of WIMPs coupling to electrons through axial-vector interactions.

It has been suggested that multicomponent models with light dark matter particles of ~MeV/c^2 mass might explain the DAMA/LIBRA modulation (27). A specific example of such a model, kinematically mixed mirror dark matter (28), was shown to broadly have the right properties to explain the DAMA/LIBRA signal via dark matter–electron scattering. In this model, dark matter halos are composed of a multicomponent plasma of mirror particles, each with the same mass as their standard model partners. The mirror sector is connected to the normal sector by kinetic mixing of photons and mirror photons at the level of ~10^{-9}. Whereas mirror hadrons would not induce nuclear recoils above threshold, mirror electrons ($m_{e'} = 511 \, \text{keV}/c^2$) would have a velocity dispersion large enough to induce ~keV electronic recoils.

The differential scattering rate of mirror electrons is proportional to $gNn_{e'}$, where g is the number of loosely bound electrons, assumed to be those with binding energy <1 keV (28); N is the number of target atoms; and $n_{e'}$ is the mirror electron density. To compare DAMA/LIBRA directly with XENON100, we apply a constant scaling of $g_{Xe}/g_{NaI} \cdot N_{xe}/N_{NaI} = 0.89$ to the DAMA/LIBRA spectrum and use the same procedure as in the case of axial-vector coupling: We again consider only the DAMA/LIBRA modulation signal, use the 70 summer live days, model scintillation in liquid xenon as described previously, and simply compare integral counts up to the point where the DAMA/LIBRA signal falls below the expected average XENON100 background data rate (at 13 PE), without background subtraction. This excludes the DAMA/LIBRA signal as kinematically mixed mirror dark matter at 3.6σ confidence level.

The third model we consider is luminous dark matter (29), featuring a dark matter particle with a ~keV mass splitting between states connected by a magnetic dipole moment operator. The dark matter particle upscatters in the Earth and later de-excites, possibly within a detector, with the emission of a real photon. The experimental signature of this model is a mono-energetic line from the de-excitation photon. A mass splitting δ = 3.3 keV provides a good fit to the DAMA/LIBRA signal (29), which would be explained as scattering of a real photon from the de-excitation of a ~GeV/c^2 dark matter particle that is heavy enough to undergo upscattering, but light enough to evade detection in other direct searches.

This signature is independent of the target material; only the sensitive volume affects the induced event rate. As rates are typically given per unit detector mass, scaling to volume is inversely proportional to target density. We thus apply a constant scaling factor to the differential rate in DAMA/LIBRA, which is the ratio of the target densities $\rho_{NaI}/\rho_{Xe} = 1.29$, in order to compare it to XENON100. Proceeding as in the previous two cases, we exclude the DAMA/LIBRA signal as luminous dark matter at 4.6σ confidence level. Together with the other two exclusions presented above, this robustly rules out leptophilic dark matter interactions as a cause for the DAMA/LIBRA signal.

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ECOLOGICAL THEORY

A general consumer-resource population model

Kevin D. Lafferty,[1]* Giulio DeLeo,[3] Cheryl J. Briggs,[2] Andrew P. Dobson,[4,5] Thilo Gross,[6] Armand M. Kuris[2]

Food-web dynamics arise from predator-prey, parasite-host, and herbivore-plant interactions. Models for such interactions include up to three consumer activity states (questing, attacking, consuming) and up to four resource response states (susceptible, exposed, ingested, resistant). Articulating these states into a general model allows for dissecting, comparing, and deriving consumer-resource models. We specify this general model for 11 generic consumer strategies that group mathematically into predators, parasites, and micropredators and then derive conditions for consumer success, including a universal saturating functional response. We further show how to use this framework to create simple models with a common mathematical lineage and transparent assumptions. Underlying assumptions, missing elements, and composite parameters are revealed when classic consumer-resource models are derived from the general model.

Malthus (1) first postulated that resource availability constrains consumer population growth in 1798. Since then, there have been about 1000 host-parasitoid, 3000 parasite-host, and 5000 predator-prey modeling studies, all describing interactions between consumers and their resources [summarized in (2, 3)]. Here, we show how the seven state variables and associated transitions used in classic models can comprise a general consumer-resource model that underlies the structure of all ecological food webs (4). The general model describes population rates of change for searching, or questing, (Q); handling, or attacking, (A); and feeding or consuming (C) activity states of consumers and the

corresponding susceptible (S), exposed (E), ingested (I), and resistant (R) states for resources (Fig. 1; mathematical formulation summarized in Table 1 and further detailed in tables SB1 to SB3). Transitions among states are represented by generalized functions (5) (e.g., C_{aq}, the contact/attack generalized function) that are placeholders for potential formulas that describe biological details (e.g., the mass-action equation βQS). A general model solves several problems. First, its standard structure clarifies mathematical relationships among consumer strategies and ecological generalities, such as a universal saturating functional response. Second, the general model is a common framework for building simple models with transparent assumptions. Third, deriving classic models from a general model illustrates the extent to which past results have depended on simplifying assumptions about underlying biology.

The general model is not intended to describe any particular biological system; instead it must be first tailored to a generic consumer strategy. The full range of these strategies can be modeled with combinations of eight operationally defined criteria (table SC1). These criteria include the number of attacks per questing consumer (i.e., several for a lion, one for a juvenile hookworm), intimacy with the resource (e.g., consumers can die if their resource dies, a trait that correlates with the relative time spent consuming—such as for pathogens and macroparasites), and effects on the fitness of the resource (i.e., eventually fatal for a parasitoid wasp, blocked reproduction for a rhizocephalan barnacle, intensity-dependent morbidity for the human roundworm) (6). We also distinguish consumers, such as vultures or plants, that feed on living resources from those that feed on nonliving resources. These taxon-neutral strategies differ from other familiar consumer categorizations such as carnivore and herbivore in that they do not consider the taxonomy of the consumer or of the resource.

Using these criteria, we specify the general model to four familiar consumer-resource model types (predators, pathogens, parasitoids, and macroparasites) and seven additional distinct consumer strategies that are not often modeled, but for which there is a distinct model structure (parasitic castrator, autotroph, decomposer, detritivore, scavenger, social predator, and micropredator) (6). We illustrate relationships in model structure with a consumer-resource model "phylogeny" (Fig. 2A) and a principle-component analysis (fig. SC1 and tables SC1 to SC4). The major graphical separation among generic models cor-
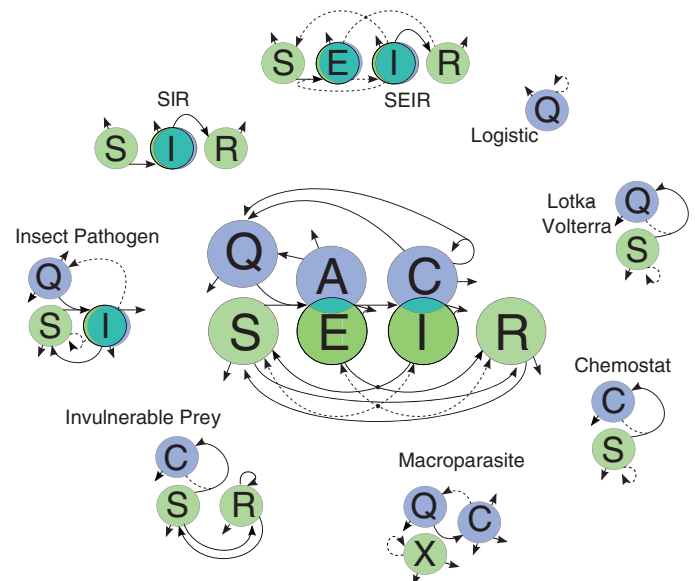
responds to multiple or single attacks by the questing state (e.g., predators versus parasites; Fig. 2A). Specifically, predators can survive a failed attack and return to questing after a meal, whereas parasite questing stages die if they fail to infect a host. Consumer-resource models can be further differentiated by life-history characteristics. For example, parasite models cluster according to a single intimate (i.e., consumer lives with its resource) attack on a resource, whereas predator models cluster around multiple nonintimate attacks. Micropredator models (including mosquitoes, some leeches, and many herbivores that eat parts of plants) differ because they make repeated nonlethal attacks on their resources. That is, the "micro" in micropredator refers to the size of the meal relative to the size of the resource, not to the size of the consumer. As a result, micropredators act like predators but affect their resources like parasites. In both the parasite and predator clusters, generic models vary according to whether more than one consumer can attack an exposed resource and whether the resource is living or nonliving. The general model thus makes it possible to compare and contrast generic consumer strategies.

The general model reveals new insights into consumer-resource dynamics. One measure of dynamics is the expected number of offspring produced by an individual consumer encountering an unexploited resource population, otherwise known as R_0 (7). R_0 defines the conditions under which a consumer can invade a resource population. For the 11 consumer strategies, R_0 increases with resource contact, attack success, handling rate, resource conversion rate, and consumer life span (table SD1). It has long been known that constraints on resource handling

(functional responses) (8) destabilize predator-prey dynamics by allowing prey to be released from their predators (3). Correspondingly, R_0 for all consumers, including parasites, saturates with resource density because contact rates asymptote (table SD2 and Fig. 2B). A saturating functional response prevents consumers from persisting on resources of low nutritional value even as those resources approach infinitely high densities. The universal half-saturation resource density of D_q/β (death rate of questing stages divided by per-capita contact rate; supplementary text D) implies that such constraints are greatest for consumers with durable and efficient questing states (characteristics more likely to describe a predator than a parasite). Regardless, an asymptotic contact rate means that all parasites are along a continuum from density-dependent to frequency-dependent transmission (9). Furthermore, the structure of R_0 differs among predators, micropredators, and parasites (boxes in Fig. 2; table SD1), indicating how different consumer strategies should be favored by longevity and body size (6).

Consumers have five distinct types of ontogenetic diet shifts that require composites of the general model (Fig. 3). Specifically, parasites with complex life cycles can have three types of ontogenetic diet shifts among life stages: (i) sequential host (schistosome), (ii) trophically transmitted (fish tapeworm), and (iii) vector transmitted (malaria). Such host shifts can correspond to different consumer strategies (e.g., for schistosomes, a parasitic castrator followed by a macroparasite). Most predators (e.g., dragonflies, amphibians, ant lions) have niche shifts related to metamorphoses that lead to nonoverlapping diets. In some cases, an ontogenetic diet shift accompanies a change between predation and

[1]Western Ecological Research Center, U.S. Geological Survey, Marine Science Institute, University of California–Santa Barbara, Santa Barbara, CA, USA. [2]Ecology, Evolution and Marine Biology, University of California–Santa Barbara, Santa Barbara, CA, USA. [3]Hopkins Marine Station Woods Institute for the Environment, Stanford University, Stanford, CA, USA. [4]Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA. [5]Santa Fe Institute, Hyde Park Road, Santa Fe, NM, USA. [6]Department of Engineering Mathematics, University of Bristol, Bristol, UK.
*Corresponding author. E-mail: klafferty@usgs.gov

Fig. 1. Diagram of the general consumer-resource model and its relationship to classic consumer-resource models.

Circles are state variables for questing (Q), attacking (A), and consuming (C) consumers (Y in blue/dark shading), under which are susceptible (S), exposed (E), ingested (I), and resistant (R) resources (X in green/light shading). Overlapping circles indicate that the values of the corresponding variables might be identical under some circumstances. Arrows represent transitions (of individuals or biomass) among states. A dashed line represents production or conversion (e.g., births), whereas a solid line is a transition from one state to another (implying no change in numbers from one state to the next). A solid node at intersecting arrows indicates consumer states might give birth to consumers in each state.

parasitism. In particular, the predatory (or sometimes nonfeeding) adult lays its eggs on its offspring's food. These "protelean" consumers include some macroparasites (e.g., bot flies, leaf miners), decomposers (e.g., blow flies) and many parasitoids (e.g., ichneumonid wasps, tachinid flies). Furthermore, although predators rarely engage in facultative parasitism, predators can be part-time micropredators (e.g., some leeches), scavengers (e.g., crows), or social predators (e.g., coyotes). In contrast, parasites almost always adhere to a single consumer strategy within a life stage. Other relevant complexity can be incorporated into models by subdividing states into classes (e.g., sex, size, genotype) and modifying the transitions among states to model other interspecific interactions (e.g., pollination by nectar feeders, phoresy). Ultimately, coupling consumer-resource models for multiple species leads to food-web models.

The general model is a common starting point for building simple models that have the desired balance of tractability, elegance, and analytical solutions versus a more explicit embrace of ecological mechanisms, fit to data, and accurate predictions (fig. SE1). To simplify the general model (4), the first step (as above) is to specify a generic consumer life-history strategy (table SC1; in supplementary text E we use an autotroph as an example). The next step is to delete state variables when, for instance, there is not a resistant resource state; or, for most pathogens and predators, the ingested resource is redundant; or, as for some infectious disease models, human population size is assumed constant. Then, the generalized functions need to be formulated with meaningful parameters. Once functions are formulated, time-scale separation can be used to subsume state variables by substituting an ephemeral state with its quasi-equilibrium (8). For example, a pathogen's microscopic infective stages (Q and A) can be assumed to quickly reach an equilibrium that can be absorbed into the C equation in Table 1. However, a consequence of assuming that states quickly reach equilibria is to increase the likelihood of local asymptotic stability (i.e., by reducing the dimensions of the system that can vary). This overestimate of stability increases with the time spent in the ignored state. Further assuming that some rates are fast relative to others can help simplify model structure (at the risk of simplifying dynamics), whereas composite parameters can be used to reduce the number of terms for presentation (at the risk of obscuring their meaning). Finally, there is the matter of which states to track. For instance, the abundance of subsumed states might or might not be counted as part of a consumer population (but failing to track them will underestimate the consumer population). Once these steps are complete, the resulting simplified model contains the legacy of the simplifying steps, thereby giving explicit meaning to composite parameters and derived functions.

When reducing the general model to the classic models that inspired our work, we find

that they often subsume ephemeral states (e.g., the attacking and consuming states in the Lotka-Volterra model or the free-living stages in host-pathogen models) or exclude them, or both. For instance, the Lotka-Volterra predator-prey equations, the foundation of most dynamic food-web

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Table 1. Model notation summary (supplementary text B). Dual subscripts indicate transitions between, or production to and from, states (e.g., H_{qc} is the transition rate from the consuming state to the questing state); an x or y subscript is for all states within a resource or consumer species, respectively (e.g., R_{sx} is the transition rate into the susceptible state from all resource states combined); single subscripts indicate state-specific nontransition (e.g., mortality) rates.

The general model in words

Consumer (Y)

d(Questing)/dt = Birth − Death + Handling I + Killing + Failure − Contact

d(Attacking)/dt = Contact − Death − Handling E − Resource Death − Failure

d(Consuming)/dt = Birth − Death + Handling E − Resource Death − Killing − Handling

Resource (X)

d(Susceptible)/dt = Birth − Death + Recovery + Vulnerability − Invulnerability − Contact

d(Exposed)/dt = Birth − Death − Recovery − Handling E + Contact

d(Ingested)/dt = Birth − Death − Recovery + Handling E − Killing

d(Resistant)/dt = Birth − Death + Recovery − Vulnerability + Invulnerability

With general function abbreviations

$dY_q/dt = B_{qc} − D_q + m(1-f)H_{qc} + mfA_iK_iY_c/X_i + mF_a − C_{aq}$

$dY_a/dt = C_{aq} − D_a − H_{ca} − j_aD_eY_a/X_e − F_a$

$dY_c/dt = B_{cc} − D_c + H_{ca} − j_cD_iY_c/X_i − A_iK_iY_c/X_i − m(1-f)H_{qc}$

$dX_s/dt = B_{sx} − D_s + R_{sx} + V_{sr} − I_{rs} − C_{aq}$

$dX_e/dt = B_{ex} − D_e − R_{xe} − H_{ca} + C_{aq}$

$dX_i/dt = B_{ix} − D_i − R_{xi} + H_{ca} − K_i$

$dX_r/dt = B_{rx} − D_r + R_{rx} − V_{sr} + I_{rs}$

State variables

$X = \sum X$ total resource population size

X_s = Susceptible (and unattacked) resources

X_e = Exposed resources

X_i = Ingested (i.e., infected) resources

X_r = Resistant resources

$Y = \sum Y$ total consumer population size

Y_q = Questing consumers

Y_a = Attacking consumers

Y_c = Consuming consumers

Generalized functions

A_i = aggregation of consumers per resource

B_{cc} = vertical transmission of a consumer

B_{qc} = birth (production) of new questing individuals

B_{xi} = birth of ingested resource (e.g., B_{ii} relates to vertical transmission above)

$B_{ex} = (B_{es} + B_{ee} + B_{ei} + B_{er})$

$B_{ix} = (B_{is} + B_{ie} + B_{ii} + B_{ir})$

$B_{rx} = (B_{rs} + B_{re} + B_{ri} + B_{rr})$

$B_{sx} = (B_{ss} + B_{se} + B_{si} + B_{sr})$, or $= f(X_0)$ for consumers that feed on resources that do not reproduce (carcasses, nutrients)

C_{aq} = contact/attack between questing consumers and susceptible hosts

D = background death

F_a = attacking failure

H_{ca} = handling by the attacking state

H_{qa} = return to questing after attacking (see supplementary text E)

H_{qc} = handling by the consuming state

I_{rs} = resistance

K_i = mortality/removal rate of an ingested resource

R = recovery of ingested resources

V_{sr} = susceptibility to consumers

Auxiliary parameters (1 = yes, 0 = no)

f = consumer kills the host as part of feeding

j = joint death (i.e., intimacy) between consumer and resource
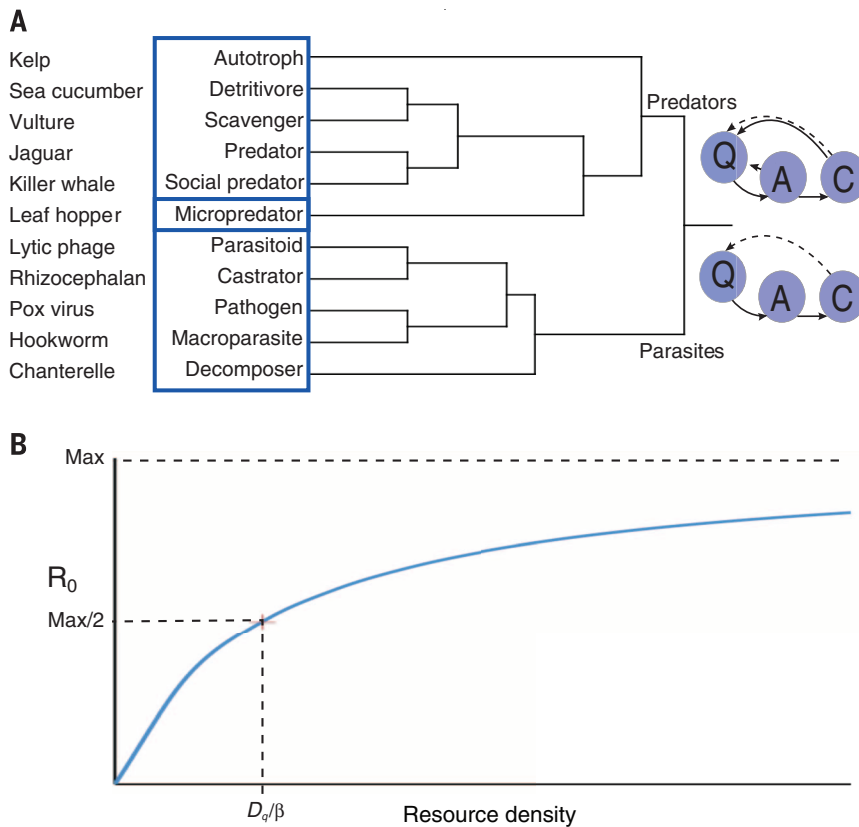
m = multiple attacks by questing state

A

B

Fig. 2. Ten consumer strategies clustered according to similarities in model structure (supplementary text C). (**A**) Dendrogram using average clustering, including example, general consumer strategy, R_0 category (blue squares), and model diagram. (**B**) Despite differences in structure, R_0 saturates with resource density for all consumer strategies (supplementary text D) with a universal half-saturation resource density of D_q/β, or the ratio of deaths per contact for the questing state.

Fig. 3. Consumer-resource models with complex life histories.

Many species change diet from one life stage to the other. This results in at least five distinct model structures, each of which has, at its core, a general model (fig. 3). For instance, protelean life histories add a new transition; specifically, the questing state returns to questing after an attack (H_{qa}). Furthermore, some protelean consumers have a free-living consumer stage (others do not).
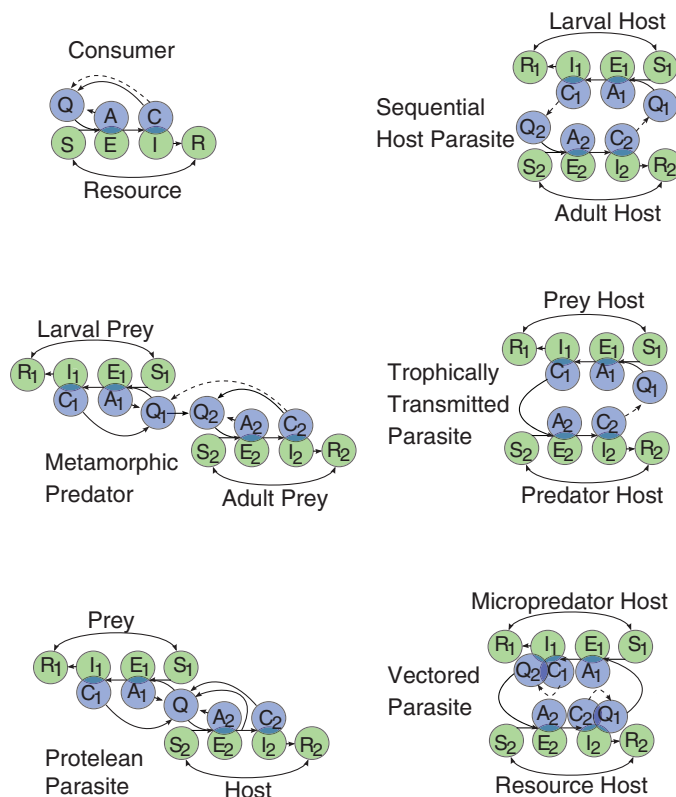
models, track only questing consumers and susceptible resources. Moreover, although the importance of a saturating functional response has been recognized in prey-predator models, classic models often assume that handling or contact is fast, or both, giving the impression that such consumers have unlimited potential to control their resources. Deriving classic models from a general-consumer resource model highlights these assumptions, specifies each model's relationship to all other consumer-resource models, and identifies the meaning of their composite parameters (table SF1).

The general consumer-resource model allows systematic mapping across consumer-resource population models. Having a common model structure exposes simplifying assumptions in classic consumer-resource models and allows us to contrast the structure of different consumer-resource relationships, specifying the conditions that favor one strategy over another. Consumer-resource interactions drive ecosystem functions, and ecosystem functions are the underlying mechanisms that govern all ecosystem services. The general model provides a useful foundation for understanding and constructing food-web models central to understanding ecological complexity.

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