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1 **SOCIAL TIPPING POINTS IN ANIMAL SOCIETIES**
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3

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Abstract

Animal social groups are complex systems that are likely to exhibit tipping points—which are defined as drastic shifts in the dynamics of systems that arise from small changes in environmental conditions—yet this concept has not been carefully applied to these systems. Here we summarize the concepts behind tipping points and describe instances in which they are likely to occur in animal societies. We also offer ways in which the study of social tipping points can open up new lines of inquiry in behavioral ecology and generate novel questions, methods, and approaches in animal behavior and other fields, including community and ecosystem ecology. While some behaviors of living systems are hard to predict, we argue that probing tipping points across animal societies and across tiers of biological organization—populations, communities, ecosystems—may help to reveal principles that transcend traditional disciplinary boundaries.

Keywords: complex system, collapse, cooperation, critical point, extinction, hysteresis, social network, personality, phase transition

60 Many animals are social, and behaviors that occur within social groups can affect individuals,
61 their immediate neighbors, and the overall performance of the society. In some cases, even small
62 changes in external environmental conditions can cause large and abrupt changes to individuals'
63 behaviors, interactions among group members, and therefore how the group functions as a
64 whole. Examples of changing environmental conditions include food deprivation, heat/cold
65 stress, predation risk, or various anthropogenic stressors. Uncovering how and why small
66 perturbations can cause marked and abrupt shifts in group dynamics is important for
67 understanding group functioning, cohesion, and responsiveness to the environment. Here, we
68 introduce the idea of tipping points, which have been used to better understand the dynamics of
69 complex systems in many fields.

70
71 The term *tipping point* was first used in the academic literature by Morton Grodzins to describe
72 racial segregation in US cities²⁵. Ecologists and climate scientists have since used tipping points
73 to better understand shifts in lake eutrophication [1], forest-grass transitions [2], and coral reef
74 states [3]. Although the idea of tipping points has been used as a popular analogy for sudden
75 changes in social systems, the conceptual framework underlying tipping points has not been
76 widely applied to questions in behavioral ecology. In this article we explain what tipping points
77 are, how they have been studied in other contexts, and how the tipping-point framework could
78 provide new insights and predictive power into the study of animal behavior.

79

80 ***What are tipping points?***

81 Tipping points are drastic shifts in the behavior of systems as a result of small changes to the
82 environment⁷. In ecology, tipping points are often referred to as *ecological thresholds* [4-6]. For

83 example, a small change in the temperature of a lake can lead to large shifts in the composition
84 of the lake's community. Other commonly cited examples of ecological tipping points include
85 sudden shifts in species dominance or population collapse [7, 8].

86
87 Similarly, in a social context, *social tipping points* occur when small changes to the physical or
88 social environment result in qualitative changes to group behavior or dynamics [9]. In animal
89 societies, tipping points could be used to explain social transitions such as the onset of collective
90 movements, shifts in group behavior from calm to agitated states, the emergence and
91 disappearance of wars between neighboring societies, the formation or disbandment of
92 cooperation, or the diffusion of new innovations. For instance, African desert locusts rapidly
93 shift between their little-observed solitary state to a swarming plague phenotype. The transition
94 between these states is density-mediated and catalyzed by positive feedback loops between
95 population density, individual activity level, and serotonin-mediated gregariousness [10-12].
96 Thus, small changes in population density can cause large and abrupt changes in both individual
97 state and group dynamics in these locusts.

98

99 **CORE CONCEPTS OF SOCIAL TIPPING POINTS**

100

101 There are several concepts that are needed to apply the conceptual framework of tipping points
102 to social systems. We describe these concepts here using an example. Social spider colonies
103 exhibit a tipping point towards violent infighting in response to heat stress (Figure 1) [13]. When
104 colonies have been in cool temperatures ($<27^{\circ}\text{C}$) they are generally calm and cooperative but
105 transition into infighting at higher temperatures ($>31^{\circ}\text{C}$). However, when the temperature cools,

106 colonies do not immediately return to their calm state upon reaching the critical 30-31°C, but
107 require much cooler temperatures (<27-28°C) to return to their prior state. Thus, at an equivalent
108 temperature, say 29°C, a colony can be characterized by high levels of infighting or calm
109 cooperation, depending on its history. Notably, the shift between calm and agitated colony
110 behavior is mediated by temperature (the external *environmental parameter*), and this shift is
111 conspicuously abrupt, which is diagnostic of social tipping points (Figure 2).

112

113 ***Behavioral States & Environmental Parameters***

114 Many animal social systems are capable of exhibiting multiple qualitatively distinct states. We
115 refer to these as *behavioral states*, such as the calm (blue) and agitated (red) colony states in the
116 spiders in Figure 1. The behavioral state expressed is dictated by the system's dynamics as well
117 as *environmental parameters* such as humidity or temperature (Figure 1, x-axis) and *internal*
118 *parameters* such as metabolic or cognitive factors. For social tipping points, we deem forces
119 acting from outside the group to be *environmental parameters* and forces emerging from within
120 the group as *internal parameters*.

121

122 Environmental parameters can be abiotic or biotic. Most studies on tipping points have examined
123 abiotic drivers [2, 5, 13], whereas relative few have examined biotic drivers, social or otherwise.
124 Abiotic parameters include temperature, light, precipitation, oxygen levels, pH, aridity,
125 anthropogenic noise, tides, and terrain [2, 5, 7]. Biotic parameters can be social (e.g. the number
126 or collective phenotypes of nearby groups) or nonsocial (e.g. predation threat, food availability,
127 or presence of parasites/disease). It is worth noting that many tipping points may be driven by
128 changes in several environmental parameters, such as the combination of heat and UV exposure.

129 Because of the potential combined effects, it is important to consider to what degree phenomena
130 like priming, enhanced lethality of multiple stressors, or cross-tolerance affect group behavior
131 [14-17]. Multiple interacting environmental parameters could be grouped into functionally
132 similar groups based on their properties or because of the shared effects that they have on social
133 groups.

134

135 *Attractors & Basins of Attraction*

136 Up to this point we have presented behavioral states as categorical (such as calm and agitated),
137 but behaviors can actually be more fluid. For example, a spider may be slightly irritated, but not
138 fully agitated. As time progresses, the spider may become calm or agitated, depending on
139 environmental parameters. In this example, the categorical states of calm and agitated are
140 referred to as *attractors* and the set of fluid states that tend towards these categorical states are
141 these attractors' *basins of attraction*. In Figure 1, the solid red and blue lines depict the agitated
142 and calm attractors for a range of environmental parameters (here, temperature). The lighter
143 shaded areas in Figure 1 are the basins of attraction for these two attractors. For intermediate
144 environmental parameters, two attractors exist. At very low temperatures, there is only one
145 attractor, the calm state, while at very high temperatures, only the agitated attractor exists. It is
146 important to emphasize that attractors can appear and disappear, depending on environmental
147 parameters.

148

149 In some cases, environmentally-driven tipping points may be irreversible. For example, events
150 such as the onset of sex change in sequentially hermaphrodites [18], the onset of epidemic
151 spawning in marine invertebrates [19], or the emergence of sexual alates in social insects [20]

152 can be one-way transitions in behavioral state driven by minor perturbations to environmental
153 parameters. In these cases, the former attractors have vanished as a consequence of the system
154 undergoing a tipping point.

155
156 In addition to the presence and number of attractors, the landscape of attraction can vary. In
157 Figure 1, this is depicted with the landscape slices above the main figure which show how the
158 geometry of the basins of attraction are modified as environmental parameters change. In each
159 case, the blue or red balls indicate the attractors at the bottom of wells symbolizing the basins of
160 attraction. The steepness of the walls of these basins of attraction determine the strength of the
161 feedback mechanisms keeping the system in a given state— the steeper the walls of the wells, the
162 quicker the system returns to the attractor state and the more resistant the state is to noise. When
163 the wells are shallow, the system returns to the attractor more slowly and drifts more widely in
164 response to noise [8, 21, 22].

165
166 ***Perturbations***

167 There are two fundamentally different ways that a system can be perturbed. Either the behavioral
168 state or the environmental parameters can be perturbed. To think about the effect of perturbations
169 to the behavioral state, consider a single slice of the landscape of attractors in Figure 1. When the
170 behavioral state is perturbed, envision the system as one of the colored balls that are subject to
171 that particular landscape. If the ball is perturbed enough that it moves to another basin of
172 attraction then the system undergoes a behavioral state change. However, this kind of
173 perturbation is not technically classified as a tipping point because the the transition was not
174 caused by changes to the external environment. In contrast, when an environmental parameter

175 changes, the landscape itself changes, which can alter the existence of attractors and the shapes
176 of their basins of attraction. In Figure 1, this is depicted by the series of slices showing the
177 landscapes governing the basins of attraction. The society moves through a tipping point when a
178 small change to environmental parameters results in a drastic enough modification to the
179 attractor landscape that the society is in an alternative basin of attraction. A critical difference
180 between the two types of perturbations is that when a tipping point occurs, the underlying
181 dynamics have changed and thus the previous regime's models and data are no longer effective
182 in describing the new regime.

183

184 Attractor states are not necessarily advantageous or disadvantageous. For example, social groups
185 might proceed from a relative calm cooperative stable state to disbandment or collapse due to
186 infighting or cheating [13, 23]. However, a system might also switch between two states that
187 perform equally well. The alternative states might even be part of a system's life history. Thus,
188 attractor states are not necessarily evolutionary stable states (ESS) nor adaptive peaks in a fitness
189 landscape, nor do they necessarily have negative consequences for social groups.

190

191 **TIPPING POINTS: FREQUENTLY ASKED QUESTIONS**

192

193 *How can we recognize tipping points?*

194 It can be difficult to recognize that a tipping point has occurred from observational data alone,
195 especially if observations are noisy. However, there are some signatures of tipping points that
196 one may recognize in their system of interest. One signature is that when a tipping point occurs,
197 small environmental changes alter system dynamics so that previous models explaining the

198 behavior of the system built under one regime are no longer predictive when the regime has
199 shifted. Although there are many reasons a model may not explain data, assuming an equilibrium
200 state, a potential indication of a tipping point is when a model explains the data well under some
201 conditions but then fails when environmental parameters change. Other possible signatures of
202 tipping points include flickering between behavioral states and delayed recovery to prior states
203 following perturbation [9].

204

205 *Are critical points and tipping points equivalent?*

206 While the terms *tipping point* and *critical point* are often used interchangeably in the literature,
207 there are distinctions. Loosely, a critical point occurs when the stability of attractors changes.
208 Tipping points require a quantifiable change in behavioral state as a result of minor changes in
209 environmental parameters. This makes all tipping points critical points, but not all critical points
210 tipping points. For example, a system moving through a critical point could have a continuous
211 behavioral state as environmental parameters change, but a system with a tipping point would
212 have a discontinuity in the behavioral state as a function of the environmental parameters (see
213 Figure 2).

214

215 *Is there hysteresis?*

216 The existence of multiple behavioral states allows for the possibility of hysteresis – a concept
217 often linked to tipping points in the literature [24-26]. Hysteresis is a system's lack of
218 reversibility as environmental parameters are varied. A system exhibits hysteresis if reverting the
219 environmental parameters in a system that has passed through a tipping point to the parameters
220 immediately preceding the change does not cause the system to revert to the previous behavioral

221 state. For example, once agitated, spider societies require cooling to far lower temperatures to
222 return them to a calm state (Figure 1). However, not all tipping points will exhibit hysteresis.
223 Tipping points and hysteresis are important to consider because it changes the way that systems
224 should be modeled. In particular, researchers may assume that their systems as reversible in
225 parameter space but, if hysteresis is present, this is not the case.

226

227 *Are there early warning signs of tipping points?*

228 One of the most challenging aspects of tipping points is anticipating when and where they are
229 likely to occur [21, 22, 27]. There are two general predictors whose presence is thought to
230 anticipate an impending tipping point. First, increased variance in a system's internal dynamics
231 is predicted to warn of an approaching tipping point [8, 28]. Destabilized dynamics, large swings
232 and oscillations, or flickering between states all potentially convey that the feedback that keeps a
233 system at one attractor state is weakening, which allows the system to wander farther from the
234 attractor. Second, the speed of recovery to baseline conditions is predicted to decrease when a
235 system is approaching its tipping point [1, 8]. This is because the strength of the feedback that
236 maintain systems in one state decreases as a system moves toward a tipping point, and therefore
237 the rate of recovery is slower. In behavior, there may be other warning signs based on individual
238 level characteristics, or early behavioral outcomes prior to more dramatic state shifts.

239

240 **APPLYING TIPPING POINTS TO ANIMAL SOCIETIES**

241

242 *What can be learned?*

243 Tipping points can inform our understanding of animal societies in a variety of ways. First,
244 documenting tipping points aids our ability to forecast dramatic state shifts in animal behavior
245 [28]. This, in turn, can help us to predict how societies will change in response to environmental
246 parameters, which is required for conservation [29-31]. Second, tipping points convey
247 information about societies' comparative sensitivity to environmental parameters. The presence
248 of abrupt tipping points, pronounced hysteresis, an inability to recover to baseline dynamics
249 following perturbation, and large differences in behavioral states all convey that the internal
250 dynamics driving a system are strongly nonlinear. Additionally, in the presence of tipping points,
251 a system's responsiveness to the environment could appear deceptively small, save for the
252 regions immediately around the tipping point. Many systems therefore may appear deceptively
253 stable, unless one specifically interrogates the limited set of conditions that trigger the system to
254 tip. Third, scrutinizing tipping points and their adaptive function may shed light on how social
255 groups are capable of incredible behavioral flexibility. For example, there is evidence that
256 societies may self-organize or evolve to keep themselves near tipping points, so that they can
257 respond dynamically to new information or environmental challenges [26, 32] and potentially
258 maximize the adaptive advantages of both order and disorder [32]. Fourth, scrutinizing tipping
259 points across tiers of biological organization may help us to determine whether there are
260 generalizable features about their dynamics that bridge tiers of biological organization. Fifth,
261 knowledge of tipping points can help guide researchers as to when a new modeling paradigm
262 may be necessary to predict system behavior.

263

264 *How can social properties affect tipping points in social systems?*

265 Many social properties could influence whether tipping points occur in a society. These include
266 relatedness and group size, presence of keystone individuals, within-group behavioral diversity,
267 group social organization, and groups' prior experience. In this section, we present a hypothetical
268 example and then use it as a lens to pose how social properties might impact tipping points.

269

270 Consider a hypothetical situation where the activity level of a group of marmosets depends on
271 the level of predation risk (Figure 3). When predation risk is low, groups are socially active and
272 have a chance of entering distracted social states. Distracted states may emerge when one
273 individual steals fruit or chases another individual, resulting in a competitive tit-for-tat game.
274 Once initiated, social activity can keep a group in an active and distracted state despite mild to
275 moderate increases in predation risk. However, at a tipping point, even a distracted group will
276 detect heightened risk, and activity will decrease in favor of vigilance. Returning back to social
277 activity will then require a large decrease in predation risk because vigilance renders a group
278 sensitive to even moderate risk. Thus, at some conditions, whether a group will be active or
279 inactive will depend on its prior state (distracted versus vigilant), creating a hysteresis window.

280

281 **Relatedness & Group Size:** Group relatedness and size likely influence tipping points.

282 Relatedness has an impact on a variety of social outcomes, including increased prosocial
283 behavior and decreased exploitation among group members [33, 34]. Thus, social feedback
284 driven by competitive interactions may be less stable between relatives [35]. Kin groups may
285 also be more likely to share information about predation risk even at risk to themselves, for
286 instance, via alarm calls [36, 37]. Group size is also likely to impact the above scenario.

287 Increasing group size could augment competitive interactions and keep individuals in a distracted

288 state for longer. Larger groups may also compete more [38] and this could increase group
289 distraction. Yet, larger groups also have more individuals with which to detect changes in the
290 environment and share information [26, 39]. The net effect of group size may therefore depend
291 on the degree to which social interactions impede individuals' probability of detecting risk and
292 the degree of information sharing.

293

294 **Keystone Individuals:** The presence of influential individuals impacts social tipping points. For
295 instance, the presence of leaders or reconciliatory individuals may prevent tit-for-tat feedback
296 loops from ever starting [40, 41]. In contrast, the presence of particularly aggressive, hungry, or
297 bold individuals could increase within-group conflict [42], thus changing the environmental
298 parameter values that result in a tipping point and the feedback strength that underlies them.

299

300 **Behavioral Diversity:** More phenotypically diverse systems are predicted to be more resistant to
301 and resilient from environmental stress [43, 44]. This, in turn, will shift the timing of tipping
302 points or cause a more linear collective response to environmental changes, i.e., eliminating
303 tipping points altogether. The so-called *portfolio effect* predicts that more diverse groups will
304 have increased odds that at least some constituents can endure novel environments, and
305 therefore, maintain group-level properties [45]. In contrast, homogeneous groups run the risk of
306 all individuals possessing the same sensitivities, making abrupt collective state shifts more likely.
307 However, even for diverse groups, there will be some environmental parameters that cause
308 tipping points in spite of any benefits.

309

310 **Social Organization:** The social structure of our marmoset groups and the space in which the
311 interactions occur also likely effect tipping points [28]. In groups that live in or build structures,
312 such as nests, the geometry of these spaces can determine the kinds of interactions that
313 individuals engage in, the degree of competition among group members, risk of predation,
314 environmental sensitivity, and so on [46]. Nests also provide some homeostatic benefits to their
315 residents [47], which will likely impact the susceptibility of groups to changes in environmental
316 parameters. For groups that live in more open environments, geographical constraints such as
317 rivers, matrix habitat, and localized resources such as fruit trees will impact individuals' position
318 in space and therefore the structure of social networks [48]. Networks, in turn, will shape
319 whether and how individuals interact and influence each other's behavior [49].

320

321 **Prior Experience:** Whether or not social groups have previously been exposed to specific
322 environmental parameters will likely impact their future tipping points [1, 5]. For instance, prior
323 experience with anthropogenic noise might prime a marmoset group and desensitize it to
324 subsequent noise exposure [50]. In the related concept of cross-tolerance [51], experience with
325 one stressor can increase the system's resistance to other stressors. The predicted outcome is
326 similar to that of priming but differs in that stressors can appear interchangeable. A final stressor
327 query is whether the social context of prior experience matters. For instance, the effects of prior
328 experience may depend on whether individuals acquired their experience in isolation, in a group
329 setting, or in a group setting that differs from their present group. The effects of such experiences
330 will likely not be equivalent.

331

332 *Organizing Social Tipping Points*

333

334 **Social Scale:** Social tipping points can be the *additive* outcome of tipping points occurring
335 within each individual (*individual-level*) or the *synergistic* outcome of interactions among
336 individuals (*group-level*). For instance, in *Polistes* paper wasps, colonies may proceed
337 nonlinearly from a quiescent state to responsive state related to increases in disturbance. This
338 could be an additive process, whereby the group response is the sum of each individual wasp's
339 threshold — beyond which it moves from inaction to agitation [52]. Alternatively, a group-level
340 response can be an emergent property, mediated by *synergistic* interactions between group
341 members. For instance, the probability of each wasp entering an agitated state may not be
342 independent from other wasps. The threshold to enter an agitated state may, for example,
343 decrease when neighbors becomes agitated. Experiments that evaluate individual responses in
344 isolation vs. group settings, in groups of various sizes, or in groups with contrasting abilities to
345 interact will be helpful for demonstrating the social scale at which tipping points operate.

346

347 **Metabolic Tipping Points:** A system may pass through a tipping point if environmental
348 parameters drive individuals into alternative metabolic states that affect individuals' behavior.
349 For example, excessive heat can force social ectotherms into collective activity either to cool
350 themselves, like collective fanning behavior in honeybees [53], or to evacuate a nest site entirely.
351 Another potential example of a metabolic tipping point is when excessive cold or aridity causes
352 collective huddling to preserve heat and water in small bodied animals [54]. Metabolic tipping
353 points can be additive or synergistic. For instance, collective huddling behavior may enable
354 groups of homeotherms to remain socially active in environments that exceed the thresholds of
355 each individual [55]. In contrast, social ectotherms may exhibit a more additive response

356 because constituents cannot share metabolic heat [56]. Other examples of metabolic tipping
357 points can occur because of contrasting hunger levels, fat stores, hypoxia, exposure to
358 contaminants, infection status, microbiomes, and so on.

359

360 **Social or cognitive Tipping Points:** Tipping points can also be mediated by social or cognitive
361 parameters, which arise because individuals' perception of their environment has changed. For
362 instance, cautious or flight-prone behavior in one group member might catalyze that behavior in
363 another individual [57]. Alternatively, observer individuals may copy the successful foraging
364 strategies of innovative group mates [58] or the migration routes of older individuals [41, 59].
365 The key ingredient for these transitions is that actors are capable of observing their environment,
366 and then adjusting their behavior accordingly. In principle, social or cognitive state transitions
367 can occur at different social scales as well. For example, each individual may independently
368 learn about its environment, and therefore, the group's behavior changes as the sum of these
369 individual assessments. However, social interactions will often result in an synergistic shift [60].

370

371

372 **WHY STUDY TIPPING POINTS IN SOCIAL BEHAVIOR?**

373

374 Many disciplines already use the ideas and terminology of tipping points to explore the
375 properties of complex systems. This leads one to ask: What strengths can behavioral ecologists
376 bring to the broader study of tipping points?

377

378 First, animal social systems provide us with the opportunity to observe interactions between
379 individual-level and group-level tipping points. Although this review pertains to social tipping
380 points in the dynamics of whole societies, individual organisms are themselves complex living
381 systems with metabolic processes that can undergo tipping points in response to environmental
382 parameters [61, 62]. One can therefore probe the scale at which tipping points occur by
383 evaluating behavioral dynamics in response to environmental drivers when individuals are in
384 isolation versus group settings or across groups of various size. Linking tiers of multi-level
385 tipping points is a problem already faced by the tipping point literature on communities and
386 ecosystems [5, 62, 63], but one fears that the problem of scale (individual versus population
387 versus community versus ecosystem) might be intractably great in such systems. Social tipping
388 points in animal societies might therefore serve as a convenient intermediate ground in which to
389 develop and critically evaluate theory on multilevel tipping points. Such individual versus group-
390 level comparisons do not have clear analogs in the application of tipping points in the physical
391 sciences. This opens the door to new lines of empirical inquiry and theory.

392

393 Second, behavioral ecologists have the ability to create large numbers of experimental systems
394 [64, 65] and manipulate environmental parameters thought to cause tipping points [12], thus
395 allowing cause-effect inferences that elude purely theoretical studies or correlative studies on
396 other living systems. General ecologists have used the tipping point framework to explore
397 contrasting ecosystem dynamics [1], shifts in community composition and functioning [3, 7], and
398 decreases in the viability of imperiled wildlife populations [30, 31]. Engineering such systems or
399 altering them experimentally with a high degree of replication is often impossible or unethical.
400 For many social systems, this is not so.

401

402 Third, using the tipping point framework has the potential to foster crosstalk between the kinds
403 of questions asked by behavioral ecologists and investigators interested in other kinds of
404 complex systems. The notion that similar principles might underlie the presence, severity,
405 timing, and recoverability of tipping points across contrasting physical and living systems is
406 intriguing, and behavioral ecologists are poised to enter this dialogue with precision.

407

408 Finally, animal societies raise our consciousness to the presence of asymmetrical interaction
409 rules, and therefore promise to inspire new kinds of tipping point models, which often assume
410 that interaction rules are simple, symmetrical, and invariant. In animals, we know that
411 individuals differ from each other in their attributes, the ways in which they interact, and the
412 social influence they exert over their groups. While behavioral ecologists have potentially much
413 to gain from the tipping point literature, the intellectual exchange promises to be bidirectional.

414

415

CONCLUSIONS

416

417 Many living systems exhibit drastic state shifts in response to small changes in environmental
418 parameters. We argue here that animal societies—like other kinds of living systems—can be
419 subject to tipping points and that a better understanding of tipping point dynamics can help us to
420 predict changes in sociality and behavior. Behavioral ecologists interested in such dynamics are
421 poised to contribute novel insights, both theoretically and empirically. The insights gleaned from
422 such studies have the potential to generate crosstalk between fields of ecology that typically
423 operate independently. The tipping-point framework in turn offers us (behavioral ecologists) a

424 variety of opportunities. First, the tipping-point framework asks us to re-examine familiar
425 topics—information spread, collective action, group formation/disbandment, etc.—from a new
426 perspective, which opens up new flavors of inquiry. Second, tipping points draw our attention to
427 possible connections between the dynamics of social systems and other kinds of complex living
428 systems — highlighting the opportunity for generalizing principles across tiers of biological
429 organization. Third, the tipping points framework draws our attention to ideas from other
430 subdisciplines of ecology and allows us to critically evaluate these ideas in a new context.
431 Finally, understanding tipping points is of conservation importance for multiple tiers of
432 biological organization, which permits basic researchers to probe tipping points while
433 simultaneously collecting data that could prove useful for applied scientists. This incipient field
434 is therefore ripe for creation and entry, and there is much for us to discover together.

435

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437

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447

448

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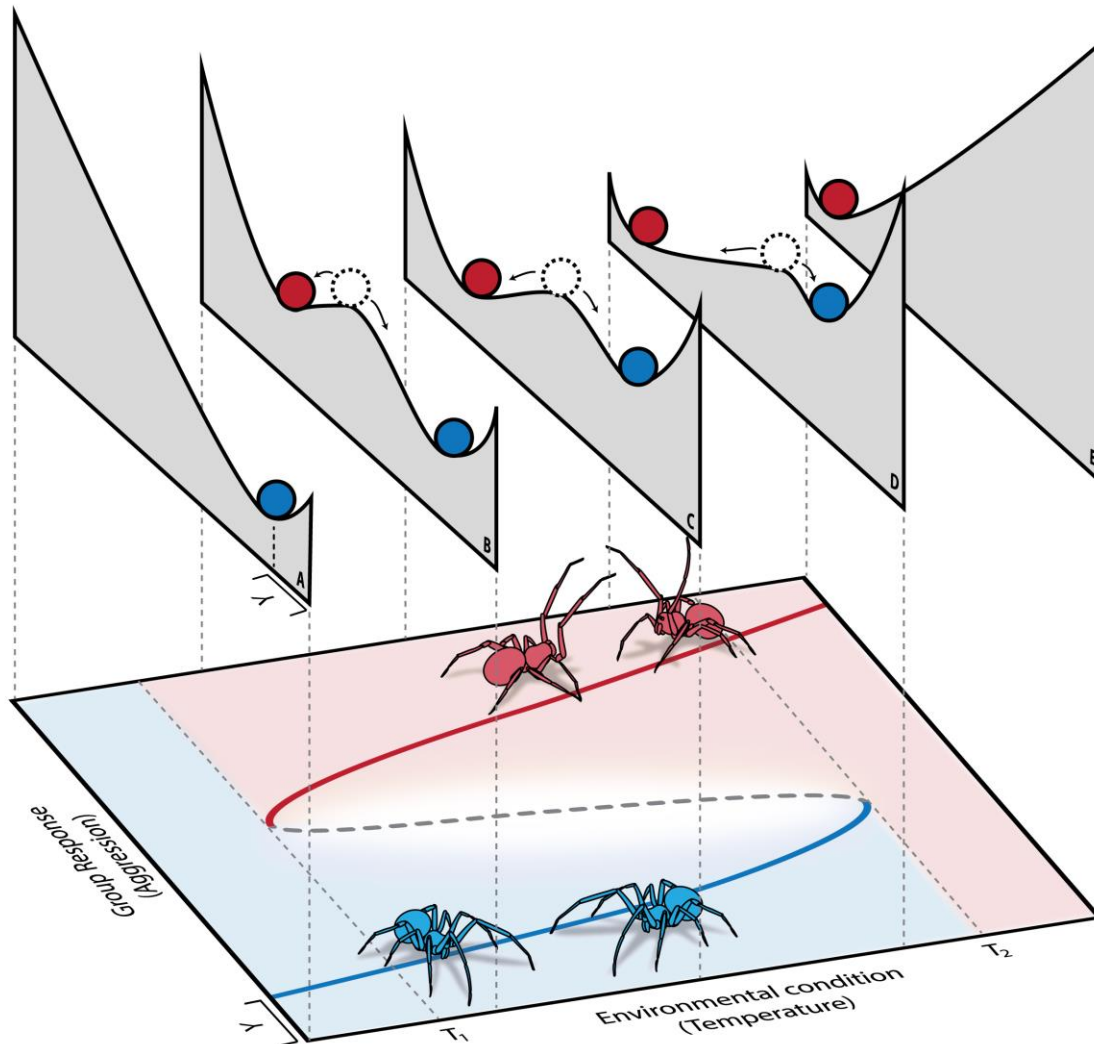
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623
 624 **Figure 1** : A hysteresis window between an environment condition (e.g., temperature) and group
 625 behavior (e.g., degree of infighting). This figure is modeled after a study on within-group
 626 conflict in response to heat stress in social spiders. Groups that have been in an agitated state
 627 (red) tend to remain agitated, whereas calm groups (blue) tend to remain calm. Therefore, there
 628 exists a set of intermediate environmental conditions ($T_1 < T < T_2$) where a group can be either
 629 calm or agitated depending on its historical dynamics. In the lower panel, solid lines represent
 630 stable equilibria states and the shaded regions show their basins of attraction. The dashed line is
 631 an unstable equilibrium, which demarks the boundary between the basins of attraction. The
 632 upper panels (A-E) provide an alternate abstraction of this system: for a given environmental
 633 condition, the group response tends to a low point on the 'landscape'. The bottoms of the troughs
 634 in the upper panels are therefore stable equilibria and correspond to the locations of the solid red
 635 and blue lines in the lower panel (see 'Y' label for an example). Tipping points occur when a
 636 stable equilibrium (solid line/trough) collides with an unstable equilibrium (dashed line/peak)

637 and is eliminated -- at this point the system transitions suddenly to the alternate remaining
638 equilibrium. In this system the tipping points are at T_1 (when the system is in the agitated state
639 and temperature is decreasing) and at T_2 (when the system is in the calm state and temperature is
640 increasing).

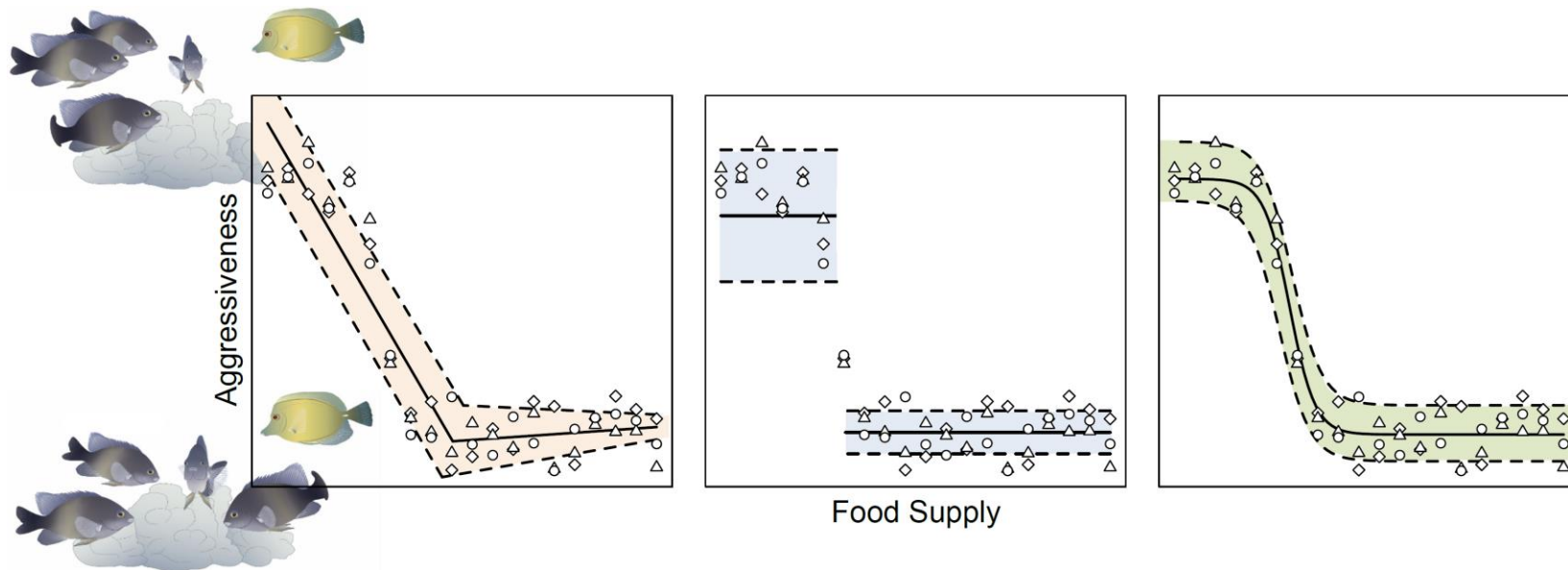


Figure 2: Social tipping points are characterized by an abrupt change in behavior state caused by small changes in environmental parameters. Here, groups of territorial damselfish (brown fishes) may respond with vigilance and inspection (top image) towards intruders or not (bottom image) depending on whether food is limited. One sign of a possible tipping point is a change point in the data, where the data suddenly appears to be nonstationary. In the plot, this is depicted as a sudden change in the mean of aggressiveness (y-axis). If a model for aggressiveness is built for conditions where food supply is low, but then applied to cases where food supply is high, the model will have very large error. This reinforces the point that the old model is no longer valid for the new data if a tipping point has occurred. The three function fitted to the identical data above have all been used to estimate the position of tipping points along environmental gradients, though the center panel reinforces the point that entirely new models may be required to explain system properties before vs. after a tipping point.

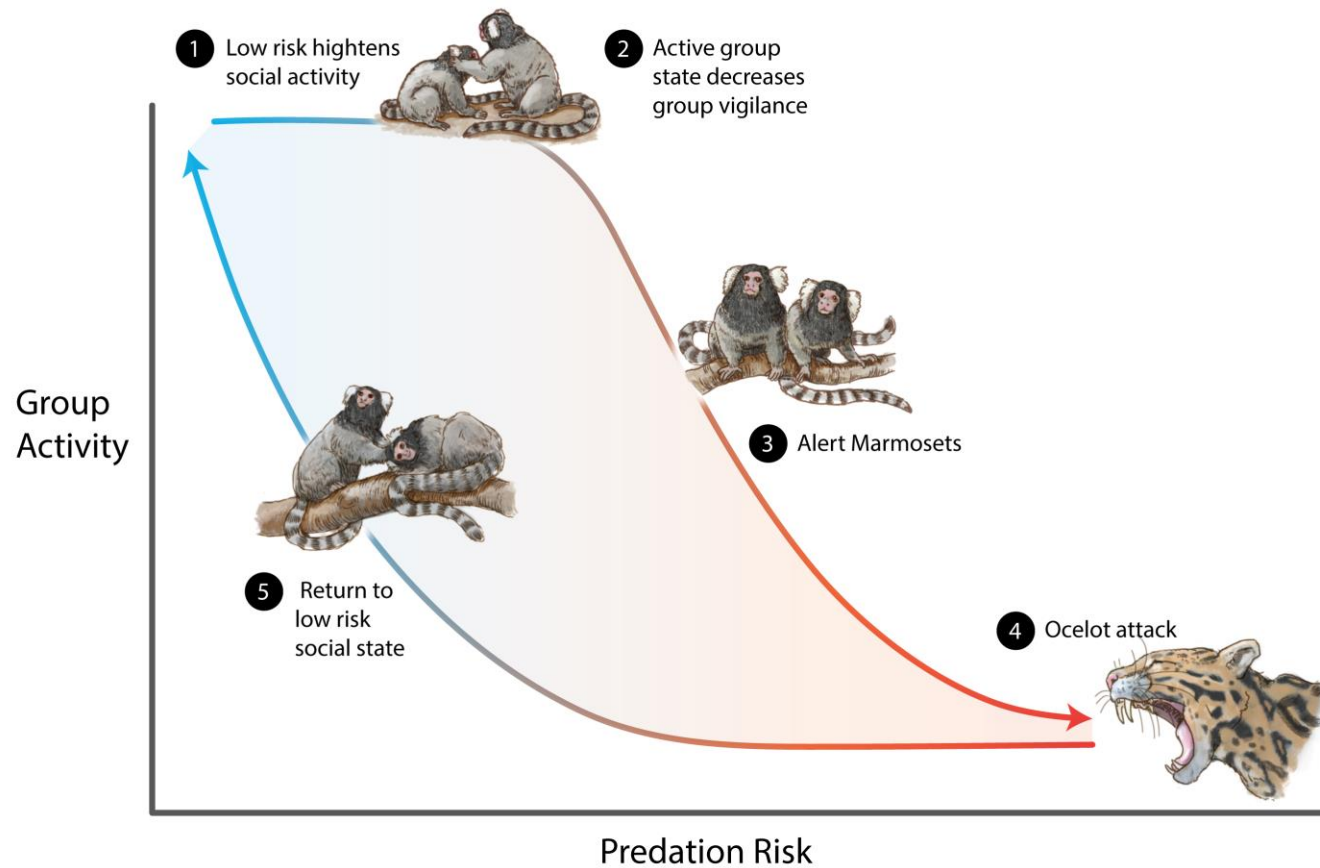


Figure 3: A hysteresis window depicting the relationship between group activity level (y-axis) in association with contrasting levels of predation risk (x-axis). At low levels of predation groups engage in social interactions that heighten group activity (1) but also distract groups from detecting small to moderate levels of predation risk (2). However, at some increased level of predation risk groups decrease activity and become vigilant (3), and extreme levels of risk will cause groups to go into hiding and cease activity (4). As risk dissipates, groups require a much lower level of risk to resume social activity (5).