

Ecosystem energetic implications of parasite and free-living biomass in three estuaries

Armand M. Kuris^{1*}, Ryan F. Hechinger^{1*}, Jenny C. Shaw¹, Kathleen L. Whitney¹, Leopoldina Aguirre-Macedo², Charlie A. Boch¹, Andrew P. Dobson³, Eleca J. Dunham⁴, Brian L. Fredensborg⁵, Todd C. Huspeni⁶, Julio Lorda¹, Luzviminda Mababa¹, Frank T. Mancini⁷, Adrienne B. Mora⁸, Maria Pickering⁹, Nadia L. Talhouk¹, Mark E. Torchin¹⁰ & Kevin D. Lafferty¹¹

Parasites can have strong impacts but are thought to contribute little biomass to ecosystems^{1–3}. We quantified the biomass of free-living and parasitic species in three estuaries on the Pacific coast of California and Baja California. Here we show that parasites have substantial biomass in these ecosystems. We found that parasite biomass exceeded that of top predators. The biomass of trematodes was particularly high, being comparable to that of the abundant birds, fishes, burrowing shrimps and polychaetes. Trophically transmitted parasites and parasitic castrators subsumed more biomass than did other parasitic functional groups. The extended phenotype biomass controlled by parasitic castrators sometimes exceeded that of their uninfected hosts. The annual production of free-swimming trematode transmission stages was greater than the combined biomass of all quantified parasites and was also greater than bird biomass. This biomass and productivity of parasites implies a profound role for infectious processes in these estuaries.

Standing stock biomass and biomass production are traditional measures of the energetics of ecosystems (see, for example, refs 4–6). Infectious agents are perceived to contribute negligible biomass to ecosystems^{1–3}. If so, it may be appropriate to set them aside from investigations of energetics, ecosystems or food webs. However, some parasites markedly influence host individuals (notably humans), wildlife populations and sometimes host communities. These effects

imply a general role for infectious processes in the dynamics of ecosystems. Here we quantify the biomass of free-living organisms and their parasites in three estuaries.

Over the course of five years we performed an extensive quantification of the free-living and infectious biomass in three estuaries in Baja California (Bahia Falsa in Bahia San Quintín (BSQ) and Estero de Punta Banda (EPB)) and California (Carpinteria Salt Marsh (CSM)). Cumulatively, the study included 199 species of free-living animals, 15 species of free-living vascular plants and 138 species (including 1 plant species) of infectious agents (see Table 1). Unless specifically mentioned, biomass refers to wet weight, including hard parts.

Here we consider the biomass of free-living and parasitic species grouped by taxonomic categories and, for parasites, by life-history strategy^{7,8}. We also determined the proportion of the mass in each host category that was parasite tissue. Additionally—because several parasites in our study were parasitic castrators, usurping the phenotype of their hosts—we noted the biomass in each estuary of castrated hosts (parasite extended phenotypes⁹). Trematode castrators in snail intermediate hosts contributed the most substantial parasitic standing crop biomass in these estuaries, so we further estimated the rates of annual productivity for this infectious component of the system (asexual production of cercariae). To illustrate more sharply the importance of parasite biomass, we compare it directly with the biomass of free-living groups, particularly with that of the bird

Table 1 | Summary of free-living groups and animal parasite functional groups in this study, and number of hosts dissected

Free-living group	No. of species	No. of individuals dissected	No. of parasite species				Sum
			Macroparasites	Trophically transmitted	Castrators	Pathogens	
Miscellaneous phyla	10	55	–	1	–	–	1
Small arthropods	33	258	–	2	–	–	2
Polychaetes	38	533	1	7	–	2	10
Bivalves	15	267	2	15	1	1	19
Snails	11	14,158	–	9	24	1	34
Burrowing shrimps	2	87	1	7	2	–	10
Crabs	3	949	1	19	2	6	28
Fishes	17	965	6	19	–	1	26
Birds	70	162	30	–	–	–	30
Total host–parasite combinations	–	–	41	79	29	11	160
Total species, life stages or individuals	199	17,434	40	72	29	9	150

Totals for numbers of parasite species may be less than the sum of the rows because some parasite species use more than one host group. Italic numbers indicate species for which we did not quantify biomass.

¹Department of Ecology, Evolution and Marine Biology and Marine Science Institute, University of California, Santa Barbara, California 93106, USA. ²Centro de Investigación y Estudios Avanzados del IPN, C.P. 97310, Mérida, Mexico. ³Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544-1003, USA. ⁴Center for Infectious Disease Dynamics, Department of Biology, Pennsylvania State University, University Park, Pennsylvania 16802, USA. ⁵Department of Biology, University of Texas Pan-American, Edinburg, Texas 78539, USA. ⁶Department of Biology, University of Wisconsin–Stevens Point, Stevens Point, Wisconsin 54481, USA. ⁷Pacific Islands Fisheries Research Center, National Marine Fisheries Service, Honolulu, Hawaii 96822, USA. ⁸Department of Biology, University of California, Riverside, California 92521, USA. ⁹Ecology and Evolutionary Biology, University of Connecticut, Storrs, 75 North Eagleville Rd. Unit 3043, Storrs, Connecticut 06269, USA. ¹⁰Smithsonian Tropical Research Institute, Apartado 0843, Ancon, Balboa 03092, Panama, Republic of Panama. ¹¹Western Ecological Research Center, US Geological Survey, Marine Science Institute, University of California, Santa Barbara, California 93106, USA.

*These authors contributed equally to this work.

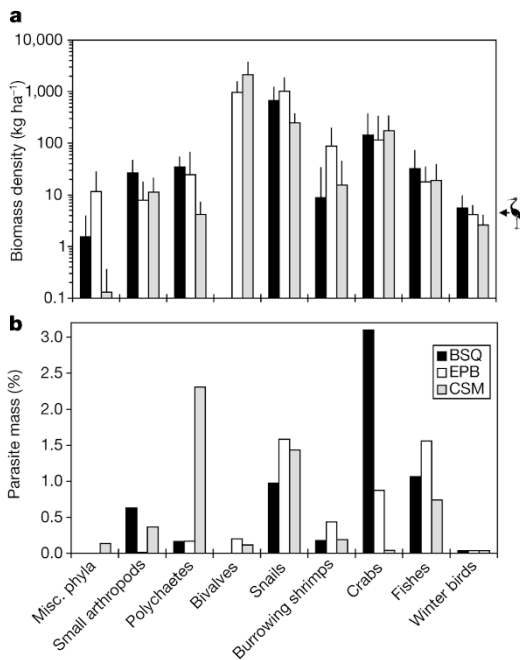


Figure 1 | Biomass of animals and proportional contribution of parasites in three estuaries. **a**, Ecosystem-level biomass density of free-living animal groups. **b**, Parasite tissue as a percentage of total biomasses. The arrow at the bird icon in **a** marks the mean biomass of winter birds (4.1 kg ha^{-1}) across the three estuaries. Error bars in **a** indicate upper 95% confidence limit. The Supplementary Information contains the standard errors and degrees of freedom for the stratified means, and confidence limits for this and all other figures.

assemblage (an obvious and important component of the estuarine ecosystem that includes most of the top predators¹⁰).

Vascular plants composed the greatest fraction of the biomass in all three estuaries: a mean of $136,166 \pm 33,848$ (95% confidence limits) kg ha^{-1} at BSQ, $61,754 \pm 14,512 \text{ kg ha}^{-1}$ at EPB, and $169,035 \pm 26,606 \text{ kg ha}^{-1}$ at CSM. At CSM, the parasitic dodder, *Cuscuta salina*, infecting leaves and stems, was 0.27% of the plant biomass. Dodder was less common at EPB and scarce at BSQ. We recognized 199 species of free-living animals and 150 species (or life stages) of metazoan parasites (Table 1).

Faunal composition was similar across these estuaries. As regards the species that contribute the top 95% of all biomass, 28% of free-living and 71% of parasite species were common to all three estuaries, and 67% of free-living species and 74% of parasite species were common to at least two estuaries. The biomasses of all free-living

animals (including their infectious agents) were 925 kg ha^{-1} at BSQ, $2,240 \text{ kg ha}^{-1}$ at EPB, and $2,594 \text{ kg ha}^{-1}$ at CSM. In the three estuaries, parasites composed 1.2%, 0.9% and 0.2% of the total animal biomass, respectively. Additionally, parasite biomasses were 6.3%, 13.2% and 3.2% of the combined biomass of their free-living trophic counterparts—that is, the main free-living groups that also feed on multiple trophic levels, namely crabs, fishes, miscellaneous phyla and birds.

For visual presentation, we combined free-living species into broad taxonomic categories (Fig. 1a and Table 1). Our estimates for free-living biomass compare with those from other estuaries (see, for example, refs 11–13). The most substantial contributors to animal biomass were the snails, bivalves and crabs. Across estuaries, the biomasses of the broad categories were generally consistent, the striking exception being the lack of bivalves at BSQ. Other biomass differences between estuaries were driven to a large extent by differences in relative habitat areas (for example marsh habitat, which was relatively extensive at CSM, supported fewer fishes and invertebrates). When all parasites were combined within the free-living groups, the total mass of parasites was generally less than 2% of the biomass of their host categories (Fig. 1b). However, the percentage of parasite biomass varied between estuaries and sometimes reached more than 3% of the mass of their free-living host groups.

The average parasite group had a biomass three orders of magnitude lower than that of the average free-living group (Fig. 2a). Certain parasitic groups dominated the parasite biomass, reaching levels similar to those of common free-living groups. For instance, the biomass of trematode worms was comparable to that of the fishes, burrowing shrimps, polychaetes or small arthropods. In all estuaries, trematode biomass exceeded bird biomass by threefold to ninefold. The epicaridean isopods were the second biggest biomass component of the parasite groups (along with tapeworms at BSQ and EPB). As with the free-living groups, biomass estimates for parasite groups were similar for all estuaries, with exceptions being the small contribution of cestodes and parasitic copepods at CSM.

Parasitic castrators and trophically transmitted parasite stages dominated parasite biomass, attaining $1\text{--}10 \text{ kg ha}^{-1}$ (Fig. 2b). This mass density was comparable to—or exceeded—that of the vertebrate groups in these estuaries. Macroparasites contributed much less to estuary biomass. This was partly due to the relatively low biomass of their principal hosts (birds and fishes). The total biomasses of the functional groups of parasites were also similar across estuaries.

A host infected with a parasitic castrator has the effective genotype of the parasite¹⁴. Hence, the entire mass of each castrated host constitutes the extended phenotype⁹ of its parasitic castrator. For a host group, the biomass of parasitically castrated hosts approached and sometimes exceeded the biomass of their uninfected hosts (Fig. 3).

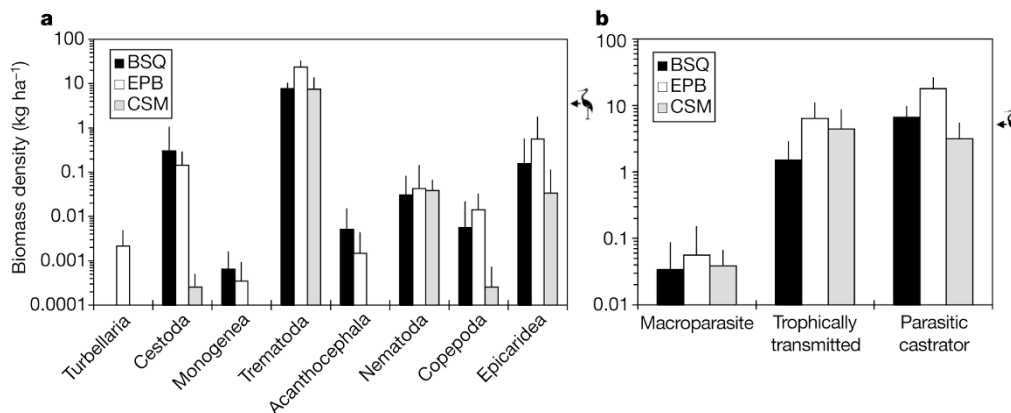


Figure 2 | Ecosystem-level biomass density of animal parasites in three estuaries. **a**, Parasites grouped by major taxon. **b**, Parasites grouped by functional group. The reference arrow at the bird icon marks the mean

winter bird mass density across the three estuaries (4.1 kg ha^{-1}). Error bars indicate upper 95% confidence limit.

For example, across the three estuaries, parasitically castrated *Cerithidea californica* commandeered 37–130% of the soft-tissue biomass compared to the uninfected snail populations (Fig. 4). Thus, parasites effectively controlled much of the host biomass of some free-living groups. This probably applies to the many other marine and aquatic systems in which hosts for parasitic castrators (for example crabs, shrimps and snails) are common.

The snail *C. californica* and its larval trematode parasitic castrators were considerable components of animal biomass. *C. californica* had the greatest biomass of any invertebrate in the two southern estuaries (569 kg ha⁻¹ at BSQ, 854 kg ha⁻¹ at EPB) and ranked eighth among the invertebrates at CSM (144 kg ha⁻¹). The larval parthenitae of 18 recognized trematode species parasitically castrated many of these snails, including almost all of the largest individuals. The trematodes average 22% of the total soft-tissue weight of individual infected snails¹⁵. In total, the trematode biomass in *C. californica* matched or exceeded the high winter biomass of birds and substantially exceeded their summer biomass (Fig. 4).

We quantified the combined cercarial production of the 18 trematode species infecting *C. californica* snails. Because their snail hosts were large and abundant, these cercariae comprised a substantial component of parasite productivity. Cercariae are released from snails in a daily pulse¹⁶ and have ephemeral life spans of about 24 h. The annual cercarial biomass produced by all *C. californica* trematodes could therefore be compared with the standing crop biomass of other (long-lived) animals. Annual production of cercariae was about threefold that of trematode parthenitae standing-stock biomass and threefold to tenfold that of winter bird biomass (Fig. 4). Further the annual production of cercariae exceeded 1.3–2.2-fold the standing stock of all parasites combined. Reproductive effort—the biomass of offspring (cercariae) produced in a year divided by the biomass of parents (infected snail soft-tissue mass)—was 0.53–0.86. This reproductive effort lies outside the range of values (0.065–0.29) reported for 13 iteroparous marine mollusc species^{17,18}. Both parthenitae in *C. californica* and cercariae produced by trematodes infecting *C. californica* had greater densities in the two southern estuaries, primarily as a result of the abundance of *C. californica* throughout the vegetated marsh at BSQ and EPB, whereas at CSM snails were rare in this extensive habitat (50–53% of all habitat area at BSQ and EPB, and 77% of that at CSM).

Our conservative estimates (see Methods) indicate that parasite biomass is comparable to that of several major groups of free-living animals and greater than that of the principal top predators in these estuaries. Parasite biomass was not equally distributed among host or parasite groups; the parasitic castrator functional group comprised most of the parasitic biomass. Consideration of the influence of their

extended phenotypes indicates a large ecological role for such parasites. Further, parasite biomass relative to the free-living biomass was up to 6–12-fold the 0.1–0.2% ‘best guess’ used for an ecosystem model of coral reefs that predicted a significant increase in trophic efficiency when parasites were included in the model¹⁹.

Large standing-stock biomass is not the only indication of energetic importance to ecosystems: productivity is also fundamental^{4,5,20}. Parasites efficiently convert food to growth and reproduction, perhaps because they are released from the homeostatic, food gathering and mobility tasks conducted by their hosts²¹. Thus, parasites—such as larval trematodes in snails—may generally have substantial biomass (like many macroorganisms) and high productivity (like microbial organisms).

Additionally, parasites drain host energy beyond that which they consume. Resistance to parasites can be energetically costly (as a result of physiological and behavioural traits to detect, prevent and respond to infection)²². In particular, immune systems require substantial standing investment and incur inductive energetic costs²³, and added to that are costs of repairing tissue damaged or consumed by parasites. If parasites have relatively high productivity compared with free-living consumers, and non-consumptive effects on their resources, their effects at the ecosystem level could be disproportionately greater than suggested by their biomass.

This investigation of the biomass of parasites at the ecosystem level fits with emerging interest in the role of parasites in food webs. Parasites can significantly affect food-web topology (for example, increasing chain length and connectance) and are commonly consumed^{24,25}. Further, by modifying the behaviour of intermediate hosts, parasites can selectively strengthen links between predator and prey²⁶. A quantification of biomass allows the assignment of mass to these potentially important parasitic nodes and therefore represents a step towards fully dynamic food-web models that incorporate infectious processes.

The substantial biomass and productivity attributed to parasites in these estuaries calls for the full integration of parasite ecology into the general body of ecological theory. Food-web analyses and ecosystem

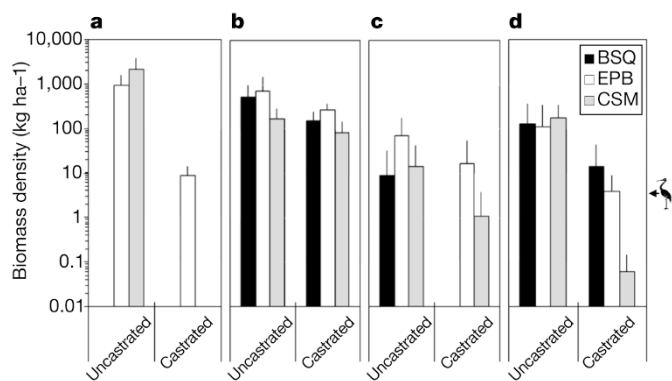


Figure 3 | Ecosystem-level biomass density of parasitically castrated (extended phenotypes) and uninfected phenotypes of hosts supporting parasitic castrators in three estuaries. a, Bivalves. b, Snails. c, Burrowing shrimps. d, Crabs. The reference arrow at the bird icon marks the mean winter bird mass density across the three estuaries (4.1 kg ha⁻¹). Error bars indicate upper 95% confidence limit.

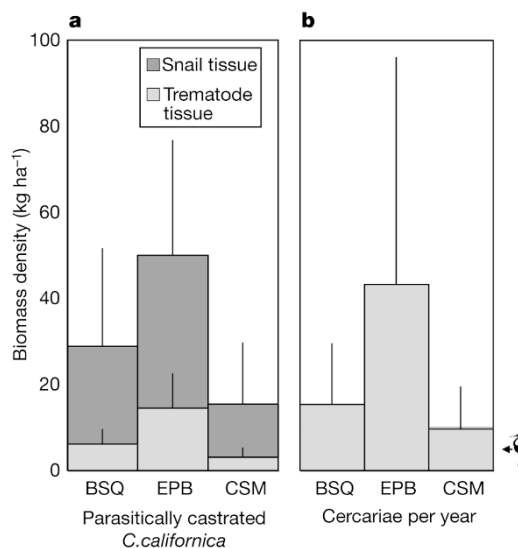


Figure 4 | Standing crop biomass and cercarial productivity of trematodes in *Cerithidea californica* snails. a, Ecosystem-level biomass density of host and parasite tissues of parasitically castrated *C. californica*. b, Biomass density of the free-swimming stages (cercariae) produced annually by infected snails. Uninfected *C. californica* tissue biomass was 78.8 ± 73.4 (95% confidence limits) kg ha⁻¹ at BSQ, 110.5 ± 119.4 kg ha⁻¹ at EPB, and 11.8 ± 9.0 kg ha⁻¹ at CSM. For clarity we do not include the snail shell mass, which is about 80% of the total mass. The reference arrow at the bird icon marks the mean winter bird-mass density across the three estuaries (4.1 kg ha⁻¹). Summer bird biomass is 0.89 kg ha⁻¹ across the three estuaries. Error bars indicate upper 95% confidence limit.

modelling that include parasites^{19,24,25,27,28} provide a starting point for this theoretical expansion.

METHODS SUMMARY

We quantified animal and plant wet biomass by sampling 23 random sites in each estuary, stratified over the four major habitats (vegetated marsh, pans, channels, and mudflats and sandflats). At each site we sampled the density and sizes of most free-living organisms more than 1 mm in body size: birds with visual surveys, fishes with nets, benthos with quadrats and cores, and plants with clip quadrats and cores. We estimated free-living animal biomass by applying weight–length curves to the sampled individuals (for birds we used average adult weight).

From each sample site we examined fishes and invertebrates for a wide range of infectious agents, focusing on metazoans. We examined all soft-tissue types in squash preparations. Ethical and pragmatic issues prevented extensive sampling of most bird species for parasites, so we performed a partial estimation of parasite communities of birds by using our own dissections and published information. In general, our methodology probably underestimated the presence of infectious disease (for example, by excluding many pathogens).

We estimated parasite biomass in our samples by multiplying species-specific estimates of individual parasite mass by their abundance²⁹ in individual hosts. We obtained the masses of most metazoan parasites by directly weighing individuals, or by estimating their mass by multiplying an estimate of their volume by a tissue density of 1.1 g ml⁻¹ (ref. 30). To generate estimates for the abundance of parasites in hosts (other than birds), we used statistical models based on data from our dissected hosts.

We estimated the annual productivity of trematode cercariae by multiplying species-specific estimates of individual cercaria mass by species-specific estimates of mean number of cercariae shed daily multiplied by infection density multiplied by 365 days.

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- Loreau, M., Roy, J. & Tilman, D. in *Parasitism and Ecosystems* (eds Thomas, F., Renaud, F. & Guégan, J.-F.) 13–21 (Oxford Univ. Press, Oxford, 2005).
- Polis, G. A. & Strong, D. R. Food web complexity and community dynamics. *Am. Nat.* **147**, 813–846 (1996).
- Poulin, R. The functional importance of parasites in animal communities: many roles at many levels? *Int. J. Parasitol.* **29**, 903–914 (1999).
- Linderman, R. L. The trophic–dynamic aspect of ecology. *Ecology* **23**, 399–418 (1942).
- Odum, E. P. Strategy of ecosystem development. *Science* **164**, 262–270 (1969).
- Yodzis, P. & Innes, S. Body size and consumer–resource dynamics. *Am. Nat.* **139**, 1151–1175 (1992).
- Kuris, A. M. & Lafferty, K. D. in *Evolutionary Biology of Host–Parasite Relationships: Theory Meets Reality* (eds Poulin, R., Morand, S. & Skorping, A.) 9–26 (Elsevier, Amsterdam, 2000).
- Lafferty, K. D. & Kuris, A. M. Trophic strategies, animal diversity and body size. *Trends Ecol. Evol.* **17**, 507–513 (2002).
- Dawkins, R. *The Extended Phenotype: The Long Reach of the Gene* (Oxford Univ. Press, Oxford, 1982).
- Erwin, R. M. Dependence of waterbirds and shorebirds on shallow-water habitats in the mid-Atlantic coastal region: An ecological profile and management recommendations. *Estuaries* **19**, 213–219 (1996).
- Spruzen, F. L., Richardson, A. M. M. & Woehler, E. J. Spatial variation of intertidal macroinvertebrates and environmental variables in Robbins Passage wetlands, NW Tasmania. *Hydrobiologia* **598**, 325–342 (2008).
- Allen, L. G. Seasonal abundance composition and productivity of the littoral fish assemblage in Upper Newport Bay, California. *Fish. Bull.* **80**, 769–790 (1982).
- Ramer, B. A., Page, G. W. & Yoklavich, M. M. Seasonal abundance habitat use and diet of shorebirds in Elkhorn Slough, California. *Western Birds* **22**, 157–174 (1991).
- O'Brien, J. & Van Wyk, P. in *Crustacean Issues: Factors in Adult Growth* (ed. Wenner, A.) 191–218 (Balkema, Rotterdam, 1985).
- Hechinger, R. F. et al. How large is the hand in the puppet? Ecological and evolutionary effects on body mass of 15 trematode parasitic castrators in their snail host. *Evol. Ecol.* doi:10.1007/s10682-008-9262-4 (in the press).
- Fingerut, J. T., Zimmer, C. A. & Zimmer, R. K. Patterns and processes of larval emergence in an estuarine parasite system. *Biol. Bull.* **205**, 110–120 (2003).
- Browne, R. A. & Russell-Hunter, W. D. Reproductive effort in molluscs. *Oecologia* **37**, 23–27 (1978).
- Hughes, R. N. & Roberts, D. J. Reproductive effort of winkles (*Littorina* spp.) with contrasted methods of reproduction. *Oecologia* **47**, 130–136 (1980).
- Arias-Gonzalez, J. E. & Morand, S. Trophic functioning with parasites: a new insight for ecosystem analysis. *Mar. Ecol. Prog. Ser.* **320**, 43–53 (2006).
- McLusky, D. S. *The Estuarine Ecosystem* 2nd edn (Blackie, Glasgow, 1989).
- Calow, P. Pattern and paradox in parasite reproduction. *Parasitology* **86**, 197–207 (1983).
- Rigby, M. C., Hechinger, R. F. & Stevens, L. Why should parasite resistance be costly? *Trends Parasitol.* **18**, 116–120 (2002).
- Lochmiller, R. L. & Deerenberg, C. Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos* **88**, 87–98 (2000).
- Lafferty, K. D., Dobson, A. P. & Kuris, A. M. Parasites dominate food web links. *Proc. Natl Acad. Sci. USA* **103**, 11211–11216 (2006).
- Lafferty, K. D. et al. in *Disease Ecology: Community Structure and Pathogen Dynamics* (eds Collinge, S. K. & Ray, C.) 119–134 (Oxford Univ. Press, Oxford, 2006).
- Lafferty, K. D. & Morris, A. K. Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology* **77**, 1390–1397 (1996).
- Huxham, M. & Raffaelli, D. Parasites and food-web patterns. *J. Anim. Ecol.* **64**, 168–176 (1995).
- Thompson, R. M., Mouritsen, K. N. & Poulin, R. Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *J. Anim. Ecol.* **74**, 77–85 (2005).
- Bush, A. O., Lafferty, K. D., Lotz, J. M. & Shostak, A. W. Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitol.* **83**, 575–583 (1997).
- Peters, R. H. *The Ecological Implications of Body Size* (Cambridge Univ. Press, Cambridge, 1983).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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