

Apparent competition couples donor and trophic control among prey of generalist predators

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Open Research Statement

Prey population time series data were taken from Georgiadis, N. J., J. G. N. Olwero, G. Ojwang, and S. S. Románach. 2007b. "Savanna Herbivore Dynamics in a Livestock-Dominated Landscape: I. Dependence on Land Use, Rainfall, Density, and Time." *Biological Conservation* 137 (3): 461–472. Predator data were from Bauer, H., G. Chapron, K. Nowell, P. Henschel, P. Funston, L. T. B. Hunter, D. W. MacDonald, and C. Packer. 2015. "Lion (*Panthera leo*) Populations Are Declining Rapidly Across Africa Except in Intensively Managed Areas." *Proceedings of the National Academy of Sciences* 112 (48): 14894–14899. These data, the

Python code used to fit models, and an associated README file, are available at Figshare:
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Artificial Intelligence (AI) Policy Statement

During development of this manuscript, generative AI (ChatGPT, OpenAI) was used to assist with (1) creating a matrix of apparent competition types; (2) identifying candidate ACDC systems and potentially relevant references through iterative literature searches; (3) exploring how predator density dependence could best be incorporated into the predator equation (Equation 3); (4) suggesting and evaluating options for model fitting and statistical analysis; (5) developing, debugging, and testing Python code used for model fitting and statistical analysis; and (6) suggesting revisions to selected passages for clarity and brevity. Accuracy of all references and code was validated by the authors.

Key words and phrases:

bottom-up control, community structure, food webs, predation, predator-prey dynamics, top-down control

Abstract

Apparent competition refers to an indirect interaction between prey populations that affect one another's abundance through shared predators. Classically, prey are reciprocally coupled, such that each can sustain and be limited by predators via trophic (top-down) control. Here, we focus on a less-examined but potentially widespread form involving primary prey that are donor (bottom-up) controlled. These sustain predators but are not regulated by them; instead, their dynamics are governed mainly by donor processes. Consequently, the indirect interaction between prey populations becomes non-reciprocal. We refer to this as Apparent Competition via Donor Control (ACDC). Under ACDC, predation mortality is largely compensatory for primary prey but additive for secondary prey. Primary prey therefore function less as victims than as resources that maintain predators, which suppress secondary prey.

We explore the occurrence of ACDC using four qualitative criteria to diagnose 20 candidate ACDC systems from the literature. These systems span terrestrial, freshwater, and marine habitats and feature diverse taxa, suggesting that ACDC can arise across a wide range of ecological settings. Some cases had previously been described as subsidy-driven predation, hyperpredation, or disturbance-mediated apparent competition, highlighting donor control as potentially a shared causal mechanism. Thus, empirical examples of ACDC may have long been available, but primary prey were not always diagnosed as donor controlled.

For systems with suitable population data, we then derive a diagnostic model framework to test whether dynamical consistency with alternative control regimes can be assessed from prey and

predator population trajectories. Applied to a recovering African large-mammal community, the fitted models classified the primary prey (plains zebra) as donor controlled in all prey pairings, while four of eight secondary prey populations exhibited dynamics consistent with trophic control, and thus ACDC.

Mechanistically, ACDC decouples energy flow from demographic impact in food webs: prey that sustain predators need not be the prey most strongly regulated by predators. A critical uncertainty is the extent to which mixed donor and trophic control modes within communities is due to ACDC operating among the prey populations of generalist predators. We hope this emphasis shifts attention to assessing the importance of ACDC in structuring food webs.

Introduction

Half a century ago, Holt (1977) introduced the concept of apparent competition as an indirect interaction between prey populations that share one or more predator species. An increase in the abundance of one prey population elevates the abundance or activity of shared predators, thereby increasing predation on and suppressing other prey populations. This outcome resembles that of interspecific competition between consumers for resources, but apparent competition operates on prey between which interspecific competition is minimal. Because most predators exploit multiple species of prey, and most prey populations share predators, apparent competition has potential to be widespread in nature. Over the last 50 years, many types of apparent competition have been described (Appendix S1), and both theory and observations have confirmed that apparent competition is pervasive in structuring ecological communities (e.g., Bascompte and Melián 2005; Holt & Bonsall 2017; Holt & Lawton 1993, 1994; Menge 1995; Schmitt 1987; Wollrab et al. 2012).

In Holt's original formulation, prey populations were controlled by the balance of donor (bottom-up) and trophic (top-down) forces, such that each prey population both influenced and responded to predator dynamics [throughout, *donor control* refers broadly to control of prey populations by density dependence or by external supply of resources, in contrast with *trophic control*, in which predators reduce prey abundance below their carrying capacity; collectively, donor control and trophic control are referred to as 'control modes']. Predators would respond numerically to the combined availability of all prey, and prey population responses were reciprocal (often symbolized as -, -). In nature, such reciprocal interactions are rarely

symmetrical. One prey population (the 'primary' prey) may disproportionately sustain predators because of its greater abundance or productivity, while remaining relatively insensitive to predator mortality. Another ('secondary' or 'subordinate') prey may be more strongly trophically controlled because of its lower abundance or productivity, or because predator mortality is more demographically consequential [throughout, primary prey refers to prey that substantially support shared predators and thereby generate or maintain predation pressure on more vulnerable secondary prey]. This asymmetric-but-reciprocal interaction—in which both primary and secondary prey populations remain responsive to changes in predator abundance (Figure 1a)—characterizes much of the apparent competition literature.

Reciprocity is not obligatory, however. Chaneton & Bonsall (2000) described an indirect interaction, which they called indirect amensalism (Figure 1b), similar to classical apparent competition in that primary prey indirectly suppress secondary prey via shared predators, while both primary and secondary prey populations remain responsive to predation. The distinguishing feature of indirect amensalism is that the effect of secondary prey on predators is so weak as to be negligible. In effect, the interaction between prey populations becomes non-reciprocal (0, −). Based on a broad sample of published predator-prey studies, Chaneton & Bonsall (2000) concluded that enemy-mediated interactions between prey are often non-reciprocal.

Trophic control of primary prey is also not obligatory. The mathematical structure of the classical theory allows primary prey to be more donor controlled than trophically controlled (Holt 1977). Holt (1984, 2008) and Holt & Lawton (1994) explicitly recognized donor-controlled predator populations, including systems in which predator abundance is maintained by external

prey subsidies or by predator spillover from source populations in spatially separated habitats that predators do not regulate locally (see also Polis et al. 1997; Polis & Strong 1996). These weaken predator–prey coupling within localities such that the interaction between primary and secondary prey populations becomes non-reciprocal. Relatedly, hyperpredation refers to cases in which abundant prey (that often are introduced or invasive) sustain elevated predator populations, thereby intensifying predation on native prey and sometimes causing their extirpation (Smith & Quin 1996). In disturbance-mediated apparent competition, disturbance improves habitat suitability for primary prey, increasing not only their abundance but also the abundance, distribution, or hunting efficiency of predators, prompting secondary prey to decline (Lamb et al. 2024; Seip 1992; Serrouya et al. 2019). Under these conditions, predation on secondary prey does not diminish even when they decline, such that the persistence of secondary prey depends on some combination of refuges, prey switching, predator saturation, or management (DeCesare et al. 2010; Sinclair et al. 1998). Typically, neither hyperpredation nor disturbance-mediated apparent competition explicitly require primary prey to be donor controlled, although this may be implied or inferred (e.g., Neufeld et al. 2026).

Here we focus on apparent competition in which primary prey are explicitly donor-controlled, which we refer to as ACDC (Apparent Competition via Donor Control; Figure 1c). Like indirect amensalism (Chaneton & Bonsall 2000), ACDC is a non-reciprocal form of enemy-mediated interaction. But whereas indirect amensalism is defined by the absence of a reciprocal effect on predators, ACDC is defined by asymmetry in prey population control: predator-sustaining primary prey remain donor controlled, while secondary prey are controlled by shared predators.

Under ACDC, therefore, secondary prey may contribute substantially to the maintenance of predator populations.

Although ACDC does not comprise a new type of apparent competition, we maintain that ACDC warrants naming and specific attention for two reasons. First, ACDC likely is not confined to systems featuring spatial subsidies, introduced prey, or disturbance. In principle, ACDC can arise wherever one or more primary prey populations sustain shared predators while remaining donor controlled. Yet, the dynamics and incidence of ACDC remain sparsely documented. The best examples feature outbreaks of rapidly increasing primary prey, driven by (and that may themselves constitute) resource pulses. For example, in Białowieża Forest, Poland, mast-driven rodent pulses increased the occurrence of rodent-hunting carnivores, that then reduced wood warbler (*Phylloscopus sibilatrix*) nest survival through increased incidental nest predation (Grendelmeier et al. 2018; Maag et al. 2024; Maziarz et al. 2019; see also Schmidt & Ostfeld 2008). Barraquand et al. (2015) modeled an apparent-interaction module in which cyclic field voles (*Microtus agrestis*) influenced red grouse (*Lagopus lagopus scoticus*) through predation by hen harriers (*Circus cyaneus*). In their model, grouse were secondary prey: they affected harrier diet and suffered harrier predation, but did not drive the harrier aggregative or numerical response. Strong harrier aggregation to voles could generate an asymmetric negative effect of voles on grouse (0, −). Conversely, high vole abundance could benefit grouse, producing apparent mutualism (0, +). Delayed predator responses after vole declines could intensify grouse predation because harriers may remain abundant when voles are scarce. Thus, the indirect effect of voles on grouse could be negative, weak, or positive depending on their relative abundance. Barraquand et al. concluded that ACDC-like dynamics may be prevalent in nature, citing hares

(*Lepus* spp), wildebeest (*Connochaetes taurinus*), sandeels (Ammodytidae), and others, and recommended that such dynamics merit further study.

The second reason to focus on ACDC is that, under ACDC, abundant, donor-controlled prey populations sustain predators through largely compensatory mortality, while additive mortality from predation characterizes less abundant (or more vulnerable) prey that share the same predators (mortality imposed by predation is compensatory when offset by a reduction in mortality imposed by other causes). Primary prey therefore function not merely as victims of predation but as drivers of predator abundance. A corollary is that primary prey should account for a large, perhaps dominant, fraction of total prey biomass (Polis & Strong 1996). This prediction remains largely untested because empirical studies rarely report the biomass *and* the modes of control of prey populations, *and* how they differentially sustain predator populations. Apparent Competition via Donor Control therefore has important but under-reported implications not only for food-web structure, but also for predator persistence, secondary prey suppression, and the interpretation of trophic control, all of which are addressed below.

We examine the properties, incidence, and significance of ACDC in ecological communities. We begin by specifying the qualifying criteria needed to diagnose ACDC. We use these criteria to identify 20 candidate systems from the literature whose attributes are assessed, and the quality of evidence for the operation of ACDC is rated. For systems with time series data available for predator, primary prey, and secondary prey populations, we next develop a quantitative framework, based on Holt's original (1977) equations, to assess whether observed dynamics are consistent with ACDC. The framework is tested using data from an African savanna system

comprised of predators and their ungulate prey, whose modes of control are largely understood from experiments and decades of observations. Finally, we consider the implications of ACDC for within- and among-food web dynamics, asking how food web structure and dynamics can be better understood by distinguishing prey that sustain predators from prey that are suppressed by predators.

Diagnosing ACDC in ecological communities

In addition to interspecific and apparent competition, other mechanisms can produce opposing prey population trajectories, including abiotic forcing, habitat change, and disease. Diagnosis of classical apparent competition begins with confirming that two or more co-occurring prey populations share one or more predators (Holt 1977). A second requirement is demonstration of numerical, functional, or aggregative responses by the predator to increases in at least one prey population. Third, another (i.e., secondary) prey population must be suppressed via trophic control. In classical apparent competition, the interaction between prey populations should be reciprocal.

To distinguish ACDC from classical apparent competition or indirect amensalism, primary prey populations must not only be abundant, but also donor controlled (Figure 1c). Thus, primary-prey dynamics must be driven mainly by resource supply, intrinsic density dependence, abiotic forcing, or other processes independent of predation. A corollary is that predation on primary prey is largely compensatory: individuals killed by predators would have been otherwise lost, such that an increase in mortality from predators results in a decrease in mortality from resource

limitation or density dependence. Conversely, predation on secondary prey is additive, with no offsetting decrease in mortality from resource limitation or density dependence, and secondary prey populations are suppressed via trophic control. Under these conditions, the primary prey population subsidizes predator abundance while experiencing little or no reciprocal suppression. Thus, in addition to the three diagnostics to identify classical apparent competition, evidence for ACDC includes a fourth criterion: donor control (and weak demographic effects of predation) of the primary prey population.

Selection and attributes of candidate ACDC systems

Trophic modules in which ACDC plausibly could be operating ('candidate systems') were identified through targeted, iterative searches of the literature conducted with ChatGPT (OpenAI) primarily on 29–30 April 2026. Searches were structured around the four diagnostic criteria for ACDC: shared predation; a numerical, aggregative, functional, or behavioral predator response to primary prey; demographic suppression of secondary prey; and donor control of primary prey. Search instructions were progressively refined to emphasize natural and human-influenced systems in which bottom-up, density-dependent, cyclic, or pulse-driven primary-prey dynamics sustained or concentrated predators that increased mortality of alternative prey. Related search concepts included apparent competition, alternative-prey effects, hyperpredation, prey subsidies, predator numerical responses, resource pulses, mast seeding, invasive prey, and disturbance-mediated apparent competition. Searches were conducted through ChatGPT's web-search functionality (including Web of Science, Scopus, Google Scholar, BIOSIS, and PubMed), rather than through a predefined bibliographic database protocol. Candidate publications

suggested by ChatGPT were treated only as leads; inclusion and scoring were based on author examination of the cited primary literature. The search was therefore targeted and non-exhaustive and was not intended to estimate the prevalence of ACDC.

Typically, no single publication documented all four criteria for a given system, so evidence was assembled across contributing publications. For each candidate system, we scored the quality of evidence supporting each criterion in cited references from 0 to 3, with '0' for not demonstrated; '1' indicating weak, indirect, or inconclusive evidence; '2' indicating credible but incomplete empirical evidence; and '3' indicating strong evidence from experimental manipulations, natural experiments, extended time series, or combinations of all three. A system was retained only when each of the four criteria scored >0 . Retained candidate systems were assigned heuristic rankings reflecting the strength of available evidence for the occurrence of ACDC, with greater weight given to criteria that were more difficult to establish and more diagnostic of ACDC.

Candidate systems were also classified by context and tempo. Context was used to categorize systems driven primarily by human activities ('human-influenced' e.g., habitat disturbance, introduced species), by natural processes ('natural'; e.g., population cycles, mast seeding), or both. The tempo of ACDC was classified as 'persistent', when donor control of primary prey was relatively continuous; as 'recurrent' or 'episodic', when periods of donor control of primary prey are interrupted by periods of trophic or balanced control of roughly equal duration; or as 'pulsed' (Ostfeld & Keesing 2000), when resource pulses produced bouts of donor control that were short compared to periods of trophic or balanced control.

After scrutiny of references and evidence, the search yielded 20 candidate ACDC systems, for which descriptive summaries are given in Appendix S2, with a condensed version of evidence for the Laikipia large-mammal system given in Table 1 as an example. With regard to the four diagnostic criteria for ACDC, evidence was strongest for the three components of classical apparent competition: a predator (or parasitoid) shared between two or more co-occurring prey populations (criterion #1) was strongly supported in 17 of 20 cases, and a predator response to increased population size of putative primary prey (criterion #2) was strongly supported in 16 of 20 cases. Evidence for suppression of secondary prey (criterion #3) also was common, with strong support in 11 systems and credible support in another 9. Evidence for criterion #4 was least prevalent: only 8 systems showed strong support for donor control of primary prey, whereas 8 were credibly and 4 were weakly supported. Thus, the main evidentiary constraint to documenting ACDC within candidate systems was whether primary prey were shown to be regulated largely by donor control.

A collective assessment of these 20 candidate systems yielded the following observations:

1. Apparent Competition via Donor Control is empirically plausible across a wide range of ecological settings, including terrestrial, freshwater, and marine biomes, featuring diverse taxa including invertebrates, vertebrate ectotherms, and vertebrate endotherms, and ranging across biomes from tropical grasslands to polar tundra.
2. Population dynamics of predators, primary prey, and secondary prey that are consistent with ACDC were caused by disturbances or other environmental changes, including invasion (Great Lakes [no. 14 in Appendix S2], Macquarie Island [16], and Canary Islands [18]), predator restoration (African savanna [1]), habitat alteration (Boreal Forest

I [11] and Boreal Forest II [13]); by persistently high resource availability (Laikipia [1], Serengeti [5], Kruger [7], Great Lakes [14], Great Barrier Reef [15], Macquarie Island [16], and Canary Islands [18]), recurrent prey cycles (Bylot Island [2], Fennoscandia [8], Ontario Mixed Forest [10], and Barents Sea [17]), and climate-driven resource pulses (Białowieża Forest [4], Humboldt Current [6], California Current [9], Antarctic Southern Ocean [12], Barents Sea I [17], Scotia Sea [19], and Barents Sea II [20]); and from short-lived resource pulses such as mast seeding (New York Mixed Forest [4]) or experimental prey supplementation (North Pacific Rim [3]).

3. The most strongly supported cases of ACDC include large mammals within an African savanna ecosystem, featured below and in Table 1), and a cyclic lemming–fox–bird system in the Arctic [2]. Lower-scoring cases were not necessarily poor examples of ACDC. Rather, they tended to involve multiple predators with hard-to-separate effects [10 and 14], environmentally forced primary-prey dynamics [20], or weak evidence that predator responses to primary prey translated into demographic suppression of secondary prey [12 and 19].
4. Apparent Competition via Donor Control manifested over a range of temporal dynamics: 10 candidate systems were classified as persistent, 9 as recurrent or episodic, and 1 as pulsed. Thus, ACDC need not operate continuously. For primary prey, the mode of population control may alternate between donor and trophic [2, 4, and 8], provided that they can maintain predators above the abundance that secondary prey alone could support. Systems exhibiting ACDC are best viewed as arranged along a continuum, varying in the strength and persistence of donor control of primary prey.

5. Candidate systems influenced by human activities were common but not dominant: 12 cases were classified as 'natural', 5 as 'human-influenced', and 3 as both.
6. Some of the candidate systems have been classified as 'subsidy-driven predation' [3 and 15], 'hyperpredation' [16 and 18], and 'disturbance-mediated apparent competition' [11 and 13], or exhibiting 'alternative-prey effects' [2, 4 and 8]. Classifying these studies as candidate ACDC systems should not replace their existing names, which describe particular contexts, mechanisms, or outcomes. In the original descriptions of these cases, the mode of control of primary prey was not required to be resolved. Donor control of primary prey is highlighted here as a potentially shared process among these systems. Examples of ACDC have long been available, therefore, but were not always recognized as such, and their details were spread across mostly separate literatures.

Our survey does not demonstrate the prevalence of ACDC in nature, because our sample of candidate systems was not derived from an unbiased survey. However, the diversity and geographical extent of candidate systems is consistent with the expectation that ACDC can arise wherever primary prey are sufficiently donor controlled to support a shared predator population, that in turn suppresses a secondary prey population. The relatively sparse documentation of ACDC is less likely due to its scarcity than to its mechanistic complexity, which requires varied and intricate data for its diagnosis.

There are also reasons why ACDC theory has received little attention. First, population modeling traditionally focused on consumer–resource relationships that are reciprocal (as opposed to non-reciprocal), with resources supporting consumers and consumers depressing resources (Holt 1977; Lotka 1925; Volterra 1926). This tendency directed attention toward how consumers and

resources influence one another, and away from resources (i.e., prey populations) that are affected minimally by their consumers (i.e., predators). Second, food web modeling often aggregated prey into trophic or functional groups, thereby obscuring differences among prey in mechanisms of demographic control (Yodzis & Winemiller 1999; Fulton et al. 2003). Lastly, donor and trophic control were long treated as separate rather than coupled processes (Barbier & Loreau 2019; DeAngelis 2012; Moore et al. 2004; Polis & Strong 1996; Zheng et al. 1997), a theme we return to below.

A quantitative framework for assessing dynamical consistency with ACDC

The preceding section emphasized that ACDC is easiest to recognize in conspicuously dynamic systems—those driven by resource pulses, prey cycles, species invasions, or habitat disturbance. In such cases, changes in primary prey or predator abundance create pronounced temporal variation that can reveal predator-mediated effects on secondary prey (and ACDC that is recurrent/episodic or pulsed). Persistent ACDC is more difficult to diagnose, especially when prey and predator populations show no marked directional change through time. In settings characterized by persistent ACDC, data on prey-specific estimates of predation mortality, attack rates, density dependence, prey productivity, and predator energetic requirements are ideal. Such data are rarely available, however. More commonly available are time series of prey and predator abundance, which may vary enough to reveal whether observed dynamics are consistent with ACDC. We therefore asked whether ACDC-like donor and trophic control could be inferred retrospectively by fitting a mechanistic model, which includes terms for both density-dependent prey limitation (i.e., donor control) and predator-mediated prey mortality (i.e., trophic control), to observed variation in prey and predator populations.

We used a slightly modified version of Holt's (1977) original apparent competition equations to assess whether prey-specific donor and trophic control could be estimated from observed prey and predator population trajectories. We refer to this formulation as the *Full* model:

$$\frac{dN_1}{dt} = r_1 N_1 - \overbrace{D_1 N_1^2}^{\text{i}} - \overbrace{\alpha_1 P N_1}^{\text{ii}} \quad (1)$$

$$\frac{dN_2}{dt} = r_2 N_2 - \overbrace{D_2 N_2^2}^{\text{iii}} - \overbrace{\alpha_2 P N_2}^{\text{iv}} \quad (2)$$

$$\frac{dP}{dt} = -r_p P - D_p P^2 + \overbrace{\varepsilon_1 \alpha_1 P N_1}^{\text{v}} + \overbrace{\varepsilon_2 \alpha_2 P N_2}^{\text{vi}} \quad (3)$$

where:

- N_1 is abundance of prey 1 [R_i]
- N_2 is abundance of prey 2 [R_i]
- P is abundance of predators
- r_i is growth rate of prey i (yr^{-1})
- D_i is intraspecific density dependence coefficient for prey i ($\text{ind}^{-1} \text{yr}^{-1}$) [r_i/K_i]
- α_i is predator attack rate on prey i ($\text{ind}^{-1} \text{yr}^{-1}$)
- ε_i is conversion coefficient of prey i to predators [Bb_i]
- r_p is baseline predator loss rate (yr^{-1}) [C]
- D_p is density dependence coefficient for predator ($\text{ind}^{-1} \text{yr}^{-1}$)

In the list above, symbols in square brackets were used by Holt (1977) for the given variable or parameter. The formulation for primary and secondary prey populations (equations 1 and 2) is algebraically equivalent to Holt's (1977) equations, after re-parameterizing prey density dependence as $D_i = r_i/K_i$ (where K_i is carrying capacity for prey species i), and prey-to-predator conversion as $\varepsilon_i = B_i b_i$ (where B_i is the conversion factor from prey i intake to predator recruitment, and b_i is caloric or energetic value of prey species i).

The formulation for predators (equation 3) differs from Holt's by the addition of a term for predator density dependence ($-D_P P^2$), following Bazykin's extension of Lotka–Volterra predator–prey models (Bazykin 1976). This term represents mechanisms causing predator self-limitation, including interference, territoriality, and other density-dependent limits on recruitment or survival. Across systems with markedly different predator abundances and prey-per-predator ratios, this term allows predator abundance to saturate as prey availability increases. Thus, attack rates remain interpretable as effective prey-specific predation coefficients rather than absorbing both prey-specific predation and predator density dependence.

Indices for donor and trophic modes of control

Equilibrium population sizes were calculated from the *Full* model by setting all derivatives to zero. For each prey species i ,

$$\frac{dN_i}{dt} = r_i N_i - D_i N_i^2 - \alpha_i P N_i = 0,$$

giving the positive equilibrium condition

$$N_i^* = \frac{r_i - \alpha_i P^*}{D_i}.$$

Predator equilibrium was obtained from

$$\frac{dP}{dt} = -r_P P - D_P P^2 + \sum_i \varepsilon_i \alpha_i P N_i = 0$$

Substituting the prey equilibrium expressions,

$$P^* = \frac{\sum_i \varepsilon_i \alpha_i r_i / D_i - r_P}{D_P + \sum_i \varepsilon_i \alpha_i^2 / D_i}.$$

The resulting P^* was then used to calculate each N_i^* . Only biologically feasible equilibria with positive prey and predator abundances were retained.

After fitting the model, the contribution of density dependence to the mortality of primary and secondary prey at equilibrium was quantified as:

$$M_{D,i} = D_i N_i^*$$

and predation mortality at equilibrium as:

$$M_{P,i} = \alpha_i P^*$$

where (N_i^*, P^*) are the equilibrium abundances from the fitted model.

For each prey species (i), the control mode index, C_i , was expressed as the log ratio of mortality related to donor versus trophic control:

$$C_i = \log_{10}(M_{D,i}/M_{P,i}) \quad (4)$$

Log-transformation places donor and trophic control on a symmetric scale centered on zero.

Values of $C_i = 0$ indicate equal donor-related and predation-related mortality; positive values indicate greater donor-related mortality, and negative values indicate greater predation mortality.

Because $\log_{10}(2) \approx 0.3$, values of this control metric within 0.3 of zero indicate that the two mortality terms differ by less than approximately twofold, and were arbitrarily interpreted as balanced control. Values of > 0.3 were classified as donor dominated, whereas values < -0.3 were classified as trophic dominated.

Alternative control regimes

Additional models were derived from the *Full* model by selectively changing or omitting one or two of the terms labeled i–iv from equations 1 and 2. This created a set of alternative models that variously require, restrict, or exclude the processes underlying ACDC. Thus, a *Forced ACDC* model was obtained by omitting terms ii and iii, thereby forcing N_I to be donor controlled and N_2

to be trophically controlled, making ACDC structurally obligatory. A *Mixed ACDC* model was derived by omitting only term ii from equation 1, leaving N_1 purely donor controlled while N_2 remained subject to both donor and trophic control. Omitting term ii from the *Forced* and *Mixed ACDC* models allowed predators to grow without impacting primary prey, in effect, mimicking compensatory mortality from predation on primary prey. This structure was consequential in fitting these models to observed predator and prey time series: when an attack-rate parameter (α_i) appeared only in the predator equation (terms v and vi in equation 3), it was constrained only by its contribution to predator growth. By contrast, when the same attack-rate parameter also appeared in the corresponding prey equation, it was constrained jointly by predator growth and prey mortality.

A third reduced model (*Donor*) was obtained by omitting terms ii and iv, making both primary and secondary prey populations exclusively donor controlled. In this model, neither ACDC nor apparent competition more broadly can operate because trophic control is absent from both prey equations. A fourth model, referred to as *No Prey Selection*, was identical to the *Full* model, except that attack rates on prey were made equal ($\alpha_1 = \alpha_2$). In this model, apparent competition (including ACDC) can operate, but depends on asymmetries between parameters other than attack rates.

Together, the five models provided an analytical framework that reveals whether observed time series are consistent with mechanisms characterizing ACDC (i.e., *Full*, *Forced ACDC*, *Mixed ACDC* or *No Prey Selection* models), or if donor control of both prey (i.e., *Donor*) is more plausible. The framework reveals (1) whether primary prey appear more donor controlled than

465 trophically controlled; (2) whether adding shared predation to density dependence better explains
466 prey population trajectories than density dependence alone; and (3) whether dynamics of
467 secondary prey populations are consistent with trophic control.

468
469 Unlike the *Full* model, reduced models cannot yield directly comparable control metrics, but
470 were informative in their responses to a standard perturbation: reducing primary prey growth by
471 6% (a sustainable harvesting rate recommended by Georgiadis et al. 2003; see the section headed
472 'Testing the framework' below). These perturbations provided validation of the causal behavior
473 implied by the fitted model structure; namely, whether secondary prey populations are released
474 from trophic control when primary prey populations are reduced (as in Figure 2c), or whether
475 dynamics of secondary prey populations are largely independent of primary prey populations.

476
477 Diagnosing ACDC is partly an identifiability problem, because similar population trajectories
478 may result from different combinations of prey density dependence, predator attack rates, and
479 predator self-limitation. Data on predator diets provide evidence of consumption, but by
480 themselves do not establish either that primary prey sustain predator abundance, that secondary
481 prey are trophically controlled, or that mortality from predation on primary prey is compensatory
482 (and thus primary prey are donor controlled). Verification requires independent evidence on
483 prey-specific vital rates, kill rates, predator demographic responses, and preferably population
484 responses to natural or experimental changes in predator or prey abundance. Thus, the model
485 framework is best viewed as a structured diagnostic aid, in that it cannot by itself confirm
486 ACDC, but it can identify when dynamics are mechanistically consistent with ACDC.

Testing the framework: Apparent Competition via Donor Control in a savanna ungulate community

Data from an African large-mammal community in the Laikipia region of northern Kenya (i.e., ACDC candidate system no. 1 in Table 1) were used to test the 5-model diagnostic framework described above. From prior studies, time series were available for both predators (Bauer et al. 2015) and prey, as were insights about modes of prey population control (Georgiadis et al. 2003; Georgiadis et al. 2007a; Georgiadis et al. 2007b; Georgiadis 2011; Ng'weno et al. 2017).

High prey and predator diversity within African savannas present high potential for apparent competition. Today, the fauna of the Laikipia region is relatively intact, but human activities shaped it historically, especially since colonization by British settlers in the early 1900s. From the mid-1950s, wild ungulates perceived by ranchers to compete with cattle (*Bos indicus*) – principally plains zebras (hereafter 'zebras', *Equus quagga*) – were lethally suppressed or excluded from many private holdings, as were large carnivores, particularly lions (*Panthera leo*). In the mid-1980s, land use began to shift from beef production to wildlife conservation, with the intent that wildlife should supplement income from cattle, initially by consumptive use, and later from ecotourism (Georgiadis et al. 2007b). The suppression of wild ungulates mostly ceased in the mid-1980s, allowing their populations to grow to their highest recorded levels in 1990-1991 (Georgiadis 2007b). Zebras increased five-fold to dominate the biomass density of wild ungulates (Georgiadis et al. 2003). Lethal control of large carnivores began to abate five years later (from the mid-1990s), allowing lions, hyenas (*C. crocuta*, *Hyaena hyaena*), leopards (*Panthera pardus*) and wild dogs (*Lycaon pictus*) to recover over the following decade (Bauer et

al. 2015; Ford et al. 2015; Frank 2011; Frank 2023). In effect, this staggered recovery of prey and then predators created an ecosystem-level perturbation experiment that yielded insights about the impact of large carnivores on a wild ungulate assemblage that initially was donor controlled.

During the period of predator recovery, some prey species declined while others remained near their density-regulated equilibria. Zebra maintained high abundances and were the most common wild ungulate within Laikipia (Georgiadis et al. 2003, Georgiadis et al. 2007b). Grant's gazelle (*Nanger granti*) and impala (*Aepyceros melampus*) populations also did not decline significantly. In contrast, populations of hartebeest (*Alcelaphus buselaphus*), waterbuck (*Kobus ellipsiprymnus*), Thomson's gazelle (*Eudorcas thomsonii*), eland (*Taurotragus oryx*), buffalo (*Syncerus caffer*), and to a lesser extent giraffe (*Giraffa camelopardalis*) all declined. By the early 2000s, the biomass density of wild ungulates collectively had declined by ~60%, relative to the early 1990s (Georgiadis et al. 2007b). Among nine hypotheses that might account for these population declines, trophic control appeared to be the most plausible cause (Georgiadis et al. 2007a), implying that predation shaped the ungulate assemblage by decreasing the biomass density of many, but not all, prey species, thereby promoting the dominance of zebra, and to a lesser extent Grant's gazelle and impala.

While most prey populations declined, zebras remained donor controlled, and they comprised the primary prey of lions and hyenas (Dheer 2016; Frank 2023; Ng'weno et al. 2019a), which is consistent with the hypothesis of ACDC. For one trophically controlled species (hartebeest), ACDC was affirmed independently by a combination of field experiments and monitoring of

primary prey (zebra), hartebeest as a focal secondary prey, and lion abundance (Ng'weno et al. 2017, Ng'weno et al. 2019a, Ng'weno et al 2019b). Population growth of hartebeest within a lion-proof sanctuary exhibited negative density dependence, while those exposed to lions exhibited an Allee effect (positive density dependence, supporting trophic control; Ng'weno et al. 2017). In addition, lions killed hartebeest selectively (but infrequently, given their scarcity), especially in proximity to their primary prey, zebras, such that areas >0.5 km from zebra herds functioned as spatial refugia for hartebeest (Ng'weno et al. 2019b).

Alternative control regimes in African ungulates

Using parameter values described in Appendix S3, parts 1a and 1b, the five models were fitted to time series data from Laikipia via a least-squares procedure outlined in Appendix S3 part 2. This procedure was implemented by a *Python 3.9.6* script developed by generative AI (ChatGPT, OpenAI). The script was tested, modified, and validated as described in Appendix S3 part 3. Both the data and the script are available from [10.6084/m9.figshare.33117608](https://doi.org/10.6084/m9.figshare.33117608).

Support for the five models varied among the eight primary–secondary prey pairings (Appendix S4; results for the best-supported model in each pairing are reported in Table 2). Model fits for primary prey (zebras) and predators were consistently good (RMSLE <0.2). Among secondary prey, model fits varied from good to adequate (RMSLE <0.3), except for one species of secondary prey (waterbuck) for which the fit was unacceptable (RMSLE = 0.73). Examples of model fits and projections are illustrated for the zebra-hartebeest pairing in Figure 2, and for other pairs in Appendix S4, Figure S4.1.

In every primary prey-secondary prey pairing, control indices (equation 4) for zebra were greater than 0.3, indicating donor control. Among secondary prey populations, half (eland, hartebeest, impala, Thomson's gazelle) appeared to be trophically controlled, exhibiting dynamics consistent with ACDC (Table 2). Among the remainder, buffalo and giraffe were donor controlled, for Grant's gazelle control was balanced, and for waterbuck control was undefined.

Fitted parameters (Table 3) revealed a consistent contrast between estimates of zebra density dependence, which were similar across all pairwise fits ($D_1 = 2.93\text{--}3.86 \times 10^{-6} \text{ ind}^{-1} \text{ yr}^{-1}$; $\text{CV} \approx 10\%$), and attack rates on zebra, which varied among pairings by more than six orders of magnitude. In this context, each estimated attack rate (α_i) is not an independent estimate of zebra vulnerability. It varies among pairwise fits because it is conditional on the secondary prey featured in each fit. Model fitting reallocates shared predator (and other) effects differently in each pair. For the intended purpose of diagnosing ACDC, it was more instructive that, in every model allowing prey-specific attack rates, the estimated attack rate on secondary prey exceeded that on zebra, and their 95% confidence intervals did not overlap.

Density dependence of predators (D_P) also varied greatly among pairings. Predators were negatively density dependent in the best-supported models for impala and Thomson's gazelle, for which the 95% confidence intervals excluded zero. For giraffe and Grant's gazelle, D_P was poorly identified, whereas for buffalo and eland its estimate reached the lower bounded value. As with the attack rates, these differences should not be interpreted as biological variation in

predator regulation. Rather, each fitted D_P represented the density-dependent limitation needed to reproduce predator dynamics in each two-prey model.

Our framework showed that models with the same predators and primary prey can generate, or at least be associated with, different control regimes for populations of secondary prey. Four of eight species of secondary prey were trophically controlled, while others were better characterized as donor controlled, and others remained poorly resolved. Such variation is expected because prey differ in vulnerability to predators, and predators differ in preference, search efficiency, and handling constraints of secondary prey. The results were broadly consistent with the original linear-model analysis of the same time series (Georgiadis et al. 2007b): trophic control was supported for declining eland, hartebeest, and Thomson's gazelle, but not for giraffe, whose decline was consistent with density dependence, or for buffalo, for which causes of decline were not diagnosed. Conversely, impala, which declined but non-significantly, appeared trophically controlled in this analysis. These results also accord with known diets of lions and hyenas, which feed less on large-bodied (>800 kg) prey, and more on abundant, mid-sized grazers that are largely donor controlled, while imposing stronger demographic effects on smaller, or more vulnerable secondary prey (Owen-Smith & Mills 2006; Radloff & Du Toit 2004; Sinclair et al. 2003).

Overall, our analyses suggest that control regimes can be inferred retrospectively from concurrent predator and prey time series, at least when some show directional change over time, and basic fixed parameters can be estimated. Applying the same framework to comparable

systems would test its generality and help distinguish robust control-regime signals from system-specific or poorly identifiable dynamics.

Implications of ACDC for community structure and dynamics

Most communities share two properties that make them susceptible to some form of apparent competition. First, most free-living predators are generalists (they consume multiple prey species), not least because diverse diets can enhance predator persistence by buffering their populations against fluctuations in individual prey, especially in variable environments (Kamaru et al. 2024; Murdoch 1969; Prokopenko et al. 2023). Consequently, most prey share natural enemies (Dunne et al. 2002; Schoener 1989). Second, communities typically comprise prey populations subject to differing balances of bottom-up and top-down control. Among prey available to any generalist predator, species differ in productivity, behavior, and life history. Their consumption by generalist predators varies with prey encounter rate, vulnerability, profitability, and handling constraints (Charnov 1976; MacArthur and Pianka 1966; Tallian et al. 2017). Consequently, the typical outcome of prey-predator interactions within communities is that some prey species are mostly donor controlled while others are mostly trophically controlled.

When this applies *within* the prey set of a generalist predator, conditions are conducive to ACDC, but they do not guarantee its expression. Donor-controlled prey may not contribute sufficiently to predator maintenance or concentration if they are difficult or unprofitable to capture or are spatially or seasonally inaccessible. Predator abundance may be constrained more

strongly by territoriality, interference, disease, den-site availability, human persecution, or by factors other than prey supply. ACDC is expected only when donor-controlled prey materially sustain or concentrate predators and those predators impose sufficiently additive mortality to exert trophic control over at least one secondary prey population.

Under ACDC, abundant, donor-controlled prey sustain predator populations without being limited by them (i.e., mortality from predation is compensatory). Weak direct effects of predation on primary prey populations do not imply weak trophic control across the community. In effect, ACDC decouples energy flow from demographic impacts of predation because the prey that mostly support predator populations need not be the prey most strongly limited by predators (Holt and Lawton 1994). Instead, trophic control is concentrated on populations of (secondary) prey that are disproportionately vulnerable to predation despite comprising a relatively small fraction of predator diets. This non-reciprocal structure allows predators to remain abundant even when secondary prey are rare or declining, because the maintenance of predator populations is underwritten partly or largely by other (typically primary) prey. Secondary prey therefore are likely to remain chronically suppressed, may fail to recover after disturbance, or may be excluded from otherwise suitable habitat.

Under these conditions, ACDC can closely resemble indirect amensalism, but with donor-controlled primary prey. Indeed, among the 34 examples provided by Chaneton and Bonsall (2000; their Table 2) are at least four in which primary prey may have been donor controlled: no. 15 'Bacterivore Protists' (Lawler et al. 1993); no. 21 'Mosquitoes' (Copeland and Craig 1992); no. 29 'Leafhoppers' (Settle and Wilson 1990); and no. 30 'Rice brown planthopper vs

detritus/plankton-feeding insects' (Settle et al. 1996). We would describe ACDC as a *dynamical mechanism* operating among prey and predators, whereas indirect amensalism is a *state* toward which such a system of interacting prey and predators is driven and maintained under persistent ACDC. In both, the extinction of secondary prey may be slowed or prevented by refuges, prey switching, or any mechanism creating 'enemy-free space'. Not every case of indirect amensalism need arise through ACDC. Chaneton & Bonsall (2000) listed several other reasons for a negligible reciprocal effect on predators from secondary prey, including poor nutritional value, phenological separation, and resistance to attack. Compared to ACDC, therefore, indirect amensalism remains a more inclusive descriptive category.

ACDC is further distinguished in that secondary prey are not demographically irrelevant to predators. Primary prey populations can sustain a predator population at abundances high enough to suppress secondary prey, but predator abundance is not necessarily determined by primary prey alone. When primary prey are abundant, predator numbers may be capped by predator territoriality, interference, disease, or other density-dependent processes (e.g., Packer et al. 2005). When primary prey are less abundant (or less catchable), predator persistence and abundance may depend increasingly on secondary prey (Kamaru et al. 2024; Stephens and Krebs 1986; Tallian et al. 2017). Thus, the importance of secondary prey for sustaining predator populations should increase when primary prey are scarce, such that secondary prey may be both victims of predation and contributors to predator persistence.

More generally, predation is associated with two well-documented regularities. Within communities, total prey biomass declines in the presence of predators (Borer et al. 2006; Katano

et al. 2015). Across communities, predator biomass increases predictably, although less than proportionally, with prey biomass, a pattern known as the Predator–Prey Power Law (Hatton et al. 2015). These regularities reflect opposing modes of control, but they are not incompatible; both arise naturally in communities comprising a mix of donor-controlled and trophic-controlled prey populations. Thus, total prey biomass declines when losses due to predation in trophic-controlled species exceed compensatory increases elsewhere in the prey community (for example, due to competitive release), while donor-controlled prey provide much of the energy that sustains predator biomass. Predator biomass covaries positively with prey biomass or productivity because both ultimately depend on resource supply and energy flow (Perkins et al. 2022). A mix of control modes can thus help explain how local suppression of prey biomass co-occurs with positive predator–prey scaling across ecosystems (although it does not by itself explain why that scaling is sublinear; see, e.g. Mazzarisi et al. 2025). Given that predator biomass should scale with the biomass of donor-controlled prey better than with total prey biomass, ACDC should tighten this correlation.

Donor and trophic modes of control can operate simultaneously and vary among species within food webs (Hunter and Price 1992; Power 1992; Polis and Strong 1996), but the degree to which control modes are mixed within (vs. among) the prey sets of individual generalist predators remains largely undefined, and constitutes a critical uncertainty highlighted by the ACDC framework. To document the prevalence of ACDC empirically, we suggest that additional studies target the conditions under which control modes of prey populations that share predators are limited by trophic control, or donor control, or both. Such studies should also report prey biomass densities through time, and the extent to which different prey populations sustain those

of shared predators. This information is essential for distinguishing systems in which shared predators merely link prey species from those in which donor-controlled prey maintain predators that impose additive mortality on (and thus trophic control over) more vulnerable, secondary prey.

Although such studies would contribute to a more complete inventory of ACDC in contemporary ecosystems, they may identify fewer cases than would have occurred under pre-industrial conditions. The global erosion of mass migrations (Fryxell & Sinclair 1988; Kauffman et al. 2021; Sola et al. 2026), megafaunal depletion (Svenning et al. 2024), predator persecution and range contraction (Torres-Romero et al. 2025; Woodroffe & Ginsberg 1998), over-harvest of abundant species (Cury et al. 2000; Essington et al. 2015; Ruzicka et al. 2024), and habitat loss and fragmentation (Fahrig 2003; Romanillos et al. 2024) – all of which may originally have featured donor-controlled prey – likely reduced, reorganized, or obscured many historical or prehistorical ACDC pathways. Conversely, humans can create novel pathways for donor control, via eutrophication, invasive prey, or other disturbances (Courchamp et al. 2003; Serrouya et al. 2021). Thus, ACDC is not only a mechanism for interpreting natural food-web structure, but also a framework for asking how anthropogenic change has reconfigured the coupling between donor control, predator persistence, and secondary-prey suppression.

Conclusions

Apparent Competition via Donor Control refers to a non-reciprocal form of apparent competition in which donor-controlled primary prey sustain predators that impose additive mortality on

secondary prey. It does not describe a new category of indirect interaction; rather, it emphasizes a perspective that may have received less attention because apparent competition has usually been framed around reciprocal prey–predator interactions, while donor control and trophic control have often been treated as separate conceptual domains (Barbier and Loreau 2019). The value of formalizing ACDC therefore lies in making this form of apparent competition explicit, diagnosable, and comparable across systems.

Apparent Competition via Donor Control merges several foundational properties of food webs into coupled donor and trophic control of prey populations. Generalist predators exploit multiple prey populations, many prey populations share predators, and prey populations within the same community typically differ in whether they are limited primarily by donor control (e.g., resources, density dependence) or trophic control (e.g., predation). ACDC is predicted to structure local communities most strongly when (and where) populations of donor-controlled (primary) prey maintain predator populations that exert trophic control over other, more vulnerable (secondary) prey populations. By defining the criteria by which ACDC can be diagnosed, we hope to focus attention on estimating the extent to which coupled donor and trophic control structure food webs. Thus, ACDC distinguishes systems in which shared predators are maintained by prey populations whose own dynamics remain largely donor controlled, while secondary prey experience additive predation. Making this distinction explicit should encourage more rigorous assessment of ACDC prevalence, strength, and persistence across ecosystems.

Apparent Competition via Donor Control exposes what is overlooked when food webs are conceived as trophic levels or functional groups governed either by donor or trophic control. It provides a framework to represent donor and trophic control as coupled processes within the same food web, linking productive prey that sustain predators with vulnerable prey that experience additive mortality. In doing so, ACDC offers a more realistic structure for interpreting familiar community-level patterns and processes.

More broadly, variation among ecosystems in degrees of donor vs. trophic control should produce systematic differences in food-web structure and dynamics. Systems dominated by productive, resilient, or pulsed prey populations that are donor-controlled may support predator populations that remain abundant despite weak reciprocal feedback from other prey populations. Such dynamics have implications both within communities, where vulnerable prey may be chronically suppressed, and among communities, where predator–prey biomass scaling may depend on the extent to which predator abundance is underwritten by donor-controlled prey. A critical uncertainty is the extent to which mixed donor and trophic control within communities is due to ACDC operating among the prey species of generalist predators.

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Conflict of Interest Statement

The authors declare no conflicts of interest.

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997

998 Table 1. A condensed description of evidence assembled to assess the African large-mammal
 999 community in Laikipia as a candidate ACDC system. Full descriptions for all candidate ACDC
 1000 systems are given in Appendix S2.

1001

System Name and Featured Species	Mechanism	Strengths and Weaknesses	Evidence and sources for the four ACDC qualifying criteria
African savanna large mammals: Laikipia region, northern Kenya Primary prey: Plains zebra (<i>Equus quagga</i>) Shared predators: Lion (<i>Panthera leo</i>); spotted hyena (<i>Crocuta crocuta</i>) Secondary Prey: Jackson's hartebeest (<i>Alcelaphus buselaphus</i>)	Rainfall- and density-regulated zebra sustain lions and hyenas, which suppress hartebeest; zebra remain comparatively insensitive to predation.	Strengths: all four criteria are supported; lion exclusion and spatial analyses strengthen causal inference. Weaknesses: hyena effects are unresolved; livestock, land use, and predator restoration may limit generality.	1. Shared predator: lions consume both prey (Ng'weno et al. 2017; Ng'weno et al. 2019a) 2. Predator response: abundant zebra supported lion recovery (Ng'weno et al. 2017; Ng'weno et al. 2019a; Georgiadis et al. 2007b). 3. Secondary suppression: lions reduce hartebeest growth and shift habitat; zebra proximity raises risk (Ng'weno et al. 2017; Ng'weno et al. 2019a; Ng'weno et al. 2019b) 4. Donor control: zebra track rainfall and density dependence (Georgiadis et al. 2003; Georgiadis et al. 2007a; Ng'weno et al. 2019a).

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Table 2. Summary of model fitting statistics and Control Indices for the best-supported models in each primary prey-secondary prey pair (complete model selection results are given in Appendix S4).

Secondary Prey	RMSLE Overall	Best-Supported Model(s) ¹	$\Delta AICc$ ²	Model Weight ³	Primary Prey Control Index ⁴	Secondary Prey Control Index ⁴
Impala	0.141	<i>Full/Mixed ACDC</i>	6.57	0.951	+0.75 (Donor)	-0.48 (Trophic)
Thomson's gazelle	0.142	<i>Full</i>	4.07	0.868	+0.51 (Donor)	-0.37 (Trophic)
Giraffe	0.160	<i>Donor</i>	7.06	0.952	+0.37 (Donor)	+6.70 (Donor)
Hartebeest	0.160	<i>Full/Mixed ACDC</i>	6.64	0.966	+0.95 (Donor)	-0.73 (Trophic)
Eland	0.160	<i>Full/Mixed ACDC</i>	10.75	0.999	+2.39 (Donor)	-0.36 (Trophic)
Grant's gazelle	0.171	<i>No Prey Selection</i>	2.05	0.500	+0.47 (Donor)	-0.17 (Balanced)
Buffalo	0.184	<i>Donor</i>	2.30	0.550	+1.79 (Donor)	+0.72 (Donor)
Waterbuck ⁵	0.424	<i>Forced ACDC/Full</i>	2.39	0.539	+0.62 (Donor)	Undefined

1. Where the best-supported models had AICc values within 2 units, both models are listed.
2. The reported $\Delta AICc$ is that of the highest-ranked model outside the best-supported model set.
3. Cumulative Akaike weight of supported model set. For impala, hartebeest, and eland, best-supported models converged on the same control regime, and their model weights were summed.
4. Control-regime classifications were calculated from the *Full* model for all pairings, even though this was not the best-supported model in 3 of 8 pairings.
5. For waterbuck, the model fit was unacceptable (RMSLE Overall>0.3).

Table 3. Estimated values (bold font) and 95% confidence intervals for the five fitted parameters in the best-supported models for each primary prey (i.e., plains zebra) – secondary prey pair.

Secondary Prey		Parameter Name and Symbol				
		Primary Prey Density Dependence	Secondary Prey Density Dependence	Primary Prey Attack Rate	Secondary Prey Attack Rate	Predator Self-Limitation
		D_1	D_2	α_i	α_e	D_P
Buffalo	Estimate	3.84E-06	7.85E-05	2.28E-05	7.54E-04	1.000E-10
	- 95% CI	3.17E-06	6.89E-05	1.00E-10	5.38E-04	1.000E-10
	+ 95% CI	4.31E-06	8.90E-05	2.65E-04	3.56E-03	8.943E-03
Eland	Estimate	3.71E-06	1.15E-05	5.08E-06	6.97E-04	1.000E-10
	- 95% CI	3.23E-06	6.27E-06	1.00E-10	6.02E-04	1.000E-10
	+ 95% CI	4.44E-06	1.81E-05	5.24E-05	7.31E-04	9.228E-04
Giraffe	Estimate	3.74E-06	7.80E-05	1.00E-10	9.67E-04	3.94E-04
	- 95% CI	3.11E-06	7.00E-05	1.00E-10	4.80E-04	4.13E-05
	+ 95% CI	4.50E-06	8.94E-05	2.66E-04	2.63E-03	9.41E-03
Grant's gazelle	Estimate	2.93E-06	2.66E-05	2.14E-04	(Not included)	2.03E-03
	- 95% CI	8.01E-07	1.47E-05	1.70E-04	-	8.53E-04
	+ 95% CI	3.64E-06	3.08E-05	5.88E-04	-	1.00E-02
Hartebeest	Estimate	3.37E-06	4.73E-05	1.14E-04	1.10E-03	4.95E-04
	- 95% CI	2.85E-06	2.86E-05	8.13E-05	9.01E-04	1.00E-10
	+ 95% CI	3.91E-06	6.01E-05	1.77E-04	1.32E-03	1.83E-03
Impala	Estimate	3.30E-06	1.15E-05	1.27E-04	1.06E-03	1.12E-03
	- 95% CI	2.71E-06	3.43E-06	8.25E-05	8.66E-04	3.36E-04
	+ 95% CI	3.87E-06	1.53E-05	1.62E-04	1.35E-03	2.00E-03
Thomson's gazelle	Estimate	3.11E-06	2.69E-05	1.79E-04	1.20E-03	1.50E-03
	- 95% CI	2.23E-06	1.59E-05	1.45E-04	8.37E-04	5.92E-04
	+ 95% CI	3.83E-06	3.73E-05	3.34E-04	1.64E-03	4.19E-03
Waterbuck	Estimate	3.86E-06	3.00E-05	4.06E-04	1.45E-03	5.78E-03
	- 95% CI	2.74E-06	-	1.32E-04	9.97E-04	1.38E-05
	+ 95% CI	5.40E-06	-	9.04E-04	2.03E-03	1.00E-02

Figure 1. Schematic comparison of mechanisms generating three types of asymmetric apparent competition (AC) between populations of two prey species (N_1 and N_2) that share a predator (P ; after Chaneeton and Bonsall 2000). The direction of energy flow is shown by green arrows. The prevailing mode of control (i.e. balance of donor vs. trophic control) is shown by blue arrows. The direction of indirect effects is shown as black dashed arrows. Arrow widths indicate relative strengths. In *Classical AC* (A), the shared predator is supported by both prey (green arrows), more so by N_1 than N_2 . Both prey are more trophic than donor controlled (blue arrows point downwards), but N_2 is more strongly trophically controlled than N_1 . This generates reciprocal indirect effects (dashed arrows) that are negative in both directions ($-$, $-$), but asymmetric. In *Indirect Amensalism* (B), both prey remain trophically controlled, but predation on N_2 has no detectable effect on P (thin green line with no arrowhead). This prevents N_2 from exerting an indirect effect on N_1 (thin black dashed line with no arrowhead), causing indirect effects to be not just asymmetric but non-reciprocal (0 , $-$). *ACDC* (C) is also non-reciprocal, but by a different mechanism: N_1 is *donor* controlled (blue arrow points *upwards* from N_1 to P), preventing N_2 from having an indirect effect on N_1 (thin black dashed line with no arrowhead). Predators are supported mostly by N_1 , but predation on N_1 is mostly compensatory. Predation is additive on N_2 , which remains trophically controlled.

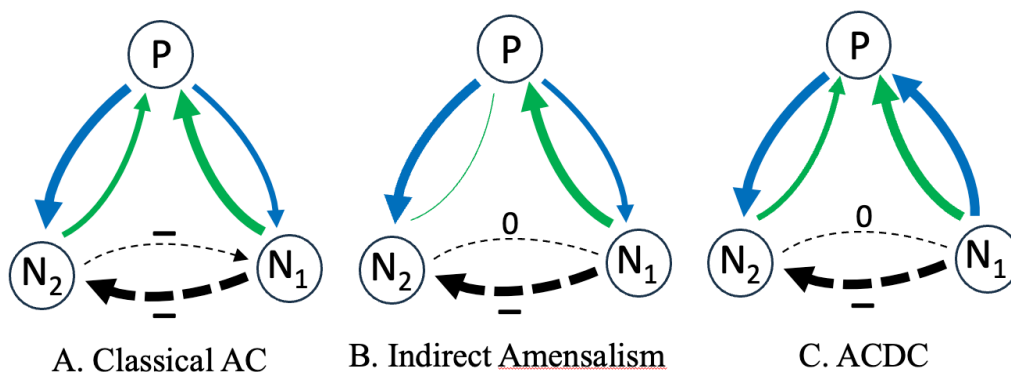
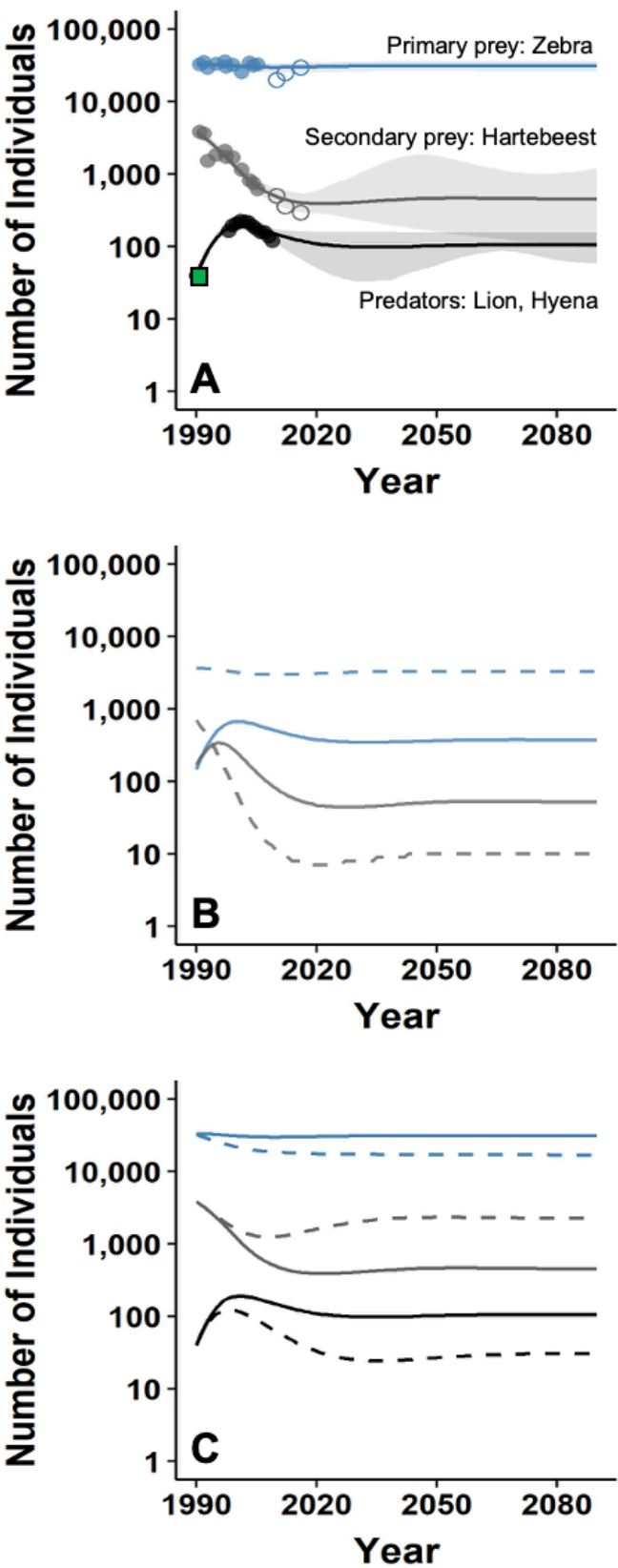


Figure 2. A) Example of 100-year projections of the *Full* model fit to population estimates (filled circles) for primary prey (zebra, in blue), secondary prey (hartebeest, in grey), and predators (lions and hyenas, in black) from the Laikipia region of northern Kenya. The initial predator value, indicated by a square, is estimated. Ninety-five percent confidence envelopes are indicated in lighter hues. Model parameters are given in Table 3. Open circles indicate population estimates that were not used in model fitting. B) Projections from the same model as in part A of annual mortality due to predation (solid lines) and to density-dependence (dashed lines). C) Comparison of population projections of the same model as in part A (solid lines) with projections following a 6% reduction in zebra growth (dashed lines). This reduced zebra and predator numbers, but increased hartebeest numbers. Colors signify the same species, and y-axes are $\log_{10}$ -transformed, in all panels. Figure created by Jacob R. Goheen.

1054 [Figure 2.]

1055



Appendix S1: Named types of apparent competition.

Authors: Nicholas J. Georgiadis, Douglas N. Kamaru, Alfred K. Kibungei, and Jacob R. Goheen

Manuscript title: Apparent competition couples donor and trophic control among prey of generalist predators

Journal: Ecology

Appendix S1. Named types of apparent competition. (Note: types are not mutually exclusive. They may mix core mechanisms, mediators, timescales, spatial or temporal contexts, directionality or outcomes, and applied conservation scenarios.)

No.	Type of Apparent Competition	Definition	Distinguishing features	Typical control structure	Comments	References
1	Classical apparent competition (numerical-response)	A negative indirect interaction between prey or host species mediated by a shared natural enemy: an increase in one prey raises enemy abundance or recruitment, thereby lowering the abundance or population growth of another prey.	Requires an enemy numerical response and enough time for it to occur. Direct competition for resources is unnecessary. Effects may be reciprocal or strongly asymmetric.	No fixed control assumption. Either prey may also be resource- or self-limited; the enemy need only generate a negative cross-effect, not be the sole or dominant limiting factor.	Holt's original formulation and the baseline against which the more specific rows below should be interpreted.	Holt (1977) Holt and Lawton (1994) Holt and Bonsall (2017)
2	Diffuse apparent competition	Negative indirect effects distributed through a web containing multiple prey or hosts and one or more shared enemies, rather than a single two-prey-one-enemy module.	Individual pairwise effects may be weak or difficult to detect even when cumulative enemy-mediated effects across the network are strong.	No fixed control assumption; control may vary among species and through time.	A scale and complexity extension of classical apparent competition, not a different causal process.	Holt (1977) Holt and Lawton (1994)
3	Parasite- or pathogen-mediated apparent competition	A shared parasite or pathogen causes one host to increase infection pressure—through reservoir competence, production of infectious stages, vector abundance, or transmission—thereby reducing another host.	The natural enemy is an infectious agent. Host competence and transmission dynamics replace or supplement the demographic response of a free-living predator.	No fixed control assumption. A reservoir host may be little affected, whereas a spillover host may be strongly disease-limited.	Often strongly asymmetric. The negative cross-effect must be mediated by the shared infectious agent.	Holt and Pickering (1985) Holt and Lawton (1994) Tompkins et. al. (2000)

Appendix S1. Named types of apparent competition (continued).

No.	Type of Apparent Competition	Definition	Distinguishing features	Typical control structure	Comments	References
4	Refuge-mediated apparent competition	One species provides physical structure or refuge that increases a consumer's local survival, persistence, or foraging activity, thereby increasing consumption of another species.	The refuge-providing species alters the enemy through habitat structure rather than through a food subsidy and need not itself be consumed.	No fixed assumption. The refuge provider may benefit, be unaffected, or be harmed; the second species experiences the negative indirect effect.	Orrock, Holt, and Baskett formalized and named this mechanism in 2010; Orrock et al. 2008 provided an influential empirical precursor.	Orrock et. al. (2008) Orrock et. al. (2010)
5	Short-term (behavior-mediated) apparent competition	A rapid negative indirect effect caused by enemy aggregation, prey switching, altered diet, or patch use before enemy reproduction changes total enemy abundance.	The response is behavioral. Total regional enemy abundance may remain unchanged, although local enemy density or activity can change through redistribution.	No fixed assumption. Depending on enemy behavior and relative prey abundance, short-term effects may instead be neutral or produce apparent mutualism.	Not synonymous with all trait-mediated apparent competition; it is defined chiefly by its rapid timescale and behavioral basis.	Holt and Kotler (1987) Holt and Bonsall (2017)
6	Stage-structured apparent competition	Apparent competition in which vulnerability, reproduction, or enemy effects differ among life stages, so that stage structure alters enemy dynamics and the indirect effects between prey.	Maturation, stage duration, and stage-specific attack rates can change coexistence, stability, and the strength of the indirect interaction.	No fixed assumption. Susceptible stages may be enemy-limited while other stages remain resource- or self-limited.	A structural extension of apparent-competition models, not a distinct mediator. Parasite- or pathogen-mediated interactions should not be subsumed under this label.	Bonsall and Holt (2003) Holt and Bonsall (2017)

Appendix S1. Named types of apparent competition (continued).

No.	Type of Apparent Competition	Definition	Distinguishing features	Typical control structure	Comments	References
7	Trait-mediated apparent competition	One prey induces a behavioral, morphological, physiological, or life-history change in a shared enemy that increases the enemy's per-capita effect on another prey.	Enemy abundance need not increase; the enemy's attack capability, preference, or other relevant trait changes.	No fixed assumption. The induced trait change must create a negative cross-effect on the second prey.	May operate rapidly or persistently. It overlaps with short-term apparent competition only when the relevant trait change is rapid and behavioral.	Abrams (1995) Ohgushi et. al. (2012) Banerji and Morin (2014)
8	Spatially subsidized apparent competition	Enemy abundance or activity in a focal habitat is supported by prey or resources from another habitat or patch, increasing enemy effects on local focal prey.	Cross-boundary movement of energy, prey, or enemies can decouple local enemy pressure from production of the focal prey.	The subsidy is exogenous or donor-controlled relative to the recipient habitat; the focal prey need not be exclusively trophically controlled.	A spatial context for classical or behavior-mediated apparent competition. Spatial heterogeneity can also weaken apparent competition and facilitate coexistence.	Holt (1984) Polis et. al. (1997)
9	Indirect amensalism	An extreme asymmetric case in which one prey strongly supports the shared enemy and depresses a second prey, while the second prey has negligible feedback on the first through the enemy.	The approximate interaction is one-way negative ($-/0$), rather than reciprocally negative ($-/-$).	The supporting prey commonly governs enemy abundance; the victim contributes little to enemy dynamics.	An interaction outcome, not a separate causal mechanism.	Chaneton and Bonsall (2000)

Appendix S1. Named types of apparent competition (continued).

No.	Type of Apparent Competition	Definition	Distinguishing features	Typical control structure	Comments	References
10	Hyperpredation (invasion-mediated apparent competition)	An introduced or newly abundant alternative prey supports a larger generalist-predator population, thereby increasing predation on a native focal prey.	Usually strongly asymmetric: the subsidizing prey is productive or resistant to predation, whereas the native focal prey is vulnerable.	The primary prey often remains resource- or self-limited or compensates for predation; the secondary prey may be strongly enemy-suppressed.	A restricted invasion-related type of apparent competition. The predator may be native or introduced. Smith and Quin introduced the term; Courchamp et al. developed the explicit model.	Smith and Quin (1996) Courchamp et. al. (2000) Roemer et. al. (2001)
11	Disturbance-mediated apparent competition (DMAC)	Habitat disturbance increases the abundance or accessibility of an alternative prey, which supports predators and thereby increases predation on a focal prey.	Canonical caribou pathway: early-seral forage increases moose or deer, which support wolves, increasing caribou mortality.	Primary prey remain donor controlled; secondary prey decline is mediated by the shared predator.	Direct effects of roads or linear features on predator travel efficiency are disturbance-mediated, but do not constitute apparent competition unless impacts on secondary prey are demonstrated.	Wittmer et. al. (2007) DeCesare et. al. (2010) DeMars et. al. (2019) Neufeld et. al. (2021)

Appendix S1. Named types of apparent competition (continued).

No.	Type of Apparent Competition	Definition	Distinguishing features	Typical control structure	Comments	References
12	Pulsed-resource apparent competition	A resource pulse increases the abundance or condition of an alternative prey and subsequently enemy abundance or activity, causing a delayed negative effect on shared focal prey.	The sequence is often lagged. Early switching or dilution can temporarily generate apparent mutualism, followed by apparent competition after the enemy numerical response.	The primary prey is temporarily bottom-up or donor-supported; focal prey may become enemy-suppressed during or after the enemy response.	Not every resource pulse produces apparent competition; the shared-prey–enemy pathway and negative cross-effect must be demonstrated.	Holt (2008) Schmidt and Ostfeld (2003)
13	Apparent Competition via Donor Control (ACDC)	A non-reciprocal apparent competition system in which a primary prey is predominantly donor- or resource-controlled and supports shared predators, while a secondary prey is substantially trophically controlled by those predators.	Classifies contrasting prey-control modes rather than a new transmission pathway; links compensatory predation on the primary prey with additive predation on the secondary prey.	Primary prey: donor- or resource-controlled. Secondary prey: trophic controlled. Predator abundance or activity is supported mainly by the primary prey.	The key diagnostic criterion is an empirically supported contrast in the prey-control modes. Can be: persistent across time; or recurrent /episodic when the system repeatedly becomes donor controlled during seasons, cycles, migrations, or environmental states but weakens, disappears, or reverses between episodes; or pulsed, which temporarily strengthens bottom-up support of a primary prey and predators, producing delayed and often transient suppression of a secondary prey.	Barraquand et. al. (2015) This paper

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Appendix S2: Descriptions and ratings of ACDC Candidate Systems

Authors: Nicholas J. Georgiadis, Douglas N. Kamaru, Alfred K. Kibungei, and Jacob R. Goheen

Manuscript title: Apparent competition couples donor and trophic control among prey of generalist predators

Journal: Ecology

Appendix S2. Descriptions and ratings of ACDC Candidate Systems

No.	System Name	System Name, Primary Prey, Predator, and Secondary Prey	Mechanism	Strengths and Weaknesses	ACDC Tempo	Natural, Human-caused, or Both	Evidence, References. amd Rating				
							Shared predator?	Predator responds to primary prey?	Secondary prey suppressed?	Primary prey donor controlled?	Weighted score
1	African savanna large mammals: Laikipia region, northern Kenya	Primary prey: Plains zebra (<i>Equus quagga</i>) Predator: Lion (<i>Panthera leo</i>); spotted hyena (<i>Crocuta crocuta</i>) Secondary prey: Jackson's hartebeest (<i>Alcelaphus buselaphus</i>)	In Laikipia, plains zebra function as a high-biomass, largely donor-controlled primary prey whose population dynamics are driven mainly by rainfall and density dependence rather than predation. This abundant and predictable prey base sustains and elevates lion and spotted hyena populations. Predators, in turn, disproportionately impact the secondary prey—Jackson's hartebeest—which are more vulnerable to predation. Empirical work shows that hartebeest experience strong suppression where lions are present, including reduced population growth, habitat shifts, and even Allee effects, while zebra remain relatively insensitive to predation pressure. The result is a classic apparent competition/donor control (ACDC) dynamic: zebra indirectly depress hartebeest by subsidizing shared predators.	Strengths: This is one of the clearest and strongest empirical ACDC examples. All key components are well supported: (i) a shared predator (lions consuming both prey), (ii) strong numerical response of the predator to the primary prey (zebra underpin lion recovery), (iii) clear and experimentally supported suppression of the secondary prey (hartebeest increase under lion exclusion and decline under exposure), and (iv) convincing evidence that the primary prey is largely donor controlled (rainfall- and density-driven zebra dynamics). The system also benefits from spatially explicit evidence (overlap in zebra–hartebeest habitat use) and quasi-experimental or exclusion-based inference, making the causal chain unusually well resolved compared to most field systems. Weaknesses: The system is not perfectly clean. The role of spotted hyenas is not explicit. Above all, the system is embedded in a livestock-influenced savanna, so broader anthropogenic context (grazing, land use, predator control) may modulate the dynamics and limit generalization to fully natural systems.	Persistent	Both	Demonstrated: lions consume both zebra and hartebeest; hartebeest suppression is strongest where lions are present, though hyenas may contribute secondarily Ng'weno et al. 2017 Ng'weno et al. 2019 Evidence rating: Strong	Demonstrated (strong): zebra are identified as the primary prey of lions in Laikipia; lion restoration was supported by abundant zebra, while zebra themselves were not shown to decline with recovering lion numbers Ng'weno et al. (2017) Ng'weno et al. (2019) Evidence rating: Strong	Demonstrated (strong): hartebeest growth shifts from negative to positive under lion exclusion; lion exposure produces an Allee effect and habitat shift . Predation risk on hartebeest increases when zebra are in the 'prey neighborhood. Evidence rating: Strong	Demonstrated (strong): zebra dynamics are driven principally by rainfall and density dependence; later analyses reaffirm rainfall- and density-based control in Laikipia. Georgiadis et al. (2003) Georgiadis et al. (2007) Ng'weno et al. (2019) Evidence rating: Strong	15
2	Bylot Island Arctic tundra vertebrates	Primary prey: Brown lemming (<i>Lemmus trimucronatus</i>) and northern collared lemming (<i>Dicrostonyx groenlandicus</i>) Predator: Arctic fox (<i>Vulpes lagopus</i>) Secondary prey: Greater snow goose (<i>Anser caerulescens atlanticus</i>); shorebirds including Baird's sandpiper (<i>Calidris bairdii</i>) and white-rumped sandpiper (<i>Calidris fuscicollis</i>)	Cyclic lemmings drive strong predator functional and numerical responses. During lemming peaks, prey switching reduces predation on bird nests (apparent mutualism). Following lemming declines, elevated predator pressure and switching increase predation on alternative prey, producing delayed apparent competition. Thus, the system exhibits lagged ACDC rather than contemporaneous ACDC.	Strengths: This is a mechanistically clean and well-documented system, with strong evidence for shared predation, prey switching, and cyclic primary prey dynamics, making it one of the best empirical tests of predator-mediated indirect interactions. The Arctic fox shows both functional and numerical responses to lemmings, and there is clear, repeatable suppression of bird nesting success when lemmings are scarce. Weaknesses: secondary prey are not suppressed when primary prey are abundant. Instead, prey switching produces contemporaneous buffering, with negative effects emerging only after a lag via predator carryover. Thus, the system is best characterized as lagged ACDC rather than true contemporaneous ACDC, and its classification depends critically on timing.	Recurrent/ Episodic	Natural	Arctic foxes prey on lemmings and on bird eggs/chicks; nest predation risk varies with lemming abundance Angelstam et al. (1984) McKinnon et al. (2014) Bêty et al. (2002) Evidence rating: Strong	Arctic fox reproductive output, den use, and foraging track lemming abundance. Angelstam et al. (1984) Bêty et al. (2002) Evidence rating: Strong	Goose nesting success and shorebird nest survival decline in low-lemming years due to increased fox predation Angelstam et al. (1984) McKinnon et al. (2014) Bêty et al. (2002) Evidence rating: Strong	Lemmings exhibit strong cyclic dynamics driven by intrinsic and seasonal processes, with predation contributing but not solely regulating dynamics Fauteux et al. (2015) Evidence rating: Strong	15

Appendix S2. Descriptions and ratings of ACDC Candidate Systems (continued)

No.	System Name	System Name, Primary Prey, Predator, and Secondary Prey	Mechanism	Strengths and Weaknesses	ACDC Tempo	Natural, Human-caused, or Both	Evidence, References. amd Rating				Weighted score
							Shared predator?	Predator responds to primary prey?	Secondary prey suppressed?	Primary prey donor controlled?	
3	Salmon-subsidized stream food web	Primary prey: Anadromous salmon (<i>Oncorhynchus gorbuscha</i> , <i>O. keta</i>) Predator: Resident fishes (especially coastrange sculpin <i>Cottus aleuticus</i>) Secondary prey: Benthic invertebrates (Ephemeroptera, Trichoptera, Diptera)	Anadromous salmon (<i>Oncorhynchus</i> spp.) deliver a large, externally generated pulse of energy to streams during spawning. Resident fishes—especially coastrange sculpin—respond to this subsidy by increasing in density and/or shifting foraging toward salmon-derived resources. This elevated predator population then intensifies predation on benthic invertebrates (e.g., Ephemeroptera, Trichoptera, Diptera), as shown experimentally when salmon subsidies are added. Thus, a donor-controlled input (salmon) boosts a shared predator, which in turn suppresses alternative prey, producing a temporally pulsed ACDC dynamic with potential lags and mixed direct–indirect pathways.	Strengths: This is a mechanistically clear, empirically supported system: salmon provide a strongly donor-controlled, externally generated subsidy; resident fishes respond numerically and/or behaviorally; and increased predation on benthic invertebrates has been demonstrated experimentally. The key ACDC pathway (donor → predator → suppression of alternative prey) is therefore well supported. Weaknesses: The system is temporally pulsed and lagged, so ACDC operates intermittently rather than persistently, making it harder to confirm. Predator responses are heterogeneous (e.g., strong for <i>Cottus aleuticus</i> , weak for <i>C. asper</i>), reducing generality. The food web is also complex, with simultaneous bottom-up (nutrient enrichment of invertebrates) and top-down effects, making net outcomes context-dependent. Finally, direct evidence that the same predator population strongly links both prey types (salmon-derived resources and invertebrates) is more limited than ideal in the retained reference set.	Persistent	Both	Implied but not directly supported by retained refs Evidence rating: Credible	Yes – sculpin density increases with salmon density Swain and Reynolds (2015) Evidence rating: Strong	Yes – experimentally increased fish predation on invertebrates under salmon subsidy Collins et al. (2016) Evidence rating: Strong	Yes – salmon are externally generated subsidy Swain and Reynolds (2015) Collins et al. (2016) Evidence rating: Strong	14.5
4	Mast/rodent–carnivore–wood warbler system	Primary prey: Forest rodents, mainly <i>Apodemus</i> spp. and bank vole (<i>Myodes glareolus</i>) Predator: Red fox (<i>Vulpes vulpes</i>) and martens, especially pine marten (<i>Martes martes</i>) Secondary prey: Wood warbler (<i>Phylloscopus sibilatrix</i>) nests	Synchronous mast seeding subsidizes forest rodents, mainly <i>Apodemus</i> mice and bank voles, which function as temporarily donor-controlled primary prey. Rodent outbreaks support numerical, aggregative, or dietary responses by generalist predators, especially red fox and pine marten, which then incidentally depredate ground nests of wood warbler. Nest survival is lower in high-rodent years, consistent with apparent competition mediated by shared predators. Best interpreted as pulsed, temporally lagged ACDC.	Strengths: Grendelmeier et al. (2018) directly measured rodents, predator occurrence, nest predation, and wood warbler nest survival in one integrated field study, and explicitly interpret the system as apparent competition. Weaknesses: the “primary prey” label should not be Microtus spp.; the dominant rodents were <i>Apodemus</i> spp. and <i>Myodes glareolus</i> . Also, the marten response alone was not statistically supported, although combined rodent-hunting mammals and foxes were. This candidate should be viewed more as a mast/rodent-pulse system rather than a <i>Microtus</i> -specific one.	Pulsed	Natural	Yes Jędrzejewski et al. (1993) Maziarz et al. (2019) Grendelmeier et al. (2018) Evidence rating: Strong	Rodent-hunting mammals, especially foxes, were more abundant in high-rodent years Pucek et al. (1993) Selva et al. (2012) Grendelmeier et al. (2018) Maag et al. (2024) Evidence rating: Credible	Wood warbler nest survival was lower in high-rodent years; rodent-hunting predators accounted for more nest predation Maziarz et al. (2019) Grendelmeier et al. (2018) Maag et al. (2024) Evidence rating: Strong	Rodent peaks followed mast/resource pulses; bottom-up/pulsed support from focal study and Białowieża rodent dynamics Pucek et al. (1993) Selva et al. (2012) Maag et al. (2024) Evidence rating: Strong	14
5	African savanna large mammals: Serengeti ecosystem	Primary prey: Blue wildebeest (<i>Connochaetes taurinus</i>); plains zebra (<i>Equus quagga</i>) Predator: Lion (<i>Panthera leo</i>); spotted Hyena (<i>Crocuta crocuta</i>) Secondary prey: Thomson’s gazelle (<i>Eudorcas thomsonii</i>); topi (<i>Damaliscus lunatus</i>)	In the Serengeti, migratory primary prey—blue wildebeest and probably plains zebra—are largely regulated by bottom-up forces (rainfall, forage, and disease release), generating high and seasonally concentrated biomass. This subsidizes predator populations, especially lions and spotted hyenas, whose abundance and spatial dynamics track the availability and accessibility of migratory herds. These predator populations then impose sustained predation pressure on resident, non-migratory secondary prey such as Thomson’s gazelle and topi, creating a predator-mediated linkage between the two prey groups consistent with ACDC.	Strengths: This is one of the strongest large-scale, real-world examples of the subsidy side of ACDC. The causal chain from migratory prey → predator numerical response is exceptionally well supported, including long-term data showing lion population expansion following wildebeest recovery and detailed studies demonstrating that predators, especially hyenas, track migratory prey biomass and accessibility. The system also clearly satisfies the shared-predator requirement, with both lions and hyenas consuming migratory and resident prey. The spatial and temporal coupling between migration, predator aggregation, and predation risk is unusually well resolved. Weaknesses: The factor preventing a “clean” ACDC classification is weaker evidence for strong, predator-driven suppression of secondary prey. While resident ungulates clearly experience predation, the degree to which this translates into sustained demographic limitation (as opposed to additive mortality or context-dependent effects) is less well established and lacks the experimental clarity seen in systems like Laikipia or Kruger.	Persistent	Natural	Demonstrated: lions and hyenas consume both migratory (primary) and resident (secondary) prey Sinclair et al. (2003) Packer et al. (2005) Evidence rating: Strong	Demonstrated (strong): lion population size increased with wildebeest recovery and remained elevated; predator dynamics track migratory prey biomass and accessibility Sinclair et al. (2003) Packer et al. (2005) Hopcraft et al. (2005) Sinclair and Arcese (1995) Evidence rating: Strong	Demonstrated (moderate): resident ungulates experience sustained predation; evidence for demographic suppression is suggestive, derived from a human-caused perturbation of the predators, but less experimental than in Laikipia/Kruger Sinclair et al. (2003) Scheel (1993) Evidence rating: Credible	Primary prey (wildebeest) are strongly influenced by wet season rainfall and forage availability. Studies have suggested zebra may be trophic controlled, but this is not supported by the quantitative assessment of ACDC in this study. Sinclair (1979) Mduma et al. (1999) Evidence rating: Strong	13.5

Appendix S2. Descriptions and ratings of ACDC Candidate Systems (continued)

No.	System Name	System Name, Primary Prey, Predator, and Secondary Prey	Mechanism	Strengths and Weaknesses	ACDC Tempo	Natural, Human-caused, or Both	Evidence, References, and Rating				Weighted score
							Shared predator?	Predator responds to primary prey?	Secondary prey suppressed?	Primary prey donor controlled?	
6	Humboldt Current anchoveta system	Primary prey: Anchoveta (<i>Engraulis ringens</i>) Predator: Fish (e.g., <i>Merluccius gayi</i>), seabirds (<i>Leucocarbo bougainvillii</i>, <i>Sula variegata</i>, <i>Pelecanus thagus</i>), marine mammals Secondary prey: Sardine (<i>Sardinops sagax</i>), silverside (<i>Odontesthes regia</i>), other pelagic fishes/invertebrates	In the Humboldt Current, Peruvian anchoveta functions as a huge, climate-sensitive forage base that supports a broad predator guild, including Chilean hake (<i>Merluccius gayi</i>), Chilean jack mackerel (<i>Trachurus murphyi</i>), chub mackerel (<i>Scomber japonicus</i>), guanay cormorant (<i>Leucocarbo bougainvillii</i>), Peruvian booby (<i>Sula variegata</i>), Peruvian pelican (<i>Pelecanus thagus</i>), pinnipeds, and other marine predators [1–3]. During warm/El Niño or low-anchoveta periods, predator diets and distributions shift toward alternative prey such as Peruvian silverside (<i>Odontesthes regia</i>), South American pilchard/sardine (<i>Sardinops sagax</i>), mesopelagic fishes, squid, and other pelagic/demersal taxa [2,3]. This creates an ACDC-like mechanism: anchoveta subsidies elevate or maintain predator demand, and when anchoveta availability falls, predation pressure can be redistributed across alternative prey.	Strengths: the system has a massive donor-like prey base, a well-documented shared predator guild, and strong predator responses to anchoveta availability. Weaknesses: It is not a clean ACDC case: anchoveta is heavily controlled by upwelling, ENSO, regime shifts, and fishing, and the evidence for population-level suppression of alternative prey by redirected predators is mostly inferred from diet switching and trophic models rather than direct demographic experiments or coordinated time series [2–4].	Recurrent/Episodic	Natural	Demonstrated: multiple predators consume anchoveta and alternative prey Gonzalez-Pestana et al. (2022) Evidence rating: Strong	Demonstrated (strong): seabird abundance, survival, and diet track anchoveta and ENSO variability Goya and Garcia-Godos (2002) Evidence rating: Strong	Moderate/inferred: predators switch to alternative prey during anchoveta decline, but population-level suppression is not well demonstrated Goya and Garcia-Godos (2002) Evidence rating: Credible	Strongly environmental: anchoveta governed by ENSO, regime shifts, and upwelling Alheit and Niquen (2004) Chavez et al. (2003) Evidence rating: Strong	13.5
7	African savanna large mammals: Kruger National Park	Primary prey: Plains zebra (<i>Equus quagga</i>); blue wildebeest (<i>Connochaetes taurinus</i>); buffalo (<i>Syncerus caffer</i>) Predator: Lion (<i>Panthera leo</i>); spotted Hyena (<i>Crocuta crocuta</i>) Secondary prey: Greater kudu (<i>Tragelaphus strepsiceros</i>), roan (<i>Hippotragus equinus</i>), sable (<i>Hippotragus niger</i>), impala (<i>Aepyceros melampus</i>), giraffa (<i>Giraffa camelopardalis</i>)	In Kruger’s savanna, abundant primary grazers—plains zebra, blue wildebeest, and buffalo—support high densities of large predators, especially lions, with spotted hyenas contributing. High predator densities then impose top-down pressure on the rarer, more vulnerable secondary prey such as greater kudu (<i>Tragelaphus strepsiceros</i>), roan (<i>Hippotragus equinus</i>), and sable (<i>Hippotragus niger</i>), contributing to their declines. However, the primary prey themselves are not purely donor-controlled: their dynamics are strongly influenced by rainfall, forage availability, and density dependence, with predation pressure switching during dry seasons and droughts.	Strengths: This is a strong and ecologically realistic ACDC candidate. The shared predator link is well documented, with lions clearly preying on both abundant grazers and rarer antelope. There is robust evidence that predator density and spatial distribution track primary prey abundance, satisfying the key subsidy requirement. At the same time, declines in kudu, roan, and sable are consistently associated with predation pressure, especially in proximity to primary prey. The system operates at large spatial and temporal scales with multiple independent datasets, making it one of the best-supported large-mammal examples of predator-mediated indirect effects. Weaknesses: Mainly that donor control of the primary prey is incomplete. Zebra and wildebeest populations are not independent of predation, such that predator–prey feedbacks can occur in both directions, depending on environmental variability (especially drought).	Persistent	Human	Demonstrated: lions prey on primary (zebra/wildebeest/bur ralo) and secondary (Gt. kudu/roan/sable) prey; other predators (hyenas) contribute Owen-Smith et al. (2005) Mills et al. (1995) Evidence rating: Strong	Demonstrated: lion density and distribution track abundance and spatial distribution of zebra/wildebeest Owen-Smith et al. (2005) Funston et al. (2003) Evidence rating: Strong	Demonstrated: kudu, roan and sable declines linked to predation Harrington et al. (1999) Owen-Smith and Mills (2006) Owen-Smith et al. (2005) Evidence rating: Strong	Zebra and wildebeest influenced strongly by rainfall and forage, but also show predator sensitivity (especially during drought) Owen-Smith and Mills (2006) Funston et al. (2003) Ogutu et al. (2011) Evidence rating: Credible	13

Appendix S2. Descriptions and ratings of ACDC Candidate Systems (continued)

No.	System Name	System Name, Primary Prey, Predator, and Secondary Prey	Mechanism	Strengths and Weaknesses	ACDC Tempo	Natural, Human-caused, or Both	Evidence, References. amd Rating				
							Shared predator?	Predator responds to primary prey?	Secondary prey suppressed?	Primary prey donor controlled?	Weighted score
8	Vole cycles–predator guild–ground birds	Primary prey: Field vole (<i>Microtus agrestis</i>), tundra/root vole (<i>Microtus oeconomus</i>), bank vole (<i>Myodes glareolus</i>) Predator: Red fox (<i>Vulpes vulpes</i>), stoat (<i>Mustela erminea</i>), least weasel (<i>Mustela nivalis</i>), pine marten (<i>Martes martes</i>), raptors incl. hen harrier (<i>Circus cyaneus</i>), common buzzard (<i>Buteo buteo</i>), owls (<i>Strix</i> spp.) Secondary prey: Black grouse (<i>Lyrurus tetrix</i>), capercaillie (<i>Tetrao urogallus</i>), red/willow grouse (<i>Lagopus lagopus</i> / L. l. scotica), other ground-nesting birds	Cyclic voles are primarily governed by bottom-up processes (resource dynamics, climate, intrinsic density dependence), producing large-amplitude fluctuations. A generalist predator guild—red fox, mustelids, raptors <i>Circus cyaneus</i>, <i>Buteo buteo</i>, <i>Strix</i> spp.)—responds numerically and functionally to vole abundance. When vole populations decline, these predators switch to alternative prey, including ground-nesting birds such as black grouse, capercaillie, and red grouse, increasing predation pressure and reducing their reproductive success. This produces phase-dependent apparent competition consistent with ACDC dynamics.	Strengths: This is a textbook apparent competition system with unusually strong empirical support. Multiple lines of evidence demonstrate predator switching, inverse relationships between vole abundance and grouse performance, and clear predator-removal effects on ground-nesting birds. The primary prey (voles) meets the donor-control definition in a broad sense, as its dynamics are dominated by bottom-up processes including resource variation, climate forcing, and intrinsic density dependence. The large amplitude of vole cycles generates a strong and temporally distinct signal, making ACDC dynamics both detectable and mechanistically interpretable. Weaknesses: The multi-predator guild introduces complexity, with different predator species responding to vole fluctuations on different timescales and through different mechanisms. This heterogeneity can blur or weaken the apparent competition signal and complicate attribution of effects to a single, unified ACDC process.	Recurrent/ Episodic	Natural	Yes — generalist predators consume both voles and grouse/nests Angelstam et al. (1984) Ludwig et al. (2020) Evidence rating: Strong	Yes — predator diet, activity, and/or abundance track vole cycles; switching occurs when voles decline Angelstam et al. (1984) Ludwig et al. (2020) Evidence rating: Strong	Yes — increased nest and adult predation on grouse; predator removal improves tetraonid success Angelstam et al. (1984) Marcström et al. (1988) Norrdahl and Korpimäki (2000) Evidence rating: Strong	Yes (broad) — vole dynamics primarily bottom-up (resource, climate, density dependence), though modified by specialist predators. Barraquand et al. (2015) Evidence rating: Credible	13
9	California Current upwelling system	Primary prey: Northern anchovy (<i>Engraulis mordax</i>) and Pacific sardine (<i>Sardinops sagax</i>) Predator: Common murre (<i>Uria aalge</i>) Secondary prey: Juvenile Chinook salmon (<i>Oncorhynchus tshawytscha</i>)	In the California Current, anchovy function as donor-controlled prey that structure predator distributions, including common murre. Rather than consistently increasing predation on juvenile Chinook salmon, anchovy abundance can reduce predation through alternative-prey buffering, whereas anchovy scarcity leads to increased predation on salmon. This system therefore exhibits sign-switching indirect interactions, consistent with an ACDC framework in which the strength and direction of predator-mediated coupling depend on the state of the donor-controlled prey. This system does not weaken ACDC. It reveals that ACDC can include both apparent competition and apparent mutualism, with the sign determined by prey state.	Strengths: Predation risk on juvenile salmon varies with the availability of alternative prey such as anchovy, which can reduce predation pressure through prey switching or dilution effects (Emmett & Sampson 2007; Phillips et al. 2021). Weaknesses: Although direct evidence for increased predation under anchovy scarcity is limited, spatial overlap and system-level correlations suggest that predator-mediated mortality may increase when alternative prey are scarce.	Recurrent/ Episodic	Natural	Murres consume both anchovy and juvenile salmon Wells et al. (2017) Thompson et al. (2022) Evidence rating: Strong	Predator diet, distribution, and reproduction track anchovy availability Warzybok et al. (2018) Thompson et al. (2022) Evidence rating: Strong	Murre predation on juvenile salmon increases when foraging on anchovy, but not necessarily trophic controlled. Wells et al. (2017) Thompson et al. (2022) Evidence rating: Strong	Sardine/anchovy dynamics driven by upwelling, climate variability, and productivity Sydeman et al. (2020) Chavez et al. (2003) Bakun (1996) Evidence rating: Credible	13

Appendix S2. Descriptions and ratings of ACDC Candidate Systems (continued)

No.	System Name	System Name, Primary Prey, Predator, and Secondary Prey	Mechanism	Strengths and Weaknesses	ACDC Tempo	Natural, Human- caused, or Both	Evidence, References. and Rating				
							Shared predator?	Predator responds to primary prey?	Secondary prey suppressed?	Primary prey donor controlled?	Weighted score
10	Temperate forest invertebrates	Primary prey: Herbivorous insects (e.g., winter moth, <i>Operophtera brumata</i> ; forest tent caterpillar, <i>Malacosoma disstria</i>) Predator: Parasitoids (e.g., ichneumonid and braconid wasps) Secondary prey: Other herbivorous insects (multiple species)	Outbreaking forest Lepidoptera (e.g., winter moth <i>Operophtera brumata</i> , forest tent caterpillar <i>Malacosoma disstria</i> , spongy moth <i>Lymantria dispar</i>) can generate strong numerical and functional responses in parasitoids (ichneumonids, braconids, tachinids). When parasitoids are sufficiently generalist and temporally synchronized, this elevated enemy pressure can spill over onto other herbivorous insects, creating parasitoid-mediated apparent competition. However, this pathway is highly contingent on parasitoid sharing, phenological overlap, and host specificity, and is often weak or absent in real forest food webs.	Strengths: This system has a clear and well-established mechanistic foundation for ACDC: parasitoids routinely attack multiple host species, and host density-dependent responses (both numerical and functional) are well documented in outbreaking forest Lepidoptera. The key ingredients—shared enemies, strong responses to primary prey, and the potential for indirect interactions—are all present. In simpler or more controlled settings (e.g., pairwise moth–parasitoid systems), parasitoid-mediated apparent competition has been directly demonstrated, confirming that the mechanism can operate. In addition, many outbreak species (e.g., <i>Operophtera brumata</i> , <i>Malacosoma disstria</i>) exhibit dynamics that are at least partly bottom-up or density-driven, satisfying the donor-control side of ACDC. The system is therefore structurally consistent and mechanistically plausible, and it likely operates intermittently during outbreak phases when parasitoid populations are elevated. Weaknesses: The main limitation is that the system is diffuse and weakly resolved empirically. Food-web studies often show limited parasitoid sharing across host species, which undermines the core AC linkage. Even where sharing exists, direct evidence that outbreak- driven parasitoid increases suppress other herbivores is scarce or inconsistent, with most support coming from short-term or simplified systems rather than full forest communities. The primary prey are also not cleanly donor-controlled, as natural enemies (including parasitoids and pathogens) contribute to outbreak collapse, blurring the bottom-up vs. top-down distinction. More broadly, phenological mismatches, host specificity, and spatial heterogeneity fragment the interaction network, preventing strong, system-wide ACDC dynamics. As a result, this is best viewed as a conditional or intermittent ACDC system, much weaker and less definitive than canonical cases with tightly coupled species and clearly demonstrated indirect suppression.	Recurrent/ Episodic	Natural	Demonstrated: parasitoids attack multiple herbivore hosts, creating shared-enemy networks Timms et al. (2012) Teder and Tammaru (2003) Evidence rating: Strong	Demonstrated (strong): parasitoid abundance and attack rates increase with primary herbivore density (outbreaks) Teder and Tammaru (2003) Hassell (2000) Evidence rating: Strong	Demonstrated (moderate): elevated parasitoid pressure can suppress or delay increases in other herbivore species Hassell (2000) Klemola et al. (2009) Evidence rating: Strong	Partial / context- dependent: herbivore outbreaks driven largely by bottom-up factors but also influenced by natural enemies (including parasitoids) Timms et al. (2012) Turchin (2013) Evidence rating: Credible	13
11	Boreal ungulate invasion system	Primary prey: White- tailed deer (<i>Odocoileus virginianus</i>) Predator: Wolf (<i>Canis lupus</i>) Secondary prey: Caribou (<i>Rangifer tarandus</i>)	In the western boreal forest, white- tailed deer (<i>Odocoileus virginianus</i>) have expanded northward due to milder winters and increased early- seral forage created by forestry and other human disturbances. This bottom-up, climate- and habitat- driven increase in deer provides a substantial energetic subsidy to wolves (<i>Canis lupus</i>), producing a strong numerical response and elevating predator densities across the landscape. Woodland caribou (<i>Rangifer tarandus</i>), which co-occur with wolves but do not benefit from these habitat changes, experience increased predation as a consequence of this inflated wolf population. Thus, deer function as a donor- controlled primary prey that indirectly suppresses caribou via shared predation, generating a classic apparent competition dynamic in which the driver is external (climate and land use) rather than trophic regulation of the primary prey.	Strengths. This is one of the clearest terrestrial ACDC cases because all four elements are well supported and tightly linked: (i) a shared predator (wolves, <i>Canis lupus</i>) demonstrably preying on both primary (deer, <i>Odocoileus virginianus</i>) and secondary prey (caribou, <i>Rangifer tarandus</i>); (ii) a strong predator numerical response to increases in the primary prey; (iii) measurable negative impacts on the secondary prey attributable to elevated predation; and (iv) a convincingly donor- controlled primary prey driven by exogenous factors (climate warming and anthropogenic habitat change). Importantly, the mechanism has been documented across multiple studies and spatial scales, not just inferred, and it aligns with independent lines of evidence on landscape change, predator movement, and ungulate dynamics. This convergence makes it a robust, policy-relevant example of apparent competition embedded within a broader ACDC framework. Weaknesses. The system is not purely trophic in its internal dynamics: it depends heavily on anthropogenic disturbance and climate forcing, raising questions about generality to undisturbed systems. Mechanistically, the pathway is also more complex than a simple three-species module—linear features and landscape fragmentation simultaneously facilitate deer expansion and increase wolf hunting efficiency, making it difficult to cleanly partition bottom-up versus top-down effects. In addition, caribou declines are influenced by multiple interacting factors (habitat loss, alternate prey such as moose, and human activity), so attributing impacts solely to deer-mediated apparent competition can be an oversimplification. Finally, the dynamics may be transient or directional (i.e., an ongoing invasion/expansion) rather than a stable, persistent ACDC state, which weakens its value as a canonical equilibrium example.	Persistent	Both	Yes Latham et al. (2011) Evidence rating: Strong	Deer expansion → strong wolf numerical response Latham et al. (2011) Latham et al. (2011) Latham et al. (2011) Evidence rating: Strong	Caribou decline linked to elevated wolf predation Latham et al. (2011) DeCesare et al. (2010) Wittmer et al. (2007) Evidence rating: Strong	Deer expansion driven by climate warming + anthropogenic forage (bottom-up), weak top-down control Dawe et al. (2014) Côté et al. (2004) Evidence rating: Credible	13

Appendix S2. Descriptions and ratings of ACDC Candidate Systems (continued)

No.	System Name	System Name, Primary Prey, Predator, and Secondary Prey	Mechanism	Strengths and Weaknesses	ACDC Tempo	Natural, Human-caused, or Both	Evidence, References. amd Rating				
							Shared predator?	Predator responds to primary prey?	Secondary prey suppressed?	Primary prey donor controlled?	Weighted score
12	Southern Ocean Antarctic krill-whales-copepods	Primary prey: Antarctic krill (<i>Euphausia superba</i>) Predator: Baleen whales, especially humpback whales (<i>Megaptera novaeangliae</i>), blue whales (<i>Balaenoptera musculus</i>), fin whales (<i>B. physalus</i>), Antarctic minke whales (<i>B. bonaerensis</i>); also penguins and albatrosses Secondary prey: Copepods, especially <i>Calanus</i> spp.; fish/myctophids are a weaker secondary pathway	In the Southern Ocean, Antarctic krill function as a dominant, bottom-up–controlled energy pathway structured by sea ice, climate, and primary production. High krill biomass supports large populations of baleen whales, penguins, and other predators, whose distribution and foraging intensity track krill availability and can locally remove substantial fractions of krill biomass. Because some predators—particularly certain baleen whales—can also exploit alternative zooplankton such as copepods (and, more weakly, myctophid fish), variation in krill availability has the potential to shift predator pressure onto these secondary prey. This creates a conditional apparent-competition pathway in which krill act as a subsidy sustaining predator populations that may indirectly affect other zooplankton, although direct empirical evidence for strong suppression of secondary prey remains limited.	Strengths: This system has exceptionally strong support for the bottom-up, donor-controlled primary prey component: Antarctic krill are tightly regulated by sea ice, climate, and primary production, and they form a dominant energy pathway in the Southern Ocean. The predator response is also well established—baleen whales, penguins, and other predators track krill spatially and temporally, with evidence that they can remove substantial fractions of local krill biomass. The system is therefore mechanistically coherent and large-scale, with clear coupling between krill dynamics and predator populations, making it one of the best marine analogues to subsidy-driven food webs. Weaknesses: The key limitation is the weak empirical evidence for effects on secondary prey, which is the most critical and least supported component of ACDC. Although models suggest that reduced krill availability could shift predation or competition onto copepods or other zooplankton, direct field demonstrations of suppression are scarce. In addition, the system is diffuse and heterogeneous: predators vary in diet breadth, copepods are not always strongly linked to whale predation, and alternative pathways (e.g., salps, fish) complicate inference. As a result, this is not a clean, canonical ACDC case, but rather a plausible, large-scale candidate in which the indirect pathway is inferred more than directly demonstrated.	Recurrent/ Episodic	Human	Yes, but unevenly. Many Southern Ocean baleen whales are strongly euphausiid-dependent, while Southern Ocean zooplankton also include copepods, salps, and other euphausiids. Bestley et al. (2020) Johnston et al. (2022) Evidence rating: Credible	Yes. Whale distribution and local consumption are linked to krill biomass; in the South Sandwich Islands region, baleen whales were estimated to consume 19–29% of available krill standing stock. Penguins and other predators also show diet, provisioning, and productivity responses to krill availability. Baines et al. (2022) Croxall et al. (1999) Evidence rating: Credible	Weak to moderate, mostly inferred. Tulloch et al. model recovering baleen whales, krill, and copepods and project increased competition under prey decline, but direct field evidence that whale recovery suppresses copepods or fish is limited. Schofield et al. (2024) Johnston et al. (2022) Evidence rating: Strong	Yes. Krill-based Southern Ocean food webs are strongly structured by sea ice, climate, primary production, and other bottom-up forcing.	12
13	Boreal forest disturbance large mammals	Primary prey: Moose (<i>Alces alces</i>) Predator: Wolves (<i>Canis lupus</i>) Secondary prey: Woodland caribou (<i>Rangifer tarandus caribou</i>)	Spruce budworm (<i>Choristoneura fumiferana</i>) outbreaks cause widespread defoliation that shifts boreal forests toward early-successional vegetation, increasing browse availability for moose (<i>Alces alces</i>). Elevated moose abundance can support higher wolf (<i>Canis lupus</i>) densities through a strong numerical response, and these wolves prey on both moose and woodland caribou (<i>Rangifer tarandus caribou</i>). Because caribou do not benefit from the increased forage and remain vulnerable to predation, they experience sustained suppression via this predator subsidy. The result is a disturbance-mediated apparent competition dynamic in which a donor-influenced increase in moose indirectly drives increased predation pressure on caribou, even though caribou are not directly linked to the original disturbance.	Strengths: This system rests on a very strong and well-documented apparent competition core: wolves respond numerically to abundant moose, and elevated predator densities are consistently linked to declines in woodland caribou. Multiple independent studies show the same directional mechanism across regions and contexts, including demographic impacts on caribou and clear predator-mediated pathways. The structure is therefore clean and canonical—shared predation, a strong predator response, and measurable suppression of the secondary prey. In addition, the disturbance component is ecologically plausible and consistent with general boreal dynamics: large-scale defoliation events are known to reset forest succession and increase early-seral forage, providing a credible pathway for boosting moose populations. Weaknesses: The key limitation is that the full ACDC chain is not directly demonstrated as a single, integrated system. In particular, the link between spruce budworm outbreaks and sustained increases in moose abundance is inferred rather than empirically established, and most of the strongest apparent competition evidence comes from systems driven by logging or fire rather than insect outbreaks. As a result, the “donor-controlled” status of moose is only partial and context-dependent, weakening the ACDC classification relative to stronger examples. More broadly, the system mixes disturbance ecology with trophic dynamics without a single study tying all components together, so it functions best as a plausible synthesis rather than a fully resolved, self-contained ACDC case.	Persistent	Natural	Wolves prey on both moose and caribou across boreal systems Wittmer et al. (2007) Serrouya et al. (2011) Evidence rating: Strong	Wolf density increases with moose to abundance (numerical response) by moose (apparent competition) Messier (1994) Evidence rating: Strong	Caribou decline due to elevated wolf predation sustained by moose (apparent competition) Wittmer et al. (2007) Serrouya et al. (2011) Hebblewhite et al. (2005) Evidence rating: Credible	Spruce budworm–driven defoliation restructures forests and promotes early-seral vegetation and browse availability relevant to moose Blais (1983) Fleming et al. (2002) Evidence rating: Credible	11.5

Appendix S2. Descriptions and ratings of ACDC Candidate Systems (continued)

No.	System Name	System Name, Primary Prey, Predator, and Secondary Prey	Mechanism	Strengths and Weaknesses	ACDC Tempo	Natural, Human-caused, or Both	Evidence, References. and Rating				
							Shared predator?	Predator responds to primary prey?	Secondary prey suppressed?	Primary prey donor controlled?	Weighted score
14	Great Lakes Alewife-salmon-native fish system	Primary prey: Invasive Alewife (<i>Alosa pseudoharengus</i>) Predator: Introduced Salmonids (e.g., <i>Oncorhynchus tshawytscha</i> , <i>O. kisutch</i>) Secondary prey: Native planktivorous fish (e.g., <i>Coregonus hoyi</i> , <i>Osmerus mordax</i>)	In the Great Lakes, invasive alewife provide a dominant pelagic prey base that supports high densities of introduced Pacific salmon. Salmon populations respond strongly to alewife abundance, with growth, condition, and overall performance closely tied to this prey resource. However, salmonids are not exclusive specialists and also consume native planktivorous fishes (e.g., <i>Coregonus hoyi</i> , <i>Osmerus mordax</i>), linking the two prey groups through shared predation. As a result, high alewife abundance sustains elevated predator pressure that contributes to suppression of native planktivores via both direct predation and broader food-web effects. Because alewife dynamics are influenced substantially by bottom-up processes and invasion history, they function as a partially donor-controlled prey, creating a managed, mixed-control ACDC system in which an abundant primary prey subsidizes predators that impact secondary prey.	Strengths: This system has unusually strong empirical support for the core ACDC mechanism. Alewife form a dominant pelagic prey base, and introduced salmonids show a clear numerical and functional response, with growth, condition, and population performance tracking alewife abundance. Salmonids also consume native planktivores (e.g., <i>Coregonus hoyi</i> , <i>Osmerus mordax</i>), establishing a well-supported shared-predator linkage. System-level syntheses further show that high alewife abundance can sustain elevated predator pressure, contributing to suppression of native prey through both direct predation and broader food-web effects. The scale, data availability, and long time series in the Great Lakes make this one of the best-documented large-scale examples of subsidy-mediated predator-prey dynamics. Weaknesses: The mechanism is not cleanly isolated as ACDC because multiple confounding processes operate simultaneously. Alewife are only partially donor-controlled, with dynamics influenced by both bottom-up forces and predation, while native planktivore declines reflect a combination of predation, competition, historical collapses, and ecosystem restructuring. Critically, predator abundance is strongly shaped by human stocking, making the predator response partly imposed rather than emergent. These factors blur causal attribution and weaken inference about purely ecological apparent competition, placing the system in a managed, mixed-control regime rather than a clear, natural ACDC case.	Persistent	Human	Demonstrated: salmonids consume both alewife and native planktivorous fish Kitchell and Crowder (1986) Brandt (1980) Evidence rating: Strong	Demonstrated (strong): salmonid growth, survival, and stocking success closely track alewife abundance Brandt (1980) Bence and Smith (1999) Evidence rating: Strong	Demonstrated (moderate-strong): native planktivorous fish suppressed via predation and indirect interactions Bence and Smith (1999) Madenjian et al. (2002) Evidence rating: Strong	Demonstrated (moderate-strong): alewife function as donor-like prey driven by invasion dynamics and bottom-up conditions, though also subject to predation Kitchell and Crowder (1986) Bunnell et al. (2014) Evidence rating: Credible	11.5
15	Coral reefs, Great Barrier Reef-centered pelagic subsidy system	Primary prey: Planktivorous reef fishes, especially damselfishes (<i>Pomacentrus</i> , <i>Chromis</i>) Predator: Coral trout (<i>Plectropomus leopardus</i>) and related piscivores Secondary prey: Small benthic-associated reef fishes, including pomacentrids and labrids	This is a plausible ACDC system in which oceanic zooplankton subsidies support planktivorous reef fishes, especially pomacentrids such as <i>Pomacentrus</i> and <i>Chromis</i> . Coral trout and related piscivores consume these planktivores as well as benthic-associated small reef fishes, including pomacentrids and labrids. If planktivore abundance is driven partly by pelagic subsidy rather than local predator control, then planktivores can elevate predator abundance or foraging intensity, increasing predation pressure on smaller benthic reef fishes. The resulting dynamic is subsidy → planktivores → piscivores → suppression of benthic fishes.	Strengths: The candidate is strong in showing the component mechanisms: pelagic zooplankton delivery to windward GBR reef faces, piscivory by coral trout, and predator-driven structure of small reef fish assemblages are all supported. Weaknesses: A weakness is that the full ACDC chain is not demonstrated in one integrated GBR dataset. The weakest link is the predator numerical response to planktivores: Skinner et al. directly supports that relationship, but in an oceanic reef system outside the GBR. Therefore, this is best classified as strong but synthetic/inferential, not a fully demonstrated ACDC case.	Persistent	Natural	Yes — <i>Plectropomus leopardus</i> consumes reef fishes including Pomacentridae and Labridae St John et al. (2001) Evidence rating: Strong	Partly supported — spatial coupling is directly shown in an oceanic reef system, but not as a GBR-specific numerical-response test Skinner et al. (2024) Evidence rating: Credible	Yes — predators structure small reef fish assemblages on the GBR Boaden and Kingsford (2015) Evidence rating: Weak	Yes — windward GBR reefs receive zooplankton subsidies used by planktivores, and pelagic subsidies can underpin reef fish productivity Hamner et al. (1988) Morais and Bellwood (2019) Evidence rating: Strong	11

Appendix S2. Descriptions and ratings of ACDC Candidate Systems (continued)

No.	System Name	System Name, Primary Prey, Predator, and Secondary Prey	Mechanism	Strengths and Weaknesses	ACDC Tempo	Natural, Human-caused, or Both	Evidence, References, and Rating				Weighted score
							Shared predator?	Predator responds to primary prey?	Secondary prey suppressed?	Primary prey donor controlled?	
16	Macquarie Island hyperpredation system (introduced mammals)	Primary prey: European rabbit (<i>Oryctolagus cuniculus</i>) Predator: Feral cat (<i>Felis catus</i>); also introduced weka (<i>Gallirallus australis</i>) Secondary prey: Macquarie parakeet (<i>Cyanoramphus novaezelandiae erythrotis</i>); burrow-nesting seabirds including Antarctic prion (<i>Pachyptila desolata</i>) and white-headed petrel (<i>Pterodroma lessonii</i>)	Macquarie Island is a strong hyperpredation / ACDC case: introduced European rabbits provided abundant, year-round prey that sustained elevated populations of introduced feral cats and also weka. Those predators then imposed severe predation on native birds, especially the Macquarie parakeet and burrow-nesting petrels such as Antarctic prion and white-headed petrel [1– al. (2000) provide the formal hyperpredation model, but 4]. Taylor specifically linked the parakeet’s rapid disappearance after 1881–1890 to rabbits increasing cats and weka, intensifying predation.	Strengths: This is a clean ACDC example because it has the full module: donor prey, shared introduced predator, vulnerable native prey, and historical extinction/suppression consistent with hyperpredation. Weaknesses: The weakness is that much of the strongest Macquarie-specific evidence is historical or diet-based rather than a modern replicated experiment; Courchamp et al. (2000) provide the formal hyperpredation model, but not a new empirical field test on Macquarie Island itself.	Persistent	Human	Cats consumed both rabbits and native birds; weka also contributed to parakeet predation Taylor (1979) Jones (1977) Brothers et al. (1985) Evidence rating: Strong	Rabbits provided abundant prey that increased or sustained cats and weka, especially through otherwise food-limited periods Taylor (1979) Jones (1977) Brothers et al. (1985) Courchamp et al. (1999) Evidence rating: Strong	Parakeet extinction strongly attributed to intensified cat/weka predation after rabbit establishment; petrels were reduced by cat predation Taylor (1979) Jones (1977) Courchamp et al. (1999) Evidence rating: Strong	Rabbits acted as a high-productivity introduced prey subsidy, not simply as prey controlled by cats Taylor (1979) Jones (1977) Courchamp et al. (1999) Evidence rating: Weak	11
17	Barents Sea capelin–cod–shrimp system	Primary prey: Capelin (<i>Mallotus villosus</i>) Predator: Atlantic cod (<i>Gadus morhua</i>) Secondary prey: Northern shrimp (<i>Pandalus borealis</i>)	In the Barents Sea, capelin is a key forage fish that strongly structures populations of Atlantic cod, a dominant generalist predator. Cod respond numerically and functionally to capelin abundance, with improved growth, condition, and recruitment during periods of high capelin biomass. When capelin stocks are high, cod predation is focused largely on capelin; when capelin collapse, cod shift to alternative prey, including northern shrimp, leading to increased predation pressure and declines in shrimp biomass. This prey-switching dynamic generates a clear indirect interaction: capelin availability modulates cod predation on shrimp. However, capelin are not consistently donor controlled. Their dynamics are influenced by climate, zooplankton availability, and strong predation from cod and other predators. Thus, while capelin can behave as a donor-like subsidy during high-abundance phases, control is mixed and variable through time.	Strengths: Atlantic cod clearly link capelin and northern shrimp through strong prey switching: cod track capelin and shift to shrimp when capelin collapse, producing a well-documented indirect effect. The signal is large-scale and repeatable (capelin collapse → shrimp decline), and supported by time series, diet data, and multispecies models. Weaknesses: Capelin are not consistently donor controlled—both bottom-up forcing and cod predation regulate them—so the system only intermittently meets ACDC assumptions. Evidence for shrimp suppression is partly indirect and confounded by environmental variability and system complexity, making attribution less clean than in simpler systems.	Recurrent/ Episodic	Natural	Demonstrated: cod consume both capelin and shrimp, with diet shifting as capelin abundance changes Varpe et al. (2005) Bogstad et al. (1997) Evidence rating: Strong	Demonstrated (strong): cod growth, recruitment, and biomass track capelin abundance Bogstad et al. (1997) Gjøsæter et al. (2009) Evidence rating: Strong	Demonstrated (strong): shrimp decline when cod switch predation following capelin collapse Gjøsæter et al. (2009) Sundby and Nakken (2008) Evidence rating: Strong	Partial / context-dependent: capelin influenced by climate, prey availability, and predation; donor-like only during high-abundance phases Varpe et al. (2005) Hjermann et al. (2004) Evidence rating: Weak	11

Appendix S2. Descriptions and ratings of ACDC Candidate Systems (continued)

No.	System Name	System Name, Primary Prey, Predator, and Secondary Prey	Mechanism	Strengths and Weaknesses	ACDC Tempo	Natural, Human- caused, or Both	Evidence, References, and Rating				
							Shared predator?	Predator responds to primary prey?	Secondary prey suppressed?	Primary prey donor controlled?	Weighted score
18	Canary Islands hyperpredation system	Primary prey: European rabbit (<i>Oryctolagus cuniculus</i>) plus other introduced mammals Predator: Feral cat (<i>Felis catus</i>) Secondary prey: Endemic giant lizards (<i>Gallotia</i> spp., especially <i>G.</i> <i>intermedia</i> , <i>G. simonyi</i> , <i>G. bravoana</i>)	This is a plausible island hyperpredation / ACDC system: introduced rabbits and other mammals provide a donor-controlled prey base that sustains feral cats (<i>Felis catus</i>), while endemic giant lizards (<i>Gallotia</i> spp.) are vulnerable secondary prey. Where rabbits are abundant, cats can persist at densities higher than lizards alone would support; predation pressure then spills over onto lizards. Where rabbits decline, cats may switch more heavily to reptiles, intensifying direct risk to giant lizards.	Strengths: the predator, primary prey, and secondary prey links are well supported: cats eat introduced mammals, rabbits are often the main biomass source, and cats prey on threatened <i>Gallotia</i> lizards. Weaknesses: the full ACDC mechanism is mostly inferential rather than demonstrated by one integrated demographic study showing rabbit abundance → cat numerical response → lizard population decline. This is a strong candidate, but not a clean, experimentally demonstrated ACDC case.	Persistent	Human	Yes — cats consume introduced mammals and native reptiles, including <i>Gallotia</i> lizards Nogales and Medina (2009) Flores Ravelo and Rando Reyes (2021) Courchamp et al. (2000) Evidence rating: Credible	Introduced mammals, especially rabbits and mice, provide the main biomass supporting cat diets across Canary habitats Nogales and Medina (2009) Flores Ravelo and Rando Reyes (2021) Flores Ravelo and Rando Reyes (2021) Evidence rating: Strong	Cats prey on critically endangered giant lizards; high reptile consumption may contribute to reduced distribution and abundance of <i>G.</i> <i>intermedia</i> Evidence rating: Weak	Rabbits are best treated as donor- controlled/subsidizin g prey in this module, rather than primarily cat- limited; this is inferred from their importance as supporting cat biomass and from general hyperpredation theory Nogales and Medina (2009) Courchamp et al. (2000) Evidence rating: Credible	9.5
19	Scotia Sea krill– large myctophid– macrozooplankton system	Primary prey: Antarctic krill (<i>Euphausia superba</i>) Predator: Large myctophids, especially <i>Electrona antarctica</i> and <i>Gymnoscopelus</i> spp. Secondary prey: Amphipods, especially <i>Themisto gaudichaudii</i> ; copepods including <i>Calanus simillimus</i> , <i>Rhincalanus gigas</i> , <i>Metridia</i> spp.	In the Scotia Sea, Antarctic krill is a major, environmentally structured energy pathway, while large myctophids feed on krill and also on copepods, amphipods, and other zooplankton. During summer, large myctophids become more krill- dependent, especially <i>Electrona antarctica</i> , and consume high proportions of krill productivity; across seasons they also impose measurable predation on <i>Themisto gaudichaudii</i> and some copepods. This creates a plausible ACDC module: krill availability can subsidize or concentrate myctophid predation, while secondary zooplankton experience predation from the same predator guild.	Strengths: mechanistic detail, direct diet data, seasonal predation-impact estimates, and a clearly documented shared-predator guild. Weakness: this is still mostly an inferred ACDC case, not a clean demographic demonstration that krill-driven increases in myctophids reduce secondary prey population growth. It is therefore a moderate candidate, stronger if framed as a seasonal, guild-level Scotia Sea system, but weaker than terrestrial examples with direct time-series evidence for predator numerical response and secondary-prey decline.	Recurrent/ Episodic	Natural	Yes Saunders et al. (2018) Saunders et al. (2019) Evidence rating: Strong	Yes, seasonally and dietarily: large myctophids become more krill-dependent in summer Saunders et al. (2018) Saunders et al. (2019) Evidence rating: Strong	Partial: predation- impact estimates are substantial for Themisto and some copepods, but population-level suppression is inferred rather than demonstrated Saunders et al. (2018) Evidence rating: Strong	Yes, broadly: krill dynamics are strongly environmentally structured, though this table does not require a separate krill-climate reference if framed conservatively Saunders et al. (2019) Evidence rating: Credible Evidence rating: Weak	9.5
20	Barents Sea capelin– zooplankton system	Primary prey: Krill: <i>Thysanoessa inermis</i> , <i>T. raschii</i> ; also amphipods such as <i>Themisto abyssorum</i> Predator: Capelin (<i>Mallotus villosus</i>) Secondary prey: Copepods: <i>Calanus finmarchicus</i> , <i>C. glacialis</i> , <i>Metridia longa</i>	In the Barents Sea, capelin are the shared planktivorous “predator” linking large zooplankton prey: krill, especially <i>Thysanoessa inermis</i> and probably <i>T. raschii</i> , and copepods, especially <i>Calanus finmarchicus</i> , <i>C. glacialis</i> , and <i>Metridia longa</i> . Smaller capelin feed heavily on copepods, while larger capelin shift toward larger zooplankton, including krill, so capelin can impose top-down grazing on copepods when capelin biomass is high. However, this is a diffuse pelagic system: krill and copepods are also affected by temperature, sea ice, Atlantic inflow, primary production, and advection.	Strengths: The trophic links are real: capelin consume both krill and copepods, capelin biomass is negatively associated with mesozooplankton biomass, and <i>Calanus finmarchicus</i> abundance can be lower when capelin biomass is high. Weaknesses: the “donor-control” part is not clean. Krill are not clearly an exogenous donor prey that subsidize capelin independently of capelin predation; rather, krill and copepods are both components of a climate- and advection-sensitive zooplankton field. Thus this is better treated as a diffuse, environmentally modulated apparent- competition candidate, not a canonical ACDC example.	Recurrent/ Episodic	Natural	Yes: capelin consume both copepods and krill, with larger capelin shifting toward krill Dalpadado and Mowbray (2013) Skjoldal (2024) Evidence rating: Strong	Moderate: capelin feeding, growth potential, and distribution are tied to zooplankton availability, but recruitment also depends on cod, herring, climate, and harvest Dalpadado and Mowbray (2013) Skjoldal (2024) Evidence rating: Strong	Yes, moderate: capelin biomass is negatively associated with mesozooplankton, and <i>C. finmarchicus</i> can be reduced where capelin biomass is high Stige et al. (2014) Kvile et al. (2022) Skjoldal (2024) Evidence rating: Credible	Weak/mixed: krill and copepod biomass are strongly structured by climate, sea ice, advection, production, and multi-predator effects Dalpadado et al. (2020) Skjoldal (2024) Evidence rating: Weak	8.5

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Appendix S3: Model parameter value estimation (Parts 1a and b), Model fitting and inference framework (Part 2), and Validation of model fitting and inference framework (Part 3)

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Manuscript title: Apparent competition couples donor and trophic control among prey of generalist predators

Journal: Ecology

Part 1a: Fixed parameter estimation

Of 10 parameters in the *Full* model, 5 were fixed. Their values were estimated from a combination of published demographic information, independent ecological datasets, and allometric relationships, such that they fell within biologically plausible ranges for African ungulates and predators, as follows:

Density independent population growth rates of prey (r_1 , r_2) were calculated from body weight (W) using the allometric equation for intrinsic growth of Sinclair (2003): $r_{max} = 1.375W^{-0.315}$. The result was multiplied by 0.5, arbitrarily chosen to account for losses due to all factors other than density dependence and predation. Body weights for each prey species are given in Table S3.1.

Table S3.1 Body weights for ungulate prey species.

Species	Body Weight (kg)
Thomson's Gazelle	21
Impala	53
Grant's Gazelle	55
Hartebeest	171
Waterbuck	210
Zebra	276
Eland	569
Buffalo	580
Giraffe	899

Prey-to-predator conversion coefficients (ε_i) were derived using an allometric function of the body weight W of prey i , $\varepsilon_i = 0.0007W_i^{0.9}$. Thus, an individual prey with larger body weight contributed more to predator recruitment, but by a smaller proportion of body weight, assuming that less of the carcass is available to predators in large prey compared to small prey. These coefficients should be interpreted as demographic conversion coefficients rather than physiological efficiencies.

Predator baseline loss rate (r_p) was fixed arbitrarily at 0.375 yr^{-1} , equivalent to annual survival of $e^{-0.375} = 0.69$ in the absence of prey-driven recruitment and predator density dependence. This value was not treated as adult mortality alone, but as an effective population-level loss rate incorporating mortality, dispersal, and failed recruitment. This interpretation is consistent with long-term lion studies showing that cub mortality is high and concentrated early in life, that recruitment is commonly measured as survival to one year, and that male takeovers and infanticide can strongly reduce cub survival (Packer et al. 2005; Loveridge et al. 2009).

Part 1b: Fitted parameter initial values

Of 10 parameters in the 5-model framework, 5 were optimized by model fitting. Their initial (seed) values were derived as follows:

Predator attack rates (α_1, α_2) were initialized from observed per-capita kill rates of lions, using the relation $k_i = \alpha_i N_i$, where k_i is the annual number of prey i killed per predator and N_i is prey abundance. Published observations indicate that lions commonly make kills at intervals of several days, with rates varying among sexes, social groups, prey sizes, and ecosystems (Schaller 1972; Funston et al. 1998). This converts to estimates of lion kill rates of ~50–70 medium-sized ungulates per lion per year.

Prey density-dependence coefficients (D_1, D_2) were initialized using the classical logistic relation $D = r/K$, where carrying capacity (K) was estimated as the abundance of each prey species in 1990, and growth rate (r) was estimated using the allometric equation for intrinsic growth of Sinclair (2003): $r_{max} = 1.375W^{-0.315}$.

Predator self-limitation (D_p) values were chosen to provide moderate predator density dependence over the observed range of predator abundances, within the range (10^{-4} – 10^{-3}), consistent with the order of magnitude needed for predator self-limitation to affect predator dynamics without overwhelming prey-driven numerical responses.

Part 2: Model fitting and inference framework

Our objective was not to reconstruct full community dynamics, but to evaluate whether the observed trajectories of secondary prey are consistent with asymmetric predator-mediated coupling to a primary prey. The minimal structure required to test this assertion included time series for predators, the primary prey (zebras), and a secondary prey species. A population time series was available for lions in Laikipia (Bauer et al. 2015) but not for hyenas. While lions and spotted hyenas differ in hunting behavior and prey-specific impacts, both are social and both exploit the same prey and carcass resources, including opportunistic scavenging from one another (Dheer 2016). They do not respond identically to changes in prey density, but both covary with prey density within systems (Hayward et al. 2007) and across systems with substantial differences in prey density (Hatton et al. 2015). To simulate total (lion + hyena) numbers, a 'predation pressure index' was derived by doubling the time series for lions, in effect, assuming that hyenas were twice as abundant as lions, but weighted as 'half-lions' to approximate allometric differences in energetic demand based on body weight (Carbone et al. 2007). This index was assumed to represent total predation pressure on prey more accurately than did lion abundance alone.

Models were fit to prey pair modules, as opposed to all prey at once. This reduced model dimensionality and limited the number of free parameters, thereby improving the identifiability of parameters within each model. This approach treats prey pairs as interaction modules embedded within a larger community. Consequently, fitted parameters should be interpreted as measuring the combined effects of related processes, rather than specific biological processes. Their fitted values may absorb the influence of unmodeled processes, such as other prey, shared

environmental forcing, prey switching, stage structure, immigration or emigration, and measurement error.

The five ODE models were fitted and implemented by a Python 3.9.6, script that was developed with ChatGPT (OpenAI; available at [10.6084/m9.figshare.33117608](https://doi.org/10.6084/m9.figshare.33117608)). The script was tested, modified, and validated as described in Part 3 (below). Inputs comprised observed prey and predator abundance time series, fixed parameter values, and starting values for fitted parameters. Primary and secondary prey were designated a priori as PREY1 and PREY2 in the input files (also available at [10.6084/m9.figshare.33117608](https://doi.org/10.6084/m9.figshare.33117608)). During fitting, the ODEs were integrated over the observation period using SciPy's `solve_ivp` (Virtanen et al. 2020), with a maximum step size of 0.5 years, and free parameters were estimated by bounded nonlinear least squares applied to log-scale residuals (bounds were 10^{-10} to 10^{-2}). The script also calculated log RMSE, log-likelihood, and AICc, generated residual diagnostics, estimated parameter uncertainty by parametric bootstrap, propagated uncertainty into 100-year projections, and calculated local parameter elasticities.

In model fitting, predator abundance was not lagged relative to prey abundance for two reasons. First, the ODE formulation represents predation as a continuous process operating within each annual interval, such that concurrent predator abundance provides the most direct index of predation pressure. Second, lags of 1–4 years did not consistently improve the fit. This was likely because time series for both predators and prey exhibited strong temporal autocorrelation, which reduces the effective independence of adjacent observations and weakens the identifiability of discrete lags. Optimizing lag length risks fitting autocorrelation structure rather than underlying mechanisms.

Part 3: Validation of model fitting and inference framework

The model fitting and inference framework was validated using a combination of analytical test cases and synthetic data generated from the same differential equations used in model fitting, as follows.

The ODE implementation and numerical integration code performed as intended. A deterministic equilibrium dataset was constructed in which prey and predator abundances were constant through time. After correcting parameter bounds to ensure that this equilibrium lay within the feasible parameter region, the fitting routine reproduced the time series to numerical precision (sum of squared log-residuals $\approx 3 \times 10^{-18}$; RMSE $\approx 10^{-10}$). This confirmed the correctness of the right-hand sides of the ODE equations, the numerical solver (`solve_ivp`), interpolation of model outputs to observation times, and construction of residuals in log-abundance space.

The fitted ODE trajectories visually reproduced observed ecological time series. This included checking that the fitted trajectories were biologically plausible and dynamically stable where expected.

The likelihood and model-selection calculations were correct. Residuals were assumed to be Gaussian in log space (corresponding to lognormal observation error in abundance). The residual variance was estimated as $\sigma^2 = SSE/n$, where SSE is the sum of squared log-residuals and n the

number of observations. The Gaussian log-likelihood was computed using this estimate, and Akaike's Information Criterion, corrected for small samples (AICc), was calculated using an effective parameter count of $k + 1$ to account for estimation of σ^2 . Likelihood magnitudes, AICc values, and their scaling with sample size and noise level were consistent with analytical expectations. Numerical safeguards (lower bounds on σ^2 and biologically motivated parameter bounds) were introduced to prevent instability near degenerate solutions.

Parameters used to generate synthetic datasets were recovered. An independent generator of synthetic data was developed that integrates the same ODE system using specified “true” parameter values and initial conditions, samples the solution at discrete observation times, and adds lognormal noise with user-controlled variance. The generator outputs data in the same format as the empirical input files and allows random deletion of predator observations to mimic incomplete sampling over time. These synthetic datasets were then fitted using the full estimation sequence. These recovery experiments confirmed that the estimated residual variance closely matched the imposed noise level ($\hat{\sigma} \approx \sigma$), that likelihood and information-criterion values behaved consistently, and that confidence intervals were asymmetric and respected parameter bounds. Parameter recovery was accurate for well-identified parameters, while several parameters (notably predator density dependence and predator effects on the primary prey) were found to be weakly identifiable under realistic noise levels and sampling intensity, leading to boundary estimates and wide confidence intervals. Because the true parameter values were known, this behavior could be unambiguously attributed to limited information content in the data rather than coding or numerical errors.

Checks of numerical robustness and optimization stability included:

- repeated refits from alternative initial parameter values, showing that optimization converged consistently,
- verification that optimum parameter values were unique (see Figure S3.1, below),
- and checking for parameter estimates equal to prescribed bounds.

Internal consistency of the inferred ecological mechanisms was verified by confirming that fitted parameters generated the expected signs and magnitudes of donor-control and trophic-control metrics, and whether long-term projections behaved consistently with the ecological interpretation of each model class.

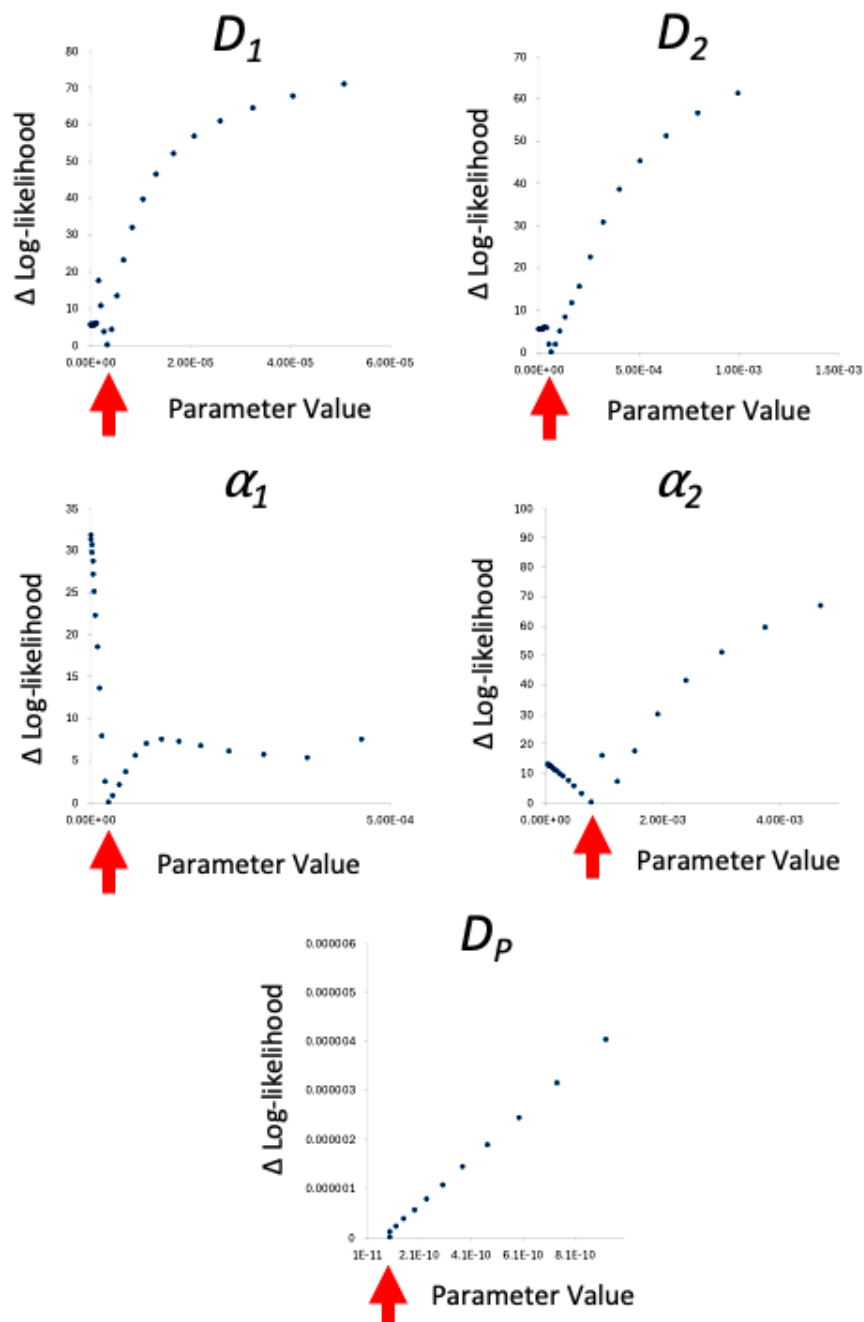
Exported metrics matched independently calculated values from the fitted residuals.

Together, these tests demonstrated that the ODE solver, optimization routine, likelihood calculations, confidence-interval procedures, and model-selection criteria were implemented correctly and behaved as expected, and that remaining uncertainty in parameter estimates reflects intrinsic limits of the data.

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Figure S3.1 Profile-likelihood validation of the ODE-fitting process. Each parameter was fixed successively across a range of values (x-axis) while the remaining parameters were re-estimated, and the resulting increase in log-likelihood loss relative to the best-fitting model was recorded ($\Delta\text{Log-likelihood}$). For most parameters, the profile has a distinct minimum at the fitted value (red arrows), demonstrating a unique best fit and confirming that model fitting recovered the likelihood optimum. The flatter, irregular profile for α_1 indicates that this parameter was more weakly identified by the data.



Appendix S4: Full ODE model fitting results for each pair of primary and secondary prey.

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Manuscript title: Apparent competition couples donor and trophic control among prey of generalist predators

Journal: Ecology

Appendix S4. Full ODE model fitting results for each pair of primary and secondary prey. Results for selected models are highlighted in bold font.

Primary Prey	Secondary Prey	MODEL	No. of Observations	No. of Parameters	SSE_log	RMSLE All	RMSLE Primary Prey	RMSLE Secondary Prey	RMSLE Predator	Log-Likelihood	AICc	Akaike Weight
Zebra	Buffalo	Forced ACDC	35	4	1.844	0.230	0.095	0.357	0.161	1.85	5.64	0.001
Zebra	Buffalo	Mixed ACDC	35	5	1.279	0.191	0.092	0.311	0.096	8.25	-4.42	0.131
Zebra	Buffalo	Full	35	5	1.273	0.191	0.092	0.310	0.096	8.33	-4.60	0.143
Zebra	Buffalo	No Prey Selection	35	4	1.361	0.197	0.098	0.295	0.151	7.16	-4.99	0.174
Zebra	Buffalo	Donor	35	5	1.179	0.184	0.091	0.296	0.098	9.68	-7.29	0.550
Zebra	Eland	Forced ACDC	35	4	1.325	0.195	0.092	0.287	0.159	7.64	-5.94	0.002
Zebra	Eland	Mixed ACDC	35	5	0.901	0.160	0.091	0.264	0.056	14.38	-16.69	0.499
Zebra	Eland	Full	35	5	0.901	0.160	0.091	0.264	0.056	14.38	-16.69	0.499
Zebra	Eland	No Prey Selection	35	4	1.796	0.227	0.098	0.355	0.154	2.31	4.72	0.000
Zebra	Eland	Donor	35	5	1.899	0.233	0.091	0.381	0.128	1.33	9.41	0.000
Zebra	Grant's gazelle	Forced ACDC	35	4	1.071	0.175	0.092	0.226	0.179	11.35	-13.37	0.235
Zebra	Grant's gazelle	Mixed ACDC	35	5	1.066	0.174	0.095	0.235	0.167	11.44	-10.82	0.066
Zebra	Grant's gazelle	Full	35	5	1.006	0.170	0.097	0.231	0.156	12.45	-12.83	0.179
Zebra	Grant's gazelle	No Prey Selection	35	4	1.026	0.171	0.100	0.232	0.158	12.10	-14.88	0.500
Zebra	Grant's gazelle	Donor	35	5	1.14	0.18	0.10	0.237	0.18	10.28	-8.49	0.020
Zebra	Giraffe	Forced ACDC	35	4	1.688	0.220	0.102	0.332	0.166	3.40	2.54	0.000
Zebra	Giraffe	Mixed ACDC	35	5	1.194	0.185	0.097	0.247	0.180	9.45	-6.84	0.006
Zebra	Giraffe	Full	35	5	1.10	0.18	0.10	0.25	0.16	10.95	-9.83	0.028
Zebra	Giraffe	No Prey Selection	35	4	1.233	0.188	0.098	0.275	0.151	8.90	-8.46	0.014
Zebra	Giraffe	Donor	35	5	0.896	0.160	0.091	0.247	0.101	14.48	-16.89	0.952
Zebra	Hartebeest	Forced ACDC	35	4	1.153	0.182	0.094	0.245	0.174	10.06	-10.79	0.034
Zebra	Hartebeest	Mixed ACDC	35	5	0.938	0.164	0.094	0.240	0.127	13.67	-15.27	0.317
Zebra	Hartebeest	Full	35	5	0.901	0.160	0.095	0.236	0.121	14.39	-16.70	0.649
Zebra	Hartebeest	No Prey Selection	35	4	1.467	0.205	0.100	0.308	0.156	5.84	-2.35	0.000
Zebra	Hartebeest	Donor	35	5	1.497	0.207	0.091	0.340	0.102	5.50	1.07	0.000
Zebra	Impala	Forced ACDC	35	4	0.905	0.161	0.092	0.193	0.176	14.31	-19.29	0.025
Zebra	Impala	Mixed ACDC	35	5	0.729	0.144	0.094	0.196	0.126	18.08	-24.09	0.277
Zebra	Impala	Full	35	5	0.693	0.141	0.095	0.189	0.124	18.97	-25.86	0.674
Zebra	Impala	No Prey Selection	35	4	0.910	0.161	0.100	0.209	0.157	14.20	-19.07	0.023
Zebra	Impala	Donor	35	5	1.009	0.170	0.091	0.227	0.164	12.40	-12.73	0.001
Zebra	Thomson's gazelle	Forced ACDC	35	4	0.953	0.165	0.099	0.200	0.177	13.41	-17.48	0.016
Zebra	Thomson's gazelle	Mixed ACDC	35	5	0.789	0.150	0.097	0.172	0.166	16.71	-21.35	0.113
Zebra	Thomson's gazelle	Full	35	5	0.702	0.142	0.099	0.168	0.148	18.74	-25.42	0.868
Zebra	Thomson's gazelle	No Prey Selection	35	4	1.079	0.176	0.100	0.243	0.156	11.23	-13.13	0.002
Zebra	Thomson's gazelle	Donor	35	5	1.243	0.188	0.092	0.267	0.168	8.75	-5.43	0.000
Zebra	Waterbuck	Forced ACDC	35	4	6.296	0.424	0.093	0.726	0.177	-19.64	48.62	0.539
Zebra	Waterbuck	Mixed ACDC	35	5	6.235	0.422	0.100	0.725	0.162	-19.47	51.01	0.163
Zebra	Waterbuck	Full	35	5	6.127	0.418	0.102	0.723	0.142	-19.17	50.40	0.221
Zebra	Waterbuck	No Prey Selection	35	4	7.050	0.449	0.098	0.770	0.181	-21.62	52.58	0.074
Zebra	Waterbuck	Donor	35	5	7.850	0.474	0.094	0.825	0.143	-23.50	59.07	0.003

Figure S4.1

Figure S4.1. Population trajectories of predators and prey pairs projected from best-supported models, using parameters given in Table 3. Population estimates (filled circles) for primary prey (zebra in blue), secondary prey (grey), and predators (lions and hyenas in black). Ninety-five percent confidence envelopes are indicated in lighter hues. Primary prey are zebras, and predators are lions and hyenas in all panels. Secondary prey trajectories are depicted for hartebeest (A), eland (B), giraffe (C), Grant's gazelle (D), impala (E), and Thomson's gazelle (F). Figure created by Jacob R. Goheen.

