/35098000

Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V. et al. (2009). Early-warning signals for critical transitions. *Nature* 461, 53-59. doi: 10.1038/nature08227

Schlaepfer, M.A., Runge, M.C., and Sherman, P.W. (2002). Ecological and evolutionary traps. *Trends Ecol. Evol.* 17, 474-480. doi: 10.1016/S0169-5347(02)02580-6

Shankar, A., Welch, K.C., Eberts, E.R., Geiser, F., Halter, S., Keicher, L. et al. (2023). Daily torpor in birds and mammals: past, present, and future of the field. *Integr. Comp. Biol.* 63, 1017-1027. doi: 10.1093/icb/icad008

Shepard, E.L.C., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A., and Vosper, S.B. (2013). Energy landscapes shape animal movement ecology. *Am. Nat.* 182, 298-312. doi: 10.1086/670726

Sih, A., Bell, A., and Johnson, J.C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* 19, 372-378. doi: 10.1016/j.tree.2004.04.009

Sih, A., Chung, H.J., Neylan, I., Ortiz-Jimenez, C., Sakai, O., and Szeligowski, R. (2023). Fear generalization and behavioral responses to multiple dangers. *Trends Ecol. Evol.* 38, 369-380. doi: 10.1016/j.tree.2023.01.009

Smith, J.A., Gaynor, K.M., and Suraci, J.P. (2021). Mismatch between risk and response may amplify lethal and non-lethal effects of humans on wild animal populations. *Front. Ecol. Evol.* 9, 604973. doi: 10.3389/fevo.2021.604973

Storms, R.F., Carere, C., Zoratto, F., and Hemelrijk, C.K. (2019). Complex patterns of collective escape in starling flocks under predation. *Behav. Ecol. Sociobiol.* 73, 10. doi:10.1007/s00265-018-2609-0

Sumpter, D.J.T. (2010). *Collective Animal Behavior*. Princeton, NJ: Princeton University Press. doi: 10.1515/9781400837106

Tishby, N., Pereira, F.C., and Bialek, W. (1999). The information bottleneck method. *Proceedings of the 37th Annual Allerton Conference on Communication, Control, and Computing,* pp. 368-377.

Taylor, K.L., Henry, C.S., and Farkas, T.E. (2023). Why fake death? Environmental and genetic control of tonic immobility in larval lacewings (Neuroptera: Chrysopidae). *J. Insect Sci.* 23, 15. doi: 10.1093/jisesa/iead042

Tognoli, E. and Kelso, J.A.S. (2014). The metastable brain. *Neuron* 81, 35-48. doi: 10.1016/j.neuron.2013.12.022.

Uchida, K., Blumstein, D.T., and Soga, M. (2024). Managing wildlife tolerance to humans for ecosystem goods and services. *Trends Ecol. Evol.* 39, 248-257. doi: 10.1016/j.tree.2023.11.011

Wilson, R.P., Quintana, F., and Hobson, V.J. (2012). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc. R. Soc. B* 279, 975-980. doi: 10.1098/rspb.2011.2105

Woo, E., Sansing, L.H., Arnsten, A.F.T., and Datta, D. (2021). Chronic stress weakens connectivity in the prefrontal cortex: architectural and molecular changes. *Chronic Stress* 5, 24705470211029254. doi: 10.1177/24705470211029254

Word, K.R., Austin, S.H., and Wingfield, J.C. (2022). Allostasis revisited: a perception, variation, and risk framework. *Front. Ecol. Evol.* 10, 954708. doi: 10.3389/fevo.2022.954708

Ydenberg, R.C., and Dill, L.M. (1986). The economics of fleeing from predators. *Adv. Study Behav.* 16, 229-249. doi: 10.1016/S0065-3454(08)60192-8