

# 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, and stabilization of protected variables. 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, torpor, collective behavior, coherence

46 **Introduction**

47 When constraints are low, flexibility can enhance fitness/performance. However, under  
48 constraints (e.g., food shortages, extreme environmental conditions and/or predation) many  
49 organisms will reduce complexity by adopting fixed behavioral patterns and/or becoming  
50 immobile (quiescent) or will become highly synchronized with one another (collective) (Geiser  
51 2021; Roelofs 2017). New tracking and machine-learning tools now make these shifts  
52 measurable across scales (Pereira et al. 2022).

53 Historically, simplification has often been interpreted as dysfunction. However, across many  
54 biological systems, simplification in function can act as a regulated survival mechanism that  
55 allows organisms to remain viable near the boundaries of their functional capacities. The primary  
56 issue confronting an organism when functioning near the boundary of its functional capacity is  
57 maintaining coordination among components, not maximizing its operational complexity.

58 Sampling the environment extensively when energy is very low can lead to starvation. Delaying  
59 response to an immediate threat can result in death. Therefore, the goal is to have enough  
60 coordination among the components of an organism to permit it to survive.

61 We refer to this pattern as the conservation of coherence (see Glossary). When coordination  
62 capacity is limited, selection should favor mechanisms to preserve coordinated function and  
63 thereby limit the degrees of freedom (behavioral, physiological, interactional) that need to be  
64 managed at one time (even at the expense of flexibility). This affords a simple evolutionary  
65 prediction grounded in the economics of behavioral and physiological coordination, that is  
66 applicable across levels of ecological organization and taxonomic groups. When demands exceed  
67 capacity, biological systems will tend to simplify to maintain coherent function because  
68 incoherence risks mortality.

## 69 **Related frameworks and the novelty of conservation of coherence**

70 There are several other theoretical frameworks which have explored how organisms maintain  
71 stability and act under uncertainty as demand increases. State-dependent decision theory models  
72 threshold-dependent behavioral switches as a function of resource state, risk, and expected  
73 fitness returns (Lima & Bednekoff 1999; Ydenberg & Dill 1986). Critical Transition Theory  
74 studies how nonlinear systems provide insight into the abrupt transitions between different states  
75 in a system and the processes that result in these transitions along with the early warning signs of  
76 these transitions (Dakos et al. 2024; Scheffer et al. 2001; Scheffer et al. 2009). An organism's  
77 robustness/resilience refers to its ability to withstand disturbances and recover from them.  
78 Typically, this involves several properties including modularity and redundancy (Crespi et al.  
79 2021; Kitano 2004). The emphasis of allostasis is on controlled adjustments to mediators or to  
80 set points. This type of response enables organisms to adapt to acute stressors and provides  
81 shorter term stability. Although the process may be successful for coping with acute stressors,  
82 prolonged activation can have cumulative costs (McEwen & Wingfield 2003; Word et al. 2022).  
83 Predictive Processing and the Free Energy Principle offer a complementary perspective that is  
84 computational in nature. These frameworks view both perception and action as forms of  
85 inference which are aimed at minimizing prediction errors, formally quantified as free energy  
86 (Friston 2010a; Friston et al. 2010; Hodson et al. 2024) within the constraints of time and energy.  
87 Table 1 compares these frameworks with conservation of coherence and highlights its unique  
88 observable predictions.

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92 **Table 1. Related frameworks for stability and control under constraint**

Framework	Key mechanisms	What it does not specify
<b>State-dependent Decision Theory</b>	Threshold-dependent behavioral switches as a function of resource state, risk, and expected fitness returns	Restructuring of coordination architecture among remaining active components
<b>Critical Transition Theory</b>	Nonlinear threshold-driven regime shifts with early warning signals and hysteresis	Whether the transition involves dimensionality compression, coupling tightening, or both
<b>Resilience/Robustness</b>	Buffering, redundancy, and modularity limit effects of perturbations	Why constrained systems converge on tighter coupling rather than maintaining modular independence
<b>Allostasis</b>	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
<b>Predictive Processing / Free Energy Principle</b>	Perception and action as inference minimizing prediction error; constraints favor less exploratory policies	Coupling reorganization at organismal/group levels or hysteresis in recovery
<b>Conservation of Coherence</b>	Capacity–demand trigger for simplified, tightly coordinated regimes preserving core function	Uniquely predicts co-occurrence of dimensionality reduction, coupling reorganization, and protected variable stabilization (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

93 **When demand exceeds capacity**

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

104 The pattern of simplified, tightly coordinated behavior predicted by this framework can be seen  
105 in the collective escape behavior in starlings when under attack by peregrine falcons. Starlings  
106 will revert to a small number of coordinated escape modes (e.g., flash expansions, blackening,  
107 splits, waves). Whether these modes also involve moment-to-moment reductions in the  
108 dimensionality of individual trajectories remains an open and testable question (Storms et al.  
109 2019). A direct means to test this would be to track individual bird movements in three  
110 dimensions before and during predator attacks. The question is whether the flock shifts to fewer  
111 independent movement patterns at the same moment that individual birds become more tightly  
112 coupled with one another.

### 113 **Why coherence is important**

114 We define coherence as the ability of functioning elements (e.g., cells, organs, behavioral  
115 components, or groups) to work together in real time in order to support continued function.

116 Coherence is a function of timing and coupling between the various elements or parts of an  
117 organism; thus, it does not depend upon the performance of individual parts alone. Biological  
118 robustness relies on decoupling and modularity to buffer against perturbation (Kitano 2004). In  
119 contrast, coherence conservation entails a narrowing of active components paired with a  
120 strengthening of the coupling among the critical components that persist.

121 When the coherence of a system changes, that change becomes visible in the number of effective  
122 degrees of freedom the system is utilizing at any point in time. Degrees of freedom refer to how  
123 many ways a system can change independently of one another. Under constraint, effective  
124 degrees of freedom decrease as components become more tightly coupled or linked. Higher  
125 degrees of freedom can afford more complex and flexible performance. However, they come at a  
126 cost. More sensors, more computation, and more control are needed to manage them (Bernstein

127 1967; Bialek 2022). The challenge of managing multiple independent variables has been  
128 formally recognized in motor coordination research, where it is known as the degrees of freedom  
129 problem (Morasso 2022). Biological systems routinely solve this problem by coupling their  
130 components together in ways that constrain the number of dimensions that need to be  
131 independently controlled. This allows them to achieve reliable performance under constraint  
132 (Latash 2024). In ecological terms, the degrees of freedom problem maps onto familiar trade-  
133 offs. A forager must simultaneously track predators, monitor patch quality, and coordinate with  
134 group members. The coordination challenge scales with the number of independent decisions  
135 required per unit of time. The degree of coherence is reflected in the data by changes in the  
136 dimensionality of an organism's behavior, such as its movement patterns, interaction patterns, or  
137 physiological states (Bialek 2022) (see Box 1).

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

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

142 **Coupling:** monitor for reorganization of the coupling structure of a system undergoing a simplification regime shift  
143 (i.e., which links strengthen/weaken), including stronger coordination among elements of the active subset, and/or  
144 suppression/loosening of other linkages.

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

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

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

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154 When coherence is maintained, animals may limit their movement to a few stereotyped patterns,  
155 reduce head and body motion, or they may use a limited number of habitual reflexes (Meier et al.  
156 2022; Roelofs 2017; Taylor et al. 2023). Groups of animals can align in terms of speed and  
157 direction to facilitate group coordination (Storms et al. 2019). Such adjustments are typically  
158 temporary and reversible. However, if the cost of switching between states is high, recovery will  
159 be disproportionately expensive. This produces a form of asymmetry, as seen in the energetic  
160 cost of torpor arousal (Geiser et al. 2014) and hysteresis in ecosystem regime shifts (Scheffer et  
161 al. 2001).

## 162 **What are the economic costs of coordination?**

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

168 When resources are limited, animals alter movement, exploration, social coordination, and  
169 defensive responses. The energetic landscape framework shows that animals traveling with  
170 limited resources will either reduce how far they travel or utilize a form of locomotion that uses  
171 significantly less energy than other forms of locomotion (Cordes et al. 2025; Shepard et al. 2013;  
172 Wilson et al. 2012).

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

177 Group coordination increases the costs associated with coordination and therefore favors the  
178 utilization of simpler rules of interaction in larger groups of animals, and results in tighter group  
179 cohesion or dispersal when the cost of flexible coordination of the behaviors of individual  
180 members of the group exceeds the benefits. This allows group members to avoid collisions,  
181 maintain cohesion, and to track neighbors. However, responses may also include fission or  
182 dispersal when alignment costs exceed benefits. Such evidence suggests that groups may  
183 preserve coherence either by aligning more tightly or dispersing when coordination costs are too  
184 high (Couzin 2009; Sumpter 2010).

### 185 **Simplification as a regime shift**

186 In ecological terms, a regime shift occurs when an organism's coordination demand exceeds its  
187 coordination capacity, triggering a rapid switch in how it regulates function. However, this often  
188 occurs at the expense of higher complexity behaviors like reproduction or exploration.

189 Behavioral ecologists have documented numerous examples of state-dependent thresholds in the  
190 literature (Lima & Bednekoff 1999; Ydenberg & Dill 1986). The idea of coherence conservation  
191 adds a unique “signature” to this study area. However, under this framework, simply decreasing  
192 the amount of behavior or energy usage does not indicate a system is displaying this signature.

193 Simpler systems of organization do not equate to being passive systems. Freezing can allow for  
194 greater operational efficiency and preparation for an activity. Torpor states have active regulation  
195 through the use of neural circuitry. Dormant microorganisms retain the ability to maintain viable  
196 cell function at a reduced level of activity and continue to possess enough sensory capacity to  
197 activate an action when reactivated (Bradley 2025; Geiser 2021; Hrvatin et al. 2020; Roelofs  
198 2017). These are simply alternative control methods, not malfunctions.

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

206 **Common signatures across biological systems**

207 The same pattern emerges across biological domains. From an ecological perspective, these  
 208 transitions are significant because they alter how organisms interact with their environment,  
 209 allocate time and energy, and respond to competitors, predators, and conspecifics.  
 210 Often systems will transition to lower cost, lower dimensional states that stabilize their most  
 211 critical variables when capacity limits are reached (see Table 2).

212 **Table 2. How constrained regimes simplify**

Biological Level	Common constraints	Coherence preserving regime	How the regime simplifies	Example Studies
<b>Cells / Microbes</b>	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
<b>Plants / Invertebrates</b>	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 & Baskin 2014; Denlinger 2002; Sakai 2021
<b>Endotherms</b>	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

<b>Vertebrates</b>	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 & Dayan 2022; Carli & Farabollini 2022
<b>Animal groups</b>	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

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214 The lower dimensional state can occur at many scales. Cells become dormant or persistent;  
 215 plants, insects and other invertebrates cease development, and endotherms will decrease their  
 216 metabolic activity by entering torpor or hibernation (Baskin & Baskin 2014; Bradley 2025;  
 217 Denlinger 2002; Geiser 2021; Letten et al. 2024). Invertebrates also display defensive states such  
 218 as tonic immobility (Sakai 2021; Taylor et al. 2023). Vertebrates defend against predators  
 219 through freezing and tonic immobility (Carli & Farabollini 2022; Roelofs 2017; Roelofs &  
 220 Dayan 2022). In addition, all members in a group will define tighter rules of interaction with  
 221 each other and subsequently cluster or polarize (Couzin 2009; Herbert-Read et al. 2011; Sumpter  
 222 2010). All of these states can be described by the joint signature (Table 2).

223 **Evolutionary consequences**

224 If conserving coherence is adaptive, selection should influence both entry into simplified states  
 225 and recovery from them. Thus, the threshold for entering simplified states should vary with  
 226 internal state (e.g., energy, health, developmental stage) and external conditions (e.g., threat  
 227 level, temperature, group density). We predict that populations will evolve differences in when  
 228 they simplify and how extreme those simplified states may become, based on how often demand  
 229 exceeds capacity. This reframes behavioral flexibility as beneficial yet costly (Auld et al. 2010;  
 230 Piersma & van Gils 2010). Organisms that are near their energetic limits may opt for quick entry

231 into simple states (e.g., torpor or habitual behavior), while less constrained organisms will have  
232 sufficient energy resources to allow them to spend longer amounts of time learning or exploring.  
233 The conservation of coherence framework also can predict why individuals within the same  
234 species differ in how they respond to similar constraints. The point at which an organism enters a  
235 simplified regime, and how quickly it makes that transition, are determined by two things: how  
236 much coordination capacity the organism has available, and the coordination demand placed on  
237 it. The various factors that can influence the capacity-demand balance include energetic reserves,  
238 environmental volatility, time-pressure, and individual differences in stress sensitivity and risk  
239 tolerance. These differences can be viewed as reflecting alternative strategies to manage  
240 coherence shaped by environmental and individual variability, rather than being characterized as  
241 just noise (Biro & Stamps 2010; Dall et al. 2004; Sih et al. 2004).

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

251 Under chronic anthropogenic stress, recovery may become slower or fail altogether. Several  
252 plausible mechanisms could drive this. Accumulated allostatic load may degrade the  
253 physiological capacity to re-expand behavioral complexity (McEwen & Wingfield 2003).

254 Persistent environmental cues may prevent organisms from detecting that conditions have  
255 improved. The chronic stress that drives prolonged simplification may simultaneously degrade  
256 the neural and social structures needed to re-expand (Girotti et al. 2024; Woo et al. 2021). As a  
257 result, systems may remain in low-flexibility states, which can have subsequent impacts on their  
258 mobility, learning, social interactions, and ultimately on the larger ecological dynamics (Gaynor  
259 et al. 2019; Lee et al. 2024; Sih et al. 2023; Uchida et al. 2024).

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

## 271 **Testing coherence conservation**

272 Conservation of coherence yields four named, testable hypotheses:

273 **H1 (Coupling–Compression Signature Hypothesis):** As coordination demand approaches or  
274 exceeds coordination capacity, effective degrees of freedom that are available at a given time  
275 should compress along with coupling among the remaining active components reorganizing and  
276 tightening. Simultaneously, critical protected variables remain stable. The aforementioned joint

277 signature can be tested by combining latent-variable dimensionality estimates with time-varying  
278 coupling metrics in multivariate behavioral, physiological, or interaction datasets (Box 1).

279 **H2 (Coordination Threshold Hypothesis):** The stimulus to simplify is not any single stressor  
280 but rather an imbalance between what the system needs to coordinate and the capacity it has to  
281 coordinate at any given moment. Stress and energy shortages can be contributors to the  
282 imbalance, but they are not necessarily required. The critical trigger is that coordination demand  
283 exceeds what the system can manage. As such, increased demands on coordination (e.g. time  
284 constraints, informational load, group density), can push thresholds to an earlier point of  
285 simplification than what would be expected even when there is only a small amount of energy  
286 savings. In contrast, added reserve capacity should enable the organism to maintain its original  
287 level of coordination longer.

288 **H3 (Hysteretic Re-expansion Hypothesis):** There are costs associated with switching into a  
289 simplified regime and rebuilding coordination capacity after exiting said regime. When these  
290 costs are present, recovery from a simplified regime should require more favorable conditions  
291 than entry. The system simplifies at one threshold. It does not re-expand until conditions improve  
292 well beyond that point. The re-expansion of dimensionality and coupling should be slower than  
293 the initial compression. The degree of asymmetry should scale with the depth and duration of  
294 simplification. This can be quantified by comparing entry versus recovery trajectories. We  
295 predict that events of simplification that are brief and shallow in nature (e.g., momentary  
296 freezing) should not display much evidence of hysteresis. On the other hand, long-duration  
297 events of significant simplification (e.g., extended torpor episodes or persistent reduction in  
298 behavioral complexity) are predicted to demonstrate considerable hysteresis. Hysteresis can also  
299 emerge from a different source. The triggering event itself may damage the system's coordination

300 apparatus. This damage can be neurological, social, or physiological (Girotti et al. 2024; Woo et  
301 al. 2021). In such scenarios, the prolongation of asymmetry does not really depend on the  
302 duration of the simplified state. Even a brief episode is predicted to produce prolonged  
303 asymmetry if the infrastructure needed for re-expansion has been compromised.

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

#### 313 **Worked example: applying H1–H4 to torpor**

314 Torpor in small endotherms provides an ideal system for testing all four hypotheses. Continuous  
315 physiological monitoring is feasible in these animals. The transitions between active states and  
316 torpid states are both discrete and repeatable. This makes it possible to observe the same process  
317 multiple times within a single individual. Testing H1 (Coupling-Compression Signature) can be  
318 accomplished by collecting continuous, multivariate physiological data (heart rate, metabolic  
319 rate, body temperature, breathing rate, and activity) with implanted logger devices and then  
320 computing effective dimensionality (e.g., PCA or factor analysis) as the organism is transitioning  
321 into torpor. The prediction is as follows. When an animal enters torpor, the number of latent  
322 modes that are needed to represent the animals physiological state will decrease. The remaining

323 active variables (body temperature and breathing) should become more tightly correlated. The  
324 framework would be challenged if metabolic rate decreased without a concurrent decrease in  
325 multivariate dimensionality or without tighter coupling among remaining variables.

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

336 To test H3 (Hysteretic Re-expansion), one would compare the rate of physiological  
337 simplification during torpor entry against the rate of re-expansion during arousal using the same  
338 multivariate metrics. The prediction is that arousal should be slower than entry into torpor. It  
339 should also require more favorable conditions (Figure 1). The degree of this asymmetry should  
340 increase as torpor bouts become longer or deeper. There are publicly available datasets that can  
341 provide an immediate opportunity to test this. For example, the Chmura et al. (2023) arctic  
342 ground squirrel body temperature archive contains 306 hibernation seasons from 199 individuals.

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

346 **Figure Legends**

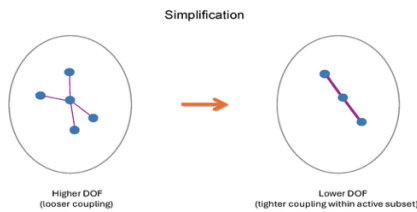
347 **Figure 1 | Capacity-demand mismatch leads to coherence-conserving simplification.**

348 (A) Simplification is predicted to lead to a joint signature. Effective degrees of freedom will  
349 compress while the coupling among the remaining active components reorganizes and tightens.  
350 Other degrees of freedom are either suppressed or decoupled (H1).

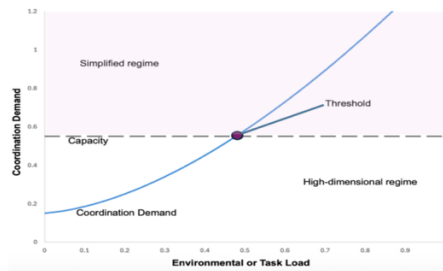
351 (B) Coordination demand increases as either environmental or task loads increase. When  
352 coordination demand exceeds coordination capacity, the system can then transition into a  
353 simplified regime (H2).

354 (C) When switching regimes and rebuilding impose costs, the thresholds for entry and exit differ.  
355 This produces hysteresis - meaning recovery to a more complex regime is slower than the  
356 transition into the simplified regime (H3). DOF, degrees of freedom.

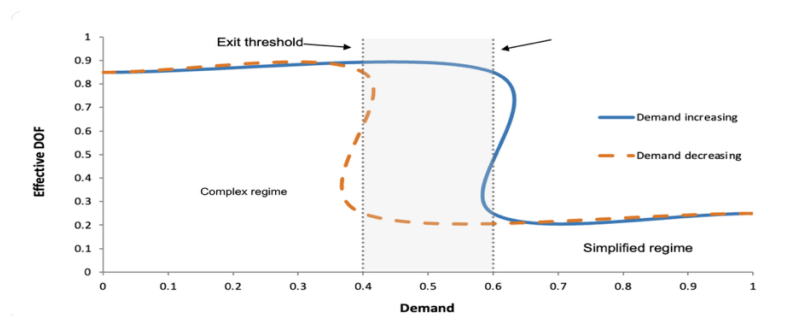
(A) H1: Coupling-compression signature



(B) H2: Coordination threshold



(C) H3: Hysteretic re-expansion



## 358 **Evaluating support across biological scales**

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

369 In plant and invertebrate diapause and dormancy, development and activity arrest while  
370 resources are redirected to protective structures (Baskin & Baskin 2014; Denlinger 2002). Tonic  
371 immobility in invertebrates collapses the behavioral repertoire to a single defensive state (Sakai  
372 2021; Taylor et al. 2023). These cases are consistent with dimensionality reduction, but coupling  
373 reorganization has not been explicitly measured. Protected variable stabilization (structural  
374 integrity, metabolic viability) is implied but not formally quantified in most studies.

375 The most compelling evidence to support a common joint signature would be torpor and  
376 hibernation. Active regulation by identified neural circuits drives torpor entry (Hrvatin et al.  
377 2020). During torpor, three main physiological parameters become tightly coupled (Geiser  
378 2021). Geiser et al. (2014) compared torpor with pathological hypothermia in similar-sized  
379 mammals. Torpor displayed coordinated reduction in metabolic rate and body temperature with  
380 body temperature defended at a lowered set point. Hypothermia did not show this, despite similar

381 reductions in both variables. This is consistent with the framework's prediction that coherent  
382 simplification produces a distinguishable signature. The same study showed that metabolic rate  
383 and body temperature follow different trajectories during entry versus arousal, consistent with  
384 recovery costs predicted by H3. Despite this evidence, relatively little research is available  
385 regarding whether the collapse in dimensionality of high-dimensional behavioral or  
386 physiological repertoires occurs at the same transition point. As a result, this leaves the full H1  
387 signature partially tested.

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

395 Collective behavior research has examined group responses to predator attacks. Research shows  
396 that when predators attack, groups consistently show increased synchronization in addition to  
397 increased group polarization (Couzin 2009; Herbert-Read et al. 2011; Sumpter 2010). Increased  
398 synchronization and group polarization are both consistent signs of increased or tighter coupling  
399 under the framework. However, Storms et al. (2019) identified several different escape patterns  
400 from starling flocks. These findings could be interpreted by some researchers as a maintained  
401 repertoire of escape behaviors instead of an example of dimensionality compression. This  
402 ambiguity further illustrates the importance of performing a dimensionality analysis on the  
403 trajectories of individual animals within a group, rather than measuring the degree of polarized

404 behavior at the group level. Notably, diversity across escape motifs is compatible with the  
405 framework. The key consideration is what happens within any single motif. If the number of  
406 independent movement dimensions drops and the coordination between individuals tightens,  
407 then the joint signature is present. The number of different motifs the flock uses over the course  
408 of an encounter is not relevant. What really matters is what occurs inside each one.

### 409 **What would falsify the framework**

410 Two scenarios would falsify the framework. The first: organisms routinely exceed their  
411 coordination capacity with no increase in failure rates and no reduction in complexity. The  
412 second: the three components of the joint signature (dimensionality compression, coupling  
413 reorganization, and protected variable stabilization) are consistently found to occur  
414 independently rather than co-occurring at the same transition. On the other hand, the fact that an  
415 organism exhibits lower levels of activity, lower rates of metabolism, or lower levels of diversity  
416 in its behavior but has undergone no changes in coupling does not provide evidence for  
417 coherence conservation.

### 418 **Discussion**

419 We have suggested that “emergency modes” across biology may be viewed as coherence-  
420 preserving regime shifts. When an organism’s ability to coordinate complex behavior is limited,  
421 it reduces the number of possible options for action and reorganizes coupling among the  
422 remaining options. This may explain why structurally similar emergency responses appear across  
423 such diverse biological systems, e.g., bacterial dormant states, freezing, torpor, habitual control,  
424 and flocking. For ecology specifically, this framework provides a unifying logic for phenomena  
425 that are currently explained by separate bodies of ecological theory, including state-dependent

426 behavior, critical transitions, energy landscapes, and collective movement, by identifying a  
427 common operational signature that connects them.

428 Considering emergency responses as regulated rather than pathological creates new  
429 considerations regarding when limits become too restrictive, when recovery occurs, and  
430 when repetitive activation of emergency responses could be detrimental. For conservation  
431 practitioners, this framework suggests that management strategies should aim to preserve  
432 recovery windows rather than simply minimizing disturbance intensity, because even  
433 moderate chronic stressors may prevent the re-expansion of complexity if they eliminate the  
434 time or energy required for recovery. This has direct implications for ecological management.  
435 Disturbance thresholds should be defined not only by population-level metrics but also by  
436 behavioral dimensionality measures that capture the coordination state of individuals and groups.  
437 Future work should attempt to clarify when hysteresis shifts from an adaptive buffer to an  
438 evolutionary constraint. It remains to be determined how selection distributes coherence across  
439 organizational levels during simplification. Furthermore, the variation in individual energy  
440 reserves and experience may shape both the initiation and recovery from a state of simplification,  
441 especially given novel anthropogenic stressors that may reduce or eliminate the windows of  
442 recovery on which these evolved mechanisms depend.

443 The presented work views emergency modes as shifts between regimes of function. Each regime  
444 shift carries a joint signature of coupling reorganization and compression of dimensionality (H1).  
445 Furthermore, entry into a new regime occurs when demands exceed current available capacity (a  
446 threshold that can be dissociated from energetic savings) (H2). Recovery can exhibit hysteresis  
447 by way of requiring more favorable conditions for exit from said regime than were needed for  
448 entry (H3). Additionally, individual simplification can enable coherence to emerge at higher

449 organizational levels (H4). Collectively, H1 through H4 provide testable predictions for future  
450 comparisons and experimental design. The major point of distinction is that all three  
451 (dimensionality compression, coupling reorganization and protected variable stabilization) must  
452 occur at the exact same switching point. Merely documenting a decline in some level of function  
453 or activity is not sufficient evidence for the conservation of coherence.

## **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, and stabilizing critical protected variables.

**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.

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