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SOCIAL TIPPING POINTS IN ANIMAL SOCIETIES

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45 **Abstract**

46 Animal social groups are complex systems that are likely to exhibit tipping points—which are

47 defined as drastic shifts in the dynamics of systems that arise from small changes in

48 environmental conditions—yet this concept has not been carefully applied to these systems. Here

49 we summarize the concepts behind tipping points and describe instances in which they are likely

50 to occur in animal societies. We also offer ways in which the study of social tipping points can

51 open up new lines of inquiry in behavioral ecology and generate novel questions, methods, and

52 approaches in animal behavior and other fields, including community and ecosystem ecology.

53 While some behaviors of living systems are hard to predict, we argue that probing tipping points

54 across animal societies and across tiers of biological organization—populations, communities,

55 ecosystems—may help to reveal principles that transcend traditional disciplinary boundaries.

56 **Keywords**: complex system, collapse, cooperation, critical point, extinction, hysteresis, social

57 network, personality, phase transition

58

59

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 cities[25]. 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   environment[7]. 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°C) they are generally calm and cooperative but

105 transition into infighting at higher temperatures (>31°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

Social Scale: Social tipping points can be the *additive* outcome of tipping points occurring

within each individual (*individual-level*) or the *synergistic* outcome of interactions among

individuals (*group-level*). For instance, in *Polistes* paper wasps, colonies may proceed

nonlinearly from a quiescent state to responsive state related to increases in disturbance. This

could be an additive process, whereby the group response is the sum of each individual wasp's

threshold — beyond which it moves from inaction to agitation [52]. Alternatively, a group-level

response can be an emergent property, mediated by *synergistic* interactions between group

members. For instance, the probability of each wasp entering an agitated state may not be

independent from other wasps. The threshold to enter an agitated state may, for example,

decrease when neighbors becomes agitated. Experiments that evaluate individual responses in

isolation vs. group settings, in groups of various sizes, or in groups with contrasting abilities to

interact will be helpful for demonstrating the social scale at which tipping points operate.

346

Metabolic Tipping Points: A system may pass through a tipping point if environmental

parameters drive individuals into alternative metabolic states that affect individuals' behavior.

For example, excessive heat can force social ectotherms into collective activity either to cool

themselves, like collective fanning behavior in honeybees [53], or to evacuate a nest site entirely.

Another potential example of a metabolic tipping point is when excessive cold or aridity causes

collective huddling to preserve heat and water in small bodied animals [54]. Metabolic tipping

points can be additive or synergistic. For instance, collective huddling behavior may enable

groups of homeotherms to remain socially active in environments that exceed the thresholds of

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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447
448   **Works Cited**

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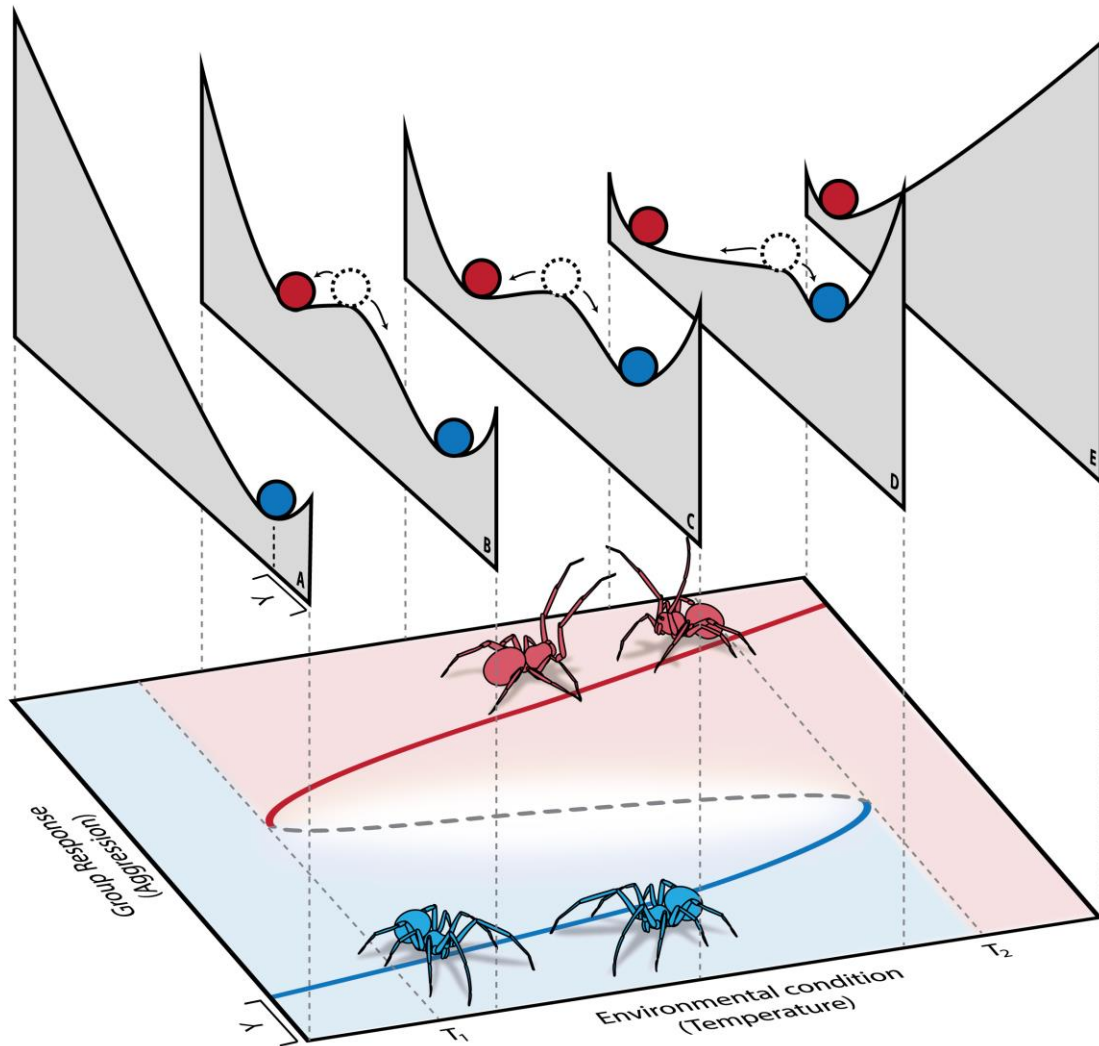
623
624 **Figure 1** : A hysteresis window between an environment condition (e.g., temperature) and group
625 behavior (e.g., degree of infighting). This figure is modeled after a study on within-group
626 conflict in response to heat stress in social spiders. Groups that have been in an agitated state
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).
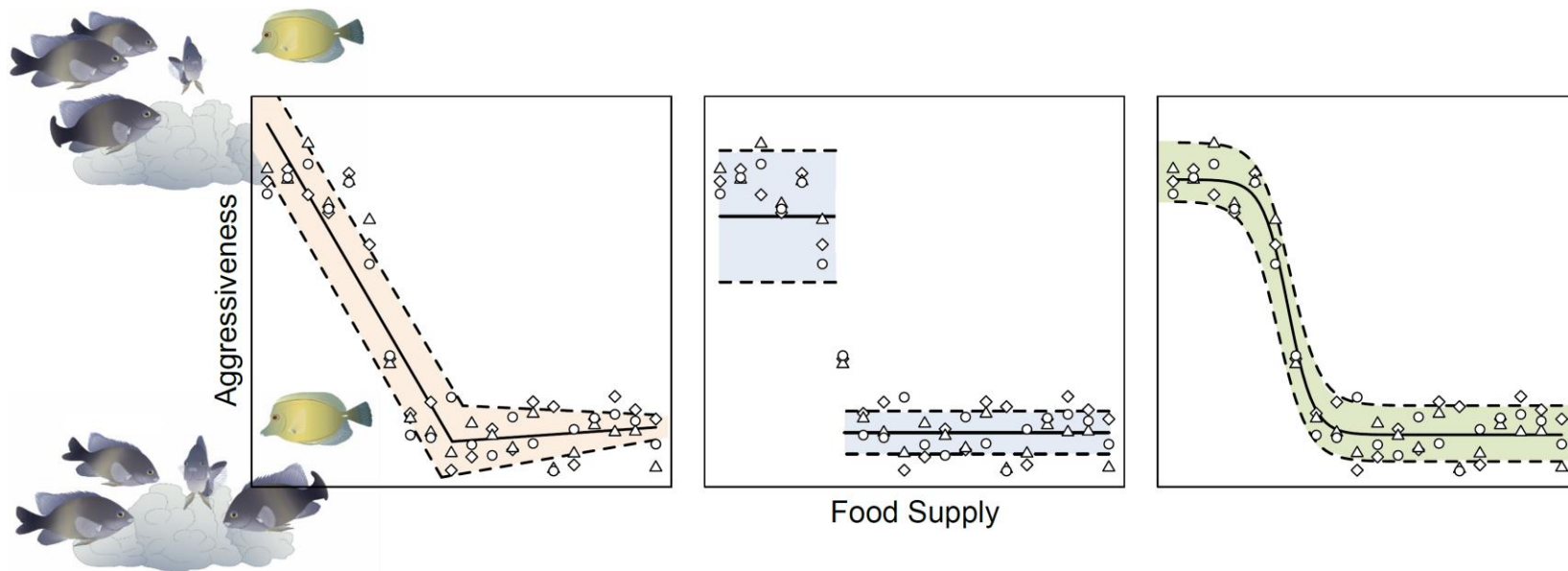
Figure 2: Social tipping points are characterized by an abrupt change in behavior state caused by small changes in environmental parameters. Here, groups of territorial damselfish (brown fishes) may respond with vigilance and inspection (top image) towards intruders or not (bottom image) depending on 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.
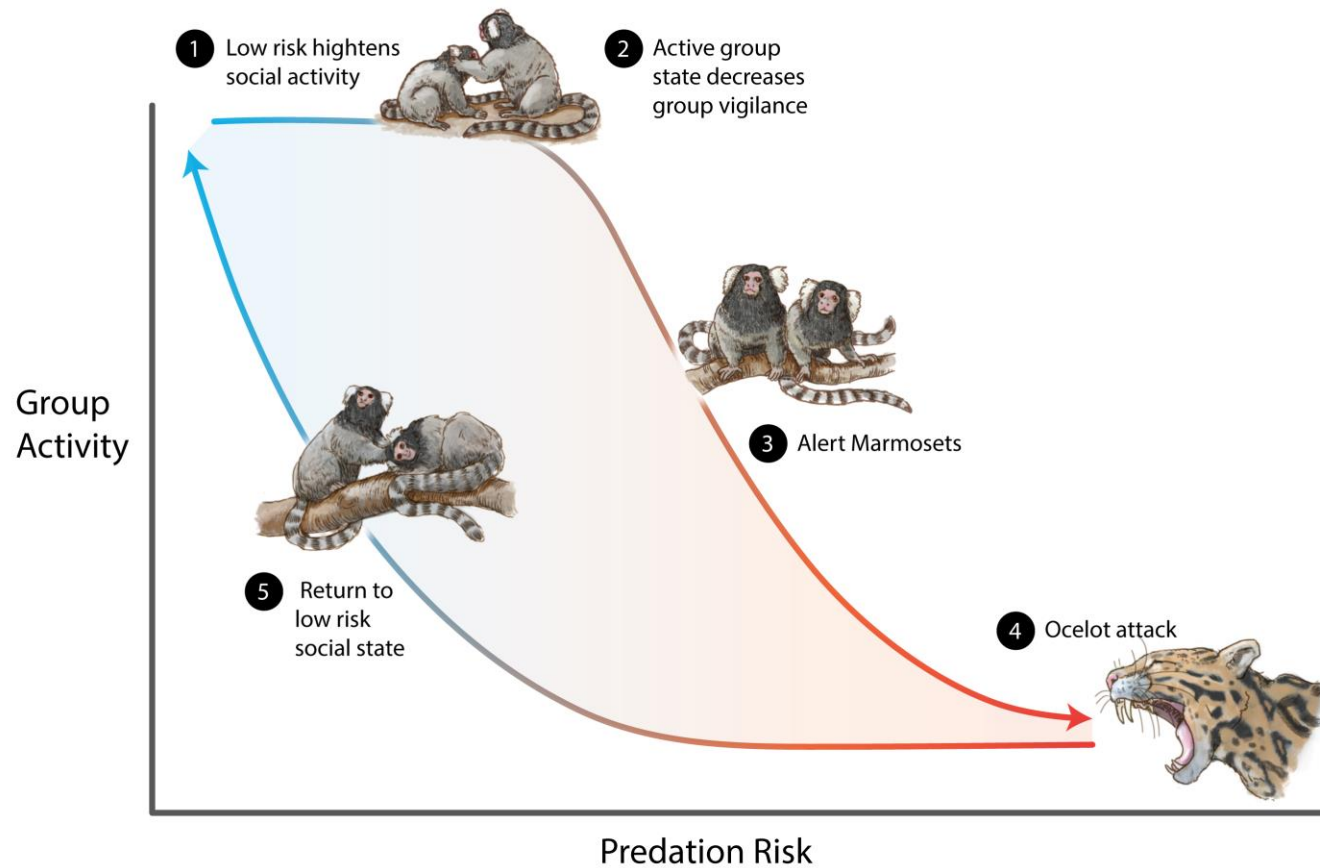
Figure 3: A hysteresis window depicting the relationship between group activity level (y-axis) in association with contrasting levels of predation risk (x-axis). At low levels of predation groups engage in social interactions that heighten group activity (1) but also distract groups from detecting small 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).