

Encounter behaviour shapes ecological distributions

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Abstract

Ecology's foundational models keep only the first moment of the stochastic distributions of encounters. Yet, encounter behaviour (how animals search, aggregate, hide and move) sets the whole distributional shape: zeros, variance, skew and, where particular behaviours build them, heavy tails. That shape decides vital rates, persistence and spatial pattern, because the rates involved are threshold-like and read the tail, not the mean. I argue that departures from the well-mixed Poisson are the rule; that identifiable, measurable behaviours generate them; that where persistence rests on a refuge, a threshold or a self-reinforcing assembly, removing them removes persistence; and that the task ahead is to derive the shape forward from measured behaviours.

The anomaly at the base of ecology

Two of the foundational theories of the life sciences (predator–prey dynamics and the spread of infection) describe the same elementary event, one individual meeting and acting upon another, and both were built on the same device: the law of mass action [1–4]. Rates are products of densities [5]; individuals are interchangeable and mix freely [6–10]. This keeps only the **first moment**. Homogeneous mixing, together with memorylessness and one-at-a-time delivery, does not merely permit a Poisson number of encounters per individual; it *requires* it: variance equals mean, and the distribution carries no information beyond the average. I take the ecological case throughout. The argument carries to transmission, since a contact is itself an encounter, but with its sign set by whose persistence is at stake: counted per susceptible, the zeros shelter hosts; counted per infector, they let chains of infection fade out [11,12].

Those three conditions (homogeneity, memorylessness, single delivery) are precisely the ones behaviour breaks. Animals school, search, hide, migrate and respond to one another [13]; in doing so they make encounter rates differ between individuals and over time, so that some individuals, for spells as long as the counting window, meet many partners while others meet none. They also deliver encounters in bursts and let one encounter change the odds of the next. The consequence is not a small correction to a Poisson world. It is that **departures from Poisson are the rule, and the well-mixed Poisson is the anomaly**: a knife-edge case, requiring the variance to equal the mean exactly, that ecology has quietly mistaken for the default. The commonest departures are over-dispersion and a surplus of zeros; heavier tails appear where particular behaviours build them. My claim goes one step further: these departures are not noise to be averaged away. Where persistence rests on a

refuge, a threshold or a self-reinforcing assembly, as in each case below, removing them removes persistence. The tails are where the ecology lives.

Why the shape, and especially the tail, is the point

For any smooth, non-linear vital rate φ acting on a variable quantity G with mean μ ,

$$\mathbb{E}[\varphi(G)] = \varphi(\mu) + 1/2 \varphi''(\mu) \text{Var}(G) + 1/6 \varphi'''(\mu) \mu_3 + \dots \quad (1)$$

This is the entire sequence of moments (μ_3 is the third central moment), each weighted by a derivative of the rate. By Jensen's inequality, curvature also fixes the sign: where the rate is convex, variation raises its expected value; where it is concave, variation lowers it. Whether dispersion helps or harms is thus set by the shape of the rate, not by the dispersion alone [14–16]. Mass action keeps the first term. Work on intraspecific variation [17–21], non-linear averaging [14,22–24], moment closure and scale transition theory (which carries the correction up to population dynamics from field-measured variances [25–27]) adds the second. In all of these, the variation is an input, whether measured, fitted or assumed; here it is generated by behaviour and derived from measurable primitives, and it is the whole shape, not only the second moment, that is at stake.

It matters because ecological rates are rarely gently curved: they are *threshold-like*. Survival collapses below a reserve floor, recruitment turns on a narrow window, populations fail below a critical density. At a true threshold the series (Eq. 1) itself breaks down, and something simpler takes its place: the expected rate becomes a tail probability, $P(G > \theta)$, the chance of clearing the threshold θ (or, for a floor, of falling short of it). The rate then depends only on that probability, which always lies between 0 and 1, so the argument holds even for tails so heavy that their higher moments, and with them the series, are infinite. And behaviour sets that tail. Over-dispersion, including a mass of zeros, is generic: almost any behaviour yields it. A genuinely heavy upper tail is not: it needs either an already heavy-tailed input carried through the process (heavy-tailed school or patch sizes) or self-reinforcing feedback that builds the tail from within. Both routes are behavioural, which is what makes the tail, not just the variance, the behavioural signal. The shape, and above all the tail, is a first-class ecological quantity, and it is set by behaviour. And the shape matters over time, not only at an instant, because the behavioural states that generate it have duration. Where they last longer than the window over which a vital rate integrates them (a starvation window, a size window, a larval stage), they do not wash out as independent fluctuations would; and the most persistent, differences in size and personality, never average out at all.

Encounter behaviour generates the shape, and it is necessary for persistence

The unifying object is the **encounter**, in its several forms: a predator meeting prey, a larva meeting its first food, an individual meeting conspecifics. Every encounter has two ends,

so the same events yield two distributions, one per party (the predator's catch and each prey's risk, for instance), and behaviour can shape the two quite differently. In each, a small set of behaviours generates a dispersed, often heavy-tailed distribution (Box 1, Fig. 2), and in each the tail is *necessary* in a precise sense: persistence rests on it, so the well-mixed baseline, which removes it, removes persistence too. The three cases share the principle but differ in *which* behaviour generates the tail and *which* tail is load-bearing: the refuge (zero) tail in predation, the survivor (upper) tail in recruitment, the big-group (upper) tail in collective response. Fig. 1 maps the behaviours to the mechanisms that generate distributional shape; Fig. 2 shows the shape each mechanism produces.

Predation and coexistence. Where a predator–prey pair is held together by encounters alone (the textbook case is Nicholson and Bailey's host–parasitoid model [28]), well-mixed encounters let the predator overexploit, and the pair collapses. Behaviour rescues it from both sides. Prey patchiness and schooling deliver encounters in clustered bursts (a compound, two-level cluster process), and area-restricted search clusters them in time. All of this fattens the upper tail of the predator's catch. But the coexistence-critical feature is the opposite one, on the prey's side: reactive schooling and refuge use *cap* the catch and pile up zeros in each prey's risk (a refuge that holds in time rather than reshuffling), so a fraction of prey always escapes. Under Poisson a fraction escapes too, but it is tied to the mean, $e^{-\lambda}$, and vanishes as predation intensifies; the behavioural refuge (the zero tail) fades far more slowly, so the prey persist, and the predator with them. It is the aggregation-of-risk stabiliser (roughly, persistence when the squared coefficient of variation of risk exceeds one [29–34]), here *generated* by behaviour rather than assumed. And because aggregation that merely tracks prey density can destabilise instead [35], what carries the weight is a refuge that behaviour holds open.

Early life and recruitment. Across taxa with a vulnerable juvenile stage (a first-feeding fish larva, an insect larva, a tree seedling), survival is a growth race through a size-dependent mortality window [36–40], so the decisive distribution is the *accumulated condition* across the cohort. Encounter behaviour still builds it. Encounter heterogeneity (the microscale food patches a first-feeding larva must find [41]) is only the seed; the tail is made by self-excitation with a permanent memory (Box 1): a larva that feeds a little better grows faster, gains a bigger gape and sharper vision, and so raises its capture rate not briefly, as area-restricted search does, but for good. A tiny head start compounds into a heavy upper tail in condition (log-normal, and with the starvation floor as an absorbing barrier, heavier still) [42]. Because the mean larva is too slow, often below the threshold outright, *under Poisson almost none clear it; only the upper tail recruits*. The tail is the year class: survivors are drawn disproportionately from the fast growers, though not universally [37,43], and both the trajectory and the tail are legible in their otolith daily increments.

Collective grouping and self-organisation. Whether fish schools, bird flocks or insect swarms, the object here is the *group-size* distribution, itself famously heavy-tailed [44,45]. It is generated by autocatalytic aggregation (joining rises with local density and group size) paired with fragmentation, a coalescence–fragmentation process. Because joining is autocatalytic, a defensive school can assemble *fast* [46,47]; under a linear (Poisson, no-

feedback) rule the group would build too slowly to be there when the predator is. So the feedback is necessary for the response to exist in time, and the defensive benefit (dilution, confusion [48,49]) is strongest in the big schools of the upper tail. Schooling is also the purest *bootstrapping* case: the behaviour generates the very density that accelerates the behaviour.

The three are not independent illustrations. Schooling generates the prey-side dispersion that predators encounter; first-feeding survival *is* escaping predation via the growth race. They are wired together, which is what sets up the emergent synthesis below. In each, though, the message is the same: the necessary tail differs by domain, but the well-mixed baseline removes precisely the part of the distribution on which persistence depends.

Behaviour (measurable primitive)	whose	Heterogeneity Cox: rate varies	Clumping compound: batches	Self-excitation Hawkes: rate rises	Self-inhibition non-Cox: rate falls
Diel vertical migration depth-time position; layer residence	both	●			
Larval food-layer search vertical position; food-layer encounter	consumer	●	○	○	
Collective grouping (schooling) acoustic school-size; NND; reaction distance	prey	●	●		●
Area-restricted search turning rate / tortuosity; giving-up time	consumer			●	
Social facilitation arrival rate of foragers to a feed	consumer			●	
Refuge use / hiding refuge-use fraction; emergence timing	prey	●			●
Territoriality / spacing nearest-neighbour distance; territory size	consumer				●
Patch depletion giving-up density; intake decline	consumer				●

● dominant mechanism ○ secondary □ well-developed family □ maths exists, not yet brought to behaviour (non-Cox)

Fig. 1. Behaviours (measurable) map to the mechanisms that break mass action. Rows are behaviours, each defined by measurable primitives (given in grey); columns are the four mechanisms by which behaviour breaks the well-mixed Poisson (heterogeneity/Cox, clumping/compound, self-excitation/Hawkes, self-inhibition/non-Cox; Box 1). Circles give the proposed mapping (filled for a behaviour's dominant mechanism, open for a secondary one), and the tags give whose behaviour it is (prey, consumer or both), though either party's behaviour can shape both ends of an encounter. Column shading marks how far the ecology has got: green, a well-developed family, routinely fitted to clustered or over-dispersed data; red, the endogenous, self-inhibiting non-Cox case, for which the mathematics exists (Box 1) but has not yet been brought to behaviour. The mapping is not

one-to-one in either direction: several behaviours converge on one mechanism (heterogeneity is fed by four), and one behaviour drives several (collective grouping, boxed, feeds heterogeneity, clumping and self-inhibition, the mechanism selected by context). Deriving each mechanism forward from its measurable primitives is the task this paper sets out; the necessity of the resulting tails is argued in the text.

Box 1 · The behavioural generators of encounter shape

The individual-level process that mass action presupposes yields a Poisson count, with a variance-to-mean ratio (VMR) of 1 and a thin tail. Each mechanism breaks one of its assumptions and reshapes a different feature of the encounter distribution. **Heterogeneity** breaks homogeneity: a rate that varies (in-patch versus out) gives a mixed-Poisson (Cox) process, in its cleanest behavioural form an interrupted Poisson process, with over-dispersion, inflated zeros, and a tail inherited from the mixing distribution (for example, the distribution of patch densities); behaviours are **patch use** and **diel vertical migration**, and the mathematics is mature. **Clumping** breaks single delivery: encounters arriving in groups rather than singly give a compound or Neyman–Scott cluster process, with a tail set by the clump-size (school) distribution; behaviours are **schooling** and **aggregation**, and the mathematics is mature. **Self-excitation** is positive feedback in which one encounter raises the rate of the next, giving a Hawkes process [50] whose tail nears a power law only close to criticality, when each encounter triggers about one more; behaviours are **area-restricted search** and **social facilitation**, and the mathematics is mature. **Self-inhibition** is negative, endogenous feedback: the process’s own history (or, in space, its neighbours) suppresses the rate, giving an inhibitory, non-Cox process that regularises the count; behaviours are **reactive closure**, **refuge use**, **territoriality** and **depletion**. Its simplest forms are standard: depletion is sampling without replacement, and closure after each encounter is a renewal process with dead time. More tellingly, the interrupted Poisson process and reactive closure are one two-state on/off machine, the switch thrown by the environment in one and by the encounter in the other; both are Markovian arrival processes with computable distributions [51–53].

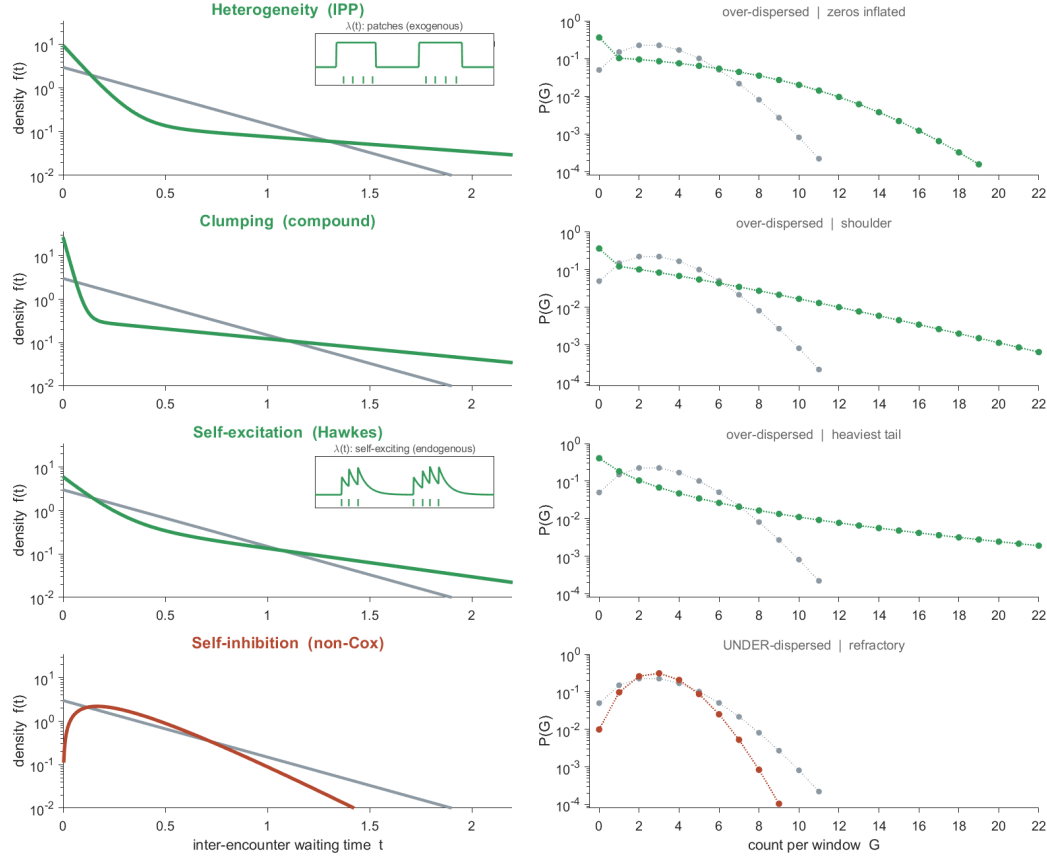


Fig. 2. Each mechanism, two views: the waiting time it produces and the count it produces. Rows are the four mechanisms of Fig. 1. The left panel is the distribution of inter-encounter waiting times; the right panel is the distribution of counts per fixed time-window, G . Together they are the two descriptions of one point process, with the mean rate as their shared summary. In every panel grey is the Poisson null (an exponential waiting time; a Poisson count) and the coloured curve the strong-behaviour case, at the *same mean* (three encounters per window). Rows 1 and 4 are each computed exactly from one two-state process, and row 2 from a compound Poisson process with near-instantaneous clumps; row 3's count uses the cluster representation of the Hawkes process, and its waiting-time panel is schematic. Parameters are illustrative. Left panels are plotted densities on a log axis; right panels are the count distribution as discrete markers with a faint dotted guide. Heterogeneity (an interrupted Poisson process, in-patch versus out-of-patch), clumping and self-excitation all over-disperse the count and fatten its tail; self-inhibition runs the other way, regularising the count (here as reactive closure: row 1's two-state on/off process, with the switch thrown by each encounter). Because heterogeneity and self-excitation share almost the same marginal shape, small insets in rows 1 and 3 show the intensity trace $\lambda(t)$ that distinguishes them: an exogenous on/off telegraph (patches) versus an endogenous, self-exciting saw-tooth. Colours follow Fig. 1 (green, well developed; red, not yet brought to behaviour).

The task: forward-derivation from measurable behaviour

The recurring lesson of Fig. 1 is that the barrier is rarely a missing distribution; it is a missing *derivation*. The mathematics exists for all four mechanisms (Box 1). What is missing, across every domain, is the same thing: a model that takes **measurable behaviours and their measurable derivatives** (swimming speeds, reaction ranges, nearest-neighbour spacings, capture success, the closure window, otolith growth increments, acoustically measured group-size distributions) and **generates** the shape of the resulting distribution, and its tail, forward, rather than fitting a curve to counts. This is the core task this paper sets. It is done analytically where the process is mature and, where it resists analysis, by agent-based simulation of the measured behaviour, reading the shape from the outcome. The reactive-closure switch has never been parameterised from measured behaviour, nor coupled to the predator’s self-excitation [51,53]. The *mapping* of behaviour to the multiplicative growth–feeding process that makes the recruitment tail is under-developed; and even where the coalescence–fragmentation formalism for group sizes exists [44,45], its merge and split *rates* have not been forward-derived from behaviour. The encouraging point is that the key inputs are measurable with existing tools across taxa. Acoustics resolves school-size distributions and closure windows in fish, and aerial imagery resolves group sizes on land; paired predator–prey tracking times the response to an encounter (zebras flee 4–5 km after meeting lions, and some stay away for an extra day [54]); automated tracking records every contact in an ant colony and how it changes after pathogen exposure [55]; and otolith microstructure and tree rings record growth trajectories in the very survivors that constitute the tail [56]. That matters doubly, because a tail is exactly what sparse counts cannot pin down: it must be derived from well-measured primitives, since it can scarcely be fitted. Derivation also separates behaviour from sampling (gut evacuation, gear selectivity and pooling across unlike samples all inflate observed dispersion), because it predicts the shape before the data are seen.

And because those primitives are set by the environment, forward-derivation is also what turns climate change from an after-the-fact correlation into a mechanism one can trace. In the ocean, for example, turbidity sets the reaction range, temperature the swimming speed, oxygen the usable habitat [57–59]; so a warming, murkier, deoxygenating ocean re-tunes the measured behaviours, reshapes the encounter distribution (its mean, but above all its *tail*) and, with it, the persistence, recruitment and pattern that hang on the tail. A model built forward from primitives can therefore say how the shape, and the tail, shift under a given driver, and the shift can be watched *directly in the primitives* (a shortened reaction distance, a slower swim, a compressed layer) rather than inferred from the population after the change has already happened. That is a different kind of forecast: mechanistic and observable at the individual scale, not a correlation fitted to the wreckage.

From encounters to pattern: the emergent synthesis

Placed on a landscape, the mechanisms can act as an **activator–inhibitor** system. Behavioural aggregation (schooling’s autocatalysis, larvae massing at patches, predators’

area-restricted search) is local positive feedback; depletion, reactive closure, escape and density limitation are negative feedbacks that cap and move the clusters. Where the inhibition reaches further than the activation, as when predators drawn to a patch deplete the prey around it, this is the classical recipe for scale-dependent self-organisation [60,61], and the excitation/inhibition duality that runs through the domains, coupled over space, makes patchy mosaics *emerge*. Because the measured primitives fix both ranges, whether it does so is a testable prediction, not an assumption. Spatial pattern is therefore not a fourth mechanism; it is what the encounter-generators do when given room. And that pattern is the substrate of spatial coexistence and biodiversity: the behaviourally generated heterogeneity is what creates refuges, fitness–density covariance and the spatial variance in competition on which coexistence rests [62–66]. So the necessity operates at *two scales*: locally, each of these systems persists through its tail; at the landscape, the same feedbacks build the pattern in which coexistence and diversity reside. Two features keep this distinct from the classical spatial theories, which mostly *assume* their interaction kernels. First, the activator–inhibitor ingredients are the *measured behaviours*, so pattern and diversity can be forward-derived rather than posited. This route has already been opened for mean densities, by deriving predator aggregation from measured area-restricted search and mussel-bed patterning from measured movement [67–69], but not yet for the shape of encounters. Second, the loop closes on itself: the pattern makes the heterogeneity that enables the coexistence that maintains the species that generate the pattern.

Conclusion

Encounter behaviour, by generating dispersed and, where it builds them, heavy-tailed encounters, is what lets predators and prey coexist, larvae recruit and groups form; and the same feedbacks, on larger spatial scales, build the pattern in which coexistence and diversity live. Because the whole chain is built from measurable behaviour, the shape of ecological distributions can be *derived* forward, from what we can measure, rather than assumed. It is also what lets us look forward in time: because the behavioural primitives are precisely the ones a changing ocean acts on (turbidity shortening reaction distances, warming altering movement, deoxygenation compressing habitat), a model derived from them can anticipate how the tails, and with them persistence, recruitment and pattern, will shift, rather than waiting to read the loss from the population after the fact. That derivation, domain by domain and driver by driver, is the programme this paper opens.

Outstanding questions

1. Reactive closure is an interrupted Poisson process whose switch is thrown by the encounter itself. Can that switch be parameterised from measured closure windows, and coupled to the predator’s self-excitation, to yield a behaviourally derived VMR? [51,53]
2. Can the merge and split rates of coalescence–fragmentation be derived from measured joining behaviour and the encounter kernel, rather than fitted to observed group-size spectra?

3. Are tails predicted more reliably when derived from measured behavioural primitives than when fitted to the sparse counts that barely resolve them? And which primitives move them most as the environment changes?
4. How long do the behavioural states that generate dispersion persist, relative to the windows over which vital rates integrate them, and which behaviours are persistent enough never to average out?
5. When does density regulation *damp* the behaviourally generated tails, and when does it *amplify* them into extinction or release?
6. Whose persistence does a given dispersion serve? The same encounter zeros that shelter prey and hosts let chains of infection die out: when does behaviour-generated dispersion favour one party over the other, and when does that asymmetry stabilise an interaction rather than destabilise it?
7. Under what conditions do the activator–inhibitor feedbacks of encounter behaviour generate spatial pattern strong enough to underwrite coexistence, and can this be measured rather than assumed?

Glossary

- **Compound (cluster) process:** encounters arrive in clumps: a Poisson number of clumps, each delivering several encounters at once or in quick succession.
- **Cox (doubly stochastic) process:** a Poisson process whose rate varies at random, driven by something other than the encounters themselves, such as moving in and out of patches.
- **Hawkes (self-exciting) process:** a process in which each encounter transiently raises the rate of further encounters, producing cascades.
- **Heavy tail:** an upper tail that decays more slowly than exponentially, so that extreme values are far more likely than under Poisson.
- **Interrupted Poisson process:** the simplest Cox process, with encounters at a constant rate while ‘on’, none while ‘off’, and random switching between the two.
- **Jensen’s inequality:** for a convex function the mean of the function exceeds the function of the mean; for a concave function the reverse holds.
- **Markovian arrival process:** a point process driven by a hidden state that can switch by itself or be switched by the events; it contains the interrupted Poisson process and reactive closure as special cases.
- **Renewal process with dead time:** after each event the process is shut for a refractory period before the next event can occur.
- **Scale transition:** the change in dynamics when a non-linear local rule is averaged over variable individuals or places.
- **Squared coefficient of variation (CV^2):** the variance divided by the squared mean; for risk across individuals, $CV^2 > 1$ is the classical criterion for aggregation to stabilise a host–parasitoid pair.

- **Variance-to-mean ratio (VMR; index of dispersion, Fano factor):** the variance of a count divided by its mean; it is 1 for Poisson, above 1 when over-dispersed and below 1 when under-dispersed.

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