

‘Biologically Degenerate, Ecologically Marginal’: Parasites as a Case Study in Societal Values Impacting Ecological Research

Meghan Barrett*, Thomas Raffel†, Bob Fischer‡


Since parasite ecology was first popularized in the late 1970s, researchers have identified and rejected many foundational assumptions about parasites that turned out to be erroneous. What explains the existence of so many erroneous assumptions about parasites and their neglect in mainstream 20th-century ecology, relative to ecologically similar organisms such as predators? We argue that longstanding negative societal values associated linguistically with parasites probably played some role in shaping negative scientific assumptions about parasites in a way different to other categories of natural enemies with different value associations. We review two examples where more recent research has corrected mistaken assumptions about parasites’ roles in ecosystems. In each case, we argue that cultural values may partially explain why earlier scientists opted not to explore hypotheses that framed parasites as powerful, important assets to their ecosystems.

Keywords

ecological theory • parasites • predators • value associations • bias

1. Introduction

No matter how much the natural sciences lay claim to a direct access to phenomena, this access will always have to be articulated in a language defined by cultural norms and traditions (Gullestad 2011).

*Department of Biology, Indiana University Indianapolis, Indiana, United States of America, meghbarr@iu.edu
 <https://orcid.org/0000-0002-1270-4983>

†Department of Biological Sciences, Oakland University, Michigan, United States of America, raffel@oakland.edu

‡Department of Philosophy, Texas State University, Texas, United States of America, fischer@txstate.edu

Received 25 March 2024; Revised 11 December 2024; Accepted 05 March 2025
doi:10.3998/ptpbio.5837

Parasite ecology research has taken off since the 1970s (Raffel et al. 2008; Moore 2012; Lively et al. 2014; Poulin 2021; but see Preston et al. 2016; Andrew et al. 2021). Many factors explain the rapid shifts in the field, including the development of key mathematical models (e.g., Anderson and May 1978), insights from community ecology (e.g., Holmes 1973), and new genetic tools (e.g., Wickström et al. 2003). This progress has overturned some erroneous hypotheses about parasites, including (1) that they are degenerate and simplified creatures; (2) that they do not play important roles in regulating ecosystem dynamics or shaping food webs; and (3) that parasites only weakly influence their hosts' evolution, population dynamics, and behavior (among others; see Mittelbach 2005; Vickerman 2009; Moore 2012; Poulin 2021).

Strikingly, such mistaken assumptions about the ecology of parasites of animal hosts (hereafter, animal parasites) appear to have been more pervasive and fundamental than in related fields, such as predator-prey ecology, resulting in a prolonged period of parasite exclusion from mainstream ecological research (as reviewed in Poulin 2021 and below). Additionally, parasites have continued to be misunderstood despite the progress in ecological parasitology. Just over a decade ago, for instance, it seemed reasonable for researchers to argue that "basic assumptions about parasites, their ubiquity, and their relevance need to be reexamined or abandoned" (Gómez and Nichols 2013, 225). More recently, researchers have claimed that parasites are still being neglected, contending that "their omission from the design and analyses of ecological studies poses real risks of flawed interpretations" (Timi and Poulin 2020, 759).

This situation raises two questions. First, what explains the accumulation of so many erroneous assumptions about animal parasites? Secondly, why have some of these assumptions lingered long after there was ample evidence against them?

Complete answers to these questions will cite many factors. Animal parasites are, of course, small and difficult to study in their natural environments (frequently, inside their hosts). And before the takeoff of ecological parasitology, researchers lacked many of the tools that are now regarded as essential to understanding parasites properly. So, it may not be surprising that earlier generations of scientists had poor models of these organisms and their ecological significance. Moreover, it takes time for scientific developments to be disseminated and fully integrated into subsequent work; so, it may not be surprising that certain errors persist decades after they are known to be errors.

While these are, no doubt, central parts of the story, our aim here is to argue for the importance of another component. As Reynolds (2018, 2) argues, the metaphors that scientists adopt "can be integral to the formulation of a theory and constitute the core of action-guiding programs of research. They also incorporate implicit value judgments about the nature of the subject matter under investigation and the proper route to its scientific understanding." And "parasite" is itself a metaphor, a piece of language originally applied to humans that was co-opted for scientific use (as we'll discuss below). We argue that the negative cultural perceptions of parasites caused a range of negative associations with the term "parasite" and its cognates, even for scientists who study these organisms, and that these negative associations resulted in cognitive biases regarding animal parasites that influenced research priorities, the development of new explanatory frameworks, and the eventual acceptance of these frameworks.

We are hardly the first to note the prevalence of erroneous assumptions about, and the neglect of, animal parasites in ecology (Moore 2012; Poulin 2021). However, previous authors have neither detailed the historical roots of this problem nor provided contrasting cases to bolster the hypothesis that cultural and linguistic value associations influenced the development of ecological theory. We do both here. We provide a novel comparison of the value associations for two categories of natural enemies, animal parasites and predators, that are commonly used as biological-social metaphors. After describing generally how language is known to impact

the development of scientific theory, we move to exploring the case of parasites and predators by: (1) demonstrating the disparity in treatment between predators and parasites in ecological literature, (2) identifying the historical origin of the relevant value associations prior to these terms' ecological adoption, and (3) providing two case studies that illustrate how these value associations impacted ecology. We conclude with some suggestions about how negative value associations in science might be addressed.

2. The Impact of Language on Scientific Theory

Scientists often borrow terminology from the broader culture to describe phenomena of interest. Often enough, the societal values associated with that language partially explain why that language is perceived to be useful, despite the ostensible desire for value neutrality in scientific discourse (e.g., Lewontin 1992, Larson 2011). One such example is the male 'king bee' (now queen bee), who reigned over honeybee colonies from Aristotle's 350 B.C.E. *History of Animals* to Hyll's 1579 beekeeping manual. Western philosopher-scientists adopted the term 'king' to describe the sex and social position of the dominant bee in each colony because of their assumptions – implicit or explicit – about who has power and who can lead (Wilson 2014a). Once adopted, the term nudged scientists towards a “general orthodoxy of the king bee,” (Wilson 2014a) hampering our understanding of bee sex and social organization (Maderspacher 2007).

The (correct) alternate hypothesis existed throughout this entire period, though it was not popularized nor rigorously tested: the 'mother' bee is mentioned in sources as far back as Aristotle's contemporaries, though, notably, none proposed that the female rules the colony (Maderspacher 2007; Grinnell 2016; Videen 2016). It was only following Queen Elizabeth I's reign (1558–1603) that the first scientific works about a *female queen* bee circulated in England (Butler's 1609 *The Feminin' Monarchie*), though her rule did nothing to change the entanglement of bee colonies and metaphoric royalty.¹

The case of the “king bee” illustrates that cultural values can subtly inform scientific theory. If those theories become prominent, then inertia can anchor the scientific community in ways of thinking that are basically misguided (Chu and Evans 2021). There is ample evidence that background beliefs can nudge scientists in many ways, affecting how researchers allocate their attention (Rees et al. 1999), how they interpret data (Brewer and Chinn 1994), what they perceive when making observations (Gunstone and White 1981), and what they judge worth communicating in their publications (Holton 1978). This can lead to long periods during which scientists try to make existing theories compatible with recalcitrant evidence (as illustrated by astronomical epicycles; Gingerich 1993) or simply miss such evidence entirely (as in the study of the evolution of the female orgasm; Lloyd 2006).

Early ecologists provide another example of cultural values informing theory, though the consequences are more complicated. When Haeckel, for instance, defined ecology as “the economy of nature” in 1869 (Egerton 2013), that phrase no longer meant something like “the order of nature,” as it had in the pre-Darwinian period. Instead, it was now informed directly by Darwin's 1859 *Origin of Species*, which systematically employs economic concepts in the theory of natural selection – competition, the division of labor, scarcity of resources, and so on – borrowed from the likes of Adam Smith and Thomas Malthus. And just as economies were thought to tend toward stable equilibria, regulated by the “invisible hand” that emerges when all actors pursue their own self-interest, Haeckel thought that ecological systems did too: such systems are

1. In the case of the “king bee,” the choice was certainly unfortunate, as the scientific use of this language was then used to legitimize human power hierarchies: Shakespeare, for instance, used the “king bee” as a metaphor for a rightly ordered patriarchal, monarchical society (1599; see also Allen 2004).

governed by the “balance of nature,” where “the absolute number of organic individuals populating our world ... remain[s] constant, and ... only the relative numbers of the individual species ... alter continually in relation to each other” (quoted in Egerton 2013, 227). Earlier biologists had understood the “balance of nature” in religious terms, attributing homeostasis to the divine ordering of the natural world. The economic view of ecological systems allowed scientists to preserve a sense of the correctness of that order without positing supernatural action. This may well have delayed scientists’ appreciation of nature’s stochasticity, not to mention many objectionable uses of the theory of natural selection to prop up certain hegemonic (power-structured and dominance-maintaining) human institutions.

These examples do not show that it is inherently objectionable to use value-laden language for scientific purposes. Instead, they illustrate the importance of thinking systematically about when and why to co-opt value-laden language for scientific purposes. In any case, our focus here is on one particular context where value-laden language had impacts on science. As mentioned earlier, we’ll explore this issue by contrasting the cases of parasites and predators. Despite ecologists’ appreciating that parasites and predators are similar in important respects, they paid parasites much less attention than predators and understood their ecological traits quite differently. Again, we do not want to suggest that values associated with parasites and parasitism were the only or even primary factors in this neglect, only that history suggests that they had some important role to play.

3. Ecological similarities, research disparities

Parasites, in a phrase, are predators that eat prey in units of less than one (Wilson 2014b, 112).

Though obviously different in many respects (Lafferty and Kuris 2002; Raffel et al. 2008), parasitism and predation share characteristics common to all consumer-resource interactions (Thomas et al. 2005b; Hall 2008). Early ecologists explicitly acknowledged this similarity – Elton (1927, 75) wrote, “it is best to treat parasites as being essentially the same as carnivores” – and other prominent ecologists have continued to associate parasites and predators (Hairston et al. 1960; Janzen 1970; Wilson 2014b). Notably, parasites were not completely ignored by all biological disciplines, such as taxonomy (“old school natural history”; Poulin 2021, 1073). Moreover, in part because parasites were targeted for eradication due to their impacts on the economy and human health (Cox 2002), parasitologists themselves began asking ecological questions about parasites long before ecologists began to seriously consider parasites as important players in ecological communities (e.g., Farley 2003; Worboys 1983). Still, it remains the case that animal parasites were at the margins of ecology throughout its early history (Jackson 2015).

This disparity in ecological research priority was apparent early in the 20th century. When reviewing recent progress in food cycles, Lindeman (1942, 405) wrote that “the various categories of parasites are somewhat comparable to those of the predators, but the details of [parasites’] energy relationships have not yet been clarified, and cannot be included.” This may be due to untested assumptions about the roles of (weak) parasites and (powerful) predators in controlling other species (about which we’ll have more to say later). Muir (Williams 1931, 26), for instance, stated that “theoretically, other things being equal, a predator should be more valuable [read: influential] than a parasite” and Elton (1927, 81) stated that “in [the food cycles of] an animal community ... parasites do not play a very important part” – without providing evidence for the claim. By comparison, the introduction of a review by Errington in 1946 suggested that studies of predation “surely number in the many thousands of titles.... Whatever else may be

said of predation, it does draw attention” (144).

The disparity grew as mid-to-late-20th century ecologists continued to demonstrate the important roles of animal predators in their ecosystems (e.g., Paine 1966; Slobodkin et al. 1967; often called ‘trophic cascades’, Paine 1980). Predators were described as “powerful” (Hutchinson 1957); “dominant” (Van Valen 1973a); “ubiquitous” (Ricklefs 1987); “major importance/regulator” (Blair 1950; Slobodkin et al. 1967); and even “keystone,” which was coined by Paine (1969a) in reference to influential, high trophic level predators before being more broadly redefined to include parasites (Power et al. 1996; Estes and Palmisano 1974). By contrast, parasites were either ignored or subsumed by predators (e.g., in Lotka-Volterra equations; Lotka 1925; Volterra 1926a, 1926b; Kingsland 2015). This systemic disparity produced an ecological literature where “competition and predation have been traditionally considered as major biotic determinants of community structure, [while] parasites have been virtually ignored” (Thomas et al. 2005a, 124).

Anderson and May’s (1978–1982) seminal models of parasite-host dynamics, drawing on the extensive predator-prey literature, began the process of integrating parasites into ecological theory in a more systematic way. As Heesterbeek and Roberts (2015) contend, while others were either pursuing highly abstract modeling or focused on understanding particular infectious agents, Anderson and May managed to model general epidemiological phenomena *without* losing sight of the biological mechanisms at work, which lent itself to improving decision-making in public health. Moreover, because they worked with a wide array of collaborators and students, Anderson and May created a new cohort of parasite and wildlife disease modelers who pushed parasite ecology research forward. As a result, the 1970s and 80s have been cited as the dawn of a parasite research revolution by many ecologists (Mittelbach 2005; Poulin 2007; Vickerman 2009; Moore 2012; Englund 2014; Jackson 2015; acknowledging that others played important roles as well, e.g., Hamilton 1980; Zuk 1982; Van Valen 1973b).

Nevertheless, the disparity in research priority between parasites and predators has persisted through the late 20th and early 21st centuries (Poulin 2021). In a study of ecological research network dynamics between 1975 and 2014, predator-prey ecology was one of the main clusters of ecological research from 1980–2014, while parasite ecology did not appear even as a sub-cluster (Réale et al. 2020). Of the 100 highest-ranked papers in ecology published between 1858 and 2014, predators featured in 45 compared to only 18 for parasites (14 of which also featured predators). The mean ranking for predator papers without parasites was 48 (published 1934–2014), including 50% of the top ten spots, while the mean ranking for parasite-only papers was 81, with only one paper in the top 50 and all published between 1978 and 1981 (Courchamp and Bradshaw, 2017).

Similarly, Loreau et al. (2005) found that the journal *Ecosystems*, chosen because it reflects the incorporation of parasites into theories about ecological systems and not simply their taxonomic inclusion, had not published a single paper on parasites, parasitism, or parasitoids from its founding in 1998 to the time of their publication (versus 110 hits for predat- between 1998 and 2005; our search of the same journal yielded 90 results for parasit- and 475 results for predat-between 1998 and 2023). The proportion of papers featuring parasites relative to predators in ecology journals from 1991 to 2006 showed predators featured in at least twice as many publications as parasites (Raffel et al. 2008). Broad topical treatment by ecologists is consistent with this analysis of the primary literature: 21st-century ecology textbooks still largely neglect parasites in comparison to predators, with the majority featuring parasites at less than 50% the rate of predators (Figure 1).

If early ecologists recognized the similarities between predators and parasites, why have parasites continued to be relegated to the margins as less important than predators in the development of ecological theories? To help answer this question, we should briefly review the

societal associations with the terms ‘parasite’ and ‘predator’ prior to their adoption by scientists.

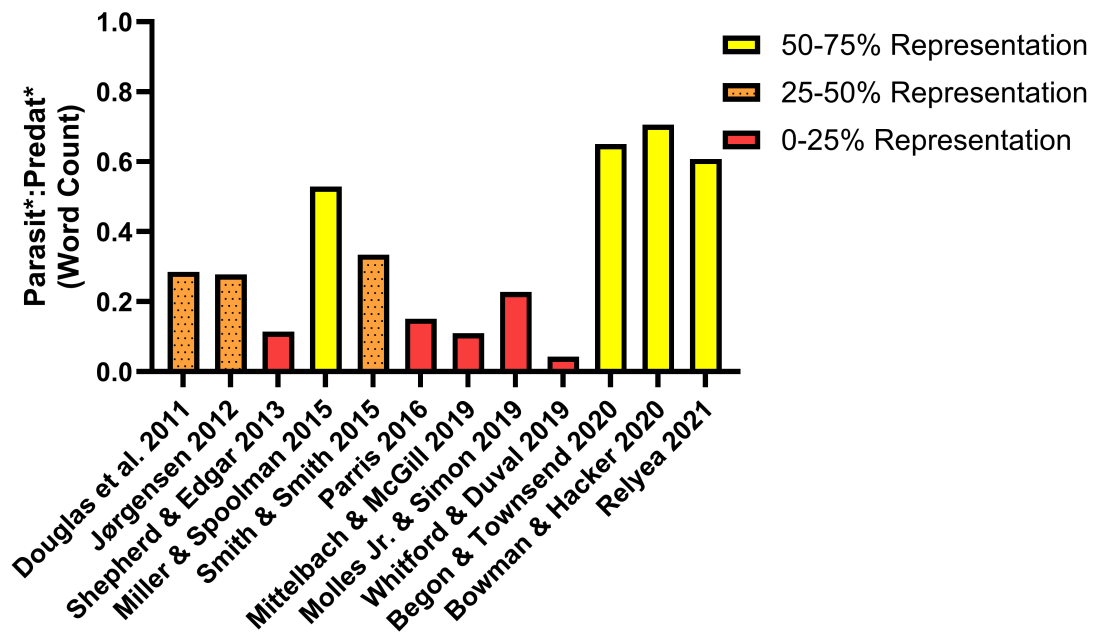


Figure 1: Parasites are neglected in ecological textbooks compared to predators. Twelve online ecology textbooks published in the last decade were searched for parasit* or predat* containing words using the ProQuest, RedShelf, or Amazon kindle search tool. The number of parasit* containing words was divided by the number of predat* containing words; a ratio of less than one means that parasites are not equivalently represented.

4. The Origins of ‘Parasite’ and ‘Predator’

‘Parasite’ has almost always been associated with weakness, dependence, lack of social importance, negativity, and threatening moral depravity. Contrary to the common supposition that the social (human) parasite is modeled off the biological parasite, the word referred solely to humans for over 2,000 years. The Greek *parasitos* dates to the 5th century B.C.; at that time, it referred to temple assistants receiving free meals in return for festival duties. Greek comedic playwrights molded the *parasitos* into a trope for the stage: irreverent flatterers dependent on free food secured at the tables of the rich. The *parasitos* was popularized as a unidimensional ‘type’ – overwhelmingly the punchline of jokes and often an example of unethical behavior (Gullestad 2011; Musolf 2014, 2016).

Ridicule morphed into vicious insult targeted at specific individuals both in creative (e.g., a 1665 satire about Pierre de Montmaur, *Epulum parasiticum*; De Smet 1996) and religious works (e.g., English Catholic scholars calling John Wycliffe “a vile heretic, a most pernicious flatterer and parasite,” Rainolds and Bruce 1593). Specific species of animal parasites (e.g., the flea) were represented as simultaneously threatening to society’s most important moral values (e.g., female virginity during the British Tudor and Victorian periods) yet individually puny/weak, often through association with socially unimportant or derided individuals (Marlowe 1592; Donne 1633; Orme 2011; Prystash 2016; Filo 2019).

‘Predator’ (meaning pillager/plunderer) appears in the 15th century, also solely in reference to humans, with a connotative duality as divinely powerful yet morally contemptible (e.g., the

disgraceful nature of the king's predation described by 15th-century political prisoner George Ashby, Bateson 1899; and Cæsar, a tyrant and 'predator' in 1584 *Don Simonides*, OED 2021). According to these authors, predators were authoritative, important male figures, generally kings and emperors ruling by a natural, divine right that justified their hostile dominance. Specific animal predator species were frequently associated with power, masculinity, wealth, and social importance (e.g., the eagle on the Roman legion standard and lions on English royal crests, among others; Mylonas 1946; Julian 2004; Hünemörder 2006; Hayes 2014; Holmes 2020). Hunting, the act of human-as-predator, was generally considered the domain of strong and able men, and in some societies became a sport associated with wealth, power, and masculinity (Goldberg 2020; some of these associations lasting to the modern era, see Littlefield 2010).

When 'parasite' was adopted and popularized in the scientific community in the 17th century, the associated values and concepts such as weakness, social (e.g., system-level) unimportance, depraved moral threat, and "negatively valued metaphors of dependence" (Osborne 2017, 212) came with the term (Gullestad 2011; Musolff 2016). Ecologist Elton (1927, 75) wrote in his foundational text, *Animal Ecology*, that "it is common to find parasites referred to as if they were in some way more morally oblique in their habits." The moral/functional degeneracy and negative dependence of even a free-living and familiar-looking brood parasite, via a social metaphor, can be clearly seen in the popular natural history works of Neltje Blanchan and her accounts of cowbirds:

Its marital and domestic character is thoroughly bad. Polygamous and utterly irresponsible for its offspring, this bird forms a striking contrast to other feathered neighbors, and indeed is almost an anomaly in the animal kingdom ... an unnatural mother may be seen skulking about in the trees and shrubbery ... selecting in a cowardly way a small nest ... there leaving the hatching and care of its young to the tender mercies of some already burdened little mother ... keeping with its unclean habits and unholy life and character. (Blanchan 1897, 49-50)²

As these examples illustrate, and as documented more thoroughly in the quotes by ecologists in supplementary table 1, the concepts of social unimportance, weakness, and degeneracy colored the way many early ecologists viewed parasites. These associations persisted and became common in the field despite the absence of scientific evidence for them; moreover, they proved to be surprisingly durable. For instance, Lack (1954) stresses parasites' unimportance, Haldane (1955) critiques this claim, but MacArthur (1958) repeats Lack's view anyway – even though MacArthur engages with Haldane's work.

'Predator', by contrast, was widely adopted by scientists in the early to mid-20th century. Animal predators were valorized as naturally powerful in their own ecosystems. At the same time, they were condemned when their actions threatened humans' safety or economic interests, and thereby the hierarchy of nature (established both through religious texts, such as the Judeo-Christian creation myth, and scientifically; Aristotle's *Scala naturae* and Linnaeus' *Systema naturae*; Pui-lan 1992; Clutton-Brock 1995). This duality helps explain humans' continual "love-hate relationship with predators" ("Predators on Top" 2018). On the one hand, they have long been culled when they've posed any threat to human interests: consider, for instance, the US decision to slaughter wolves in the late 1800s to prevent livestock predation (Dunlap 1998). However, after such threats have been minimized, predators are valorized for their critical ecosystem roles and selected as charismatic targets for conservation and ecological restoration initiatives (Dunlap 1998; Macdonald et al. 2017).

2. Her perspective is unchanged thirty years later: "this contemptible bird everyone should know if for no better reason than to despise it ... shirking as she does every motherly duty" (Blanchan 1927, 140-141).

This tension is visible, again, in the work of Blanchan (1898) who writes admiringly of “innocent birds of prey” (vii), whose “...entire structure indicates strength, ferocity, carnivorous appetite, and powerful flight, have, for their diagnostic features, strong, hooked bills...” (301) But her tone changes significantly when birds of prey threaten the anthropocentric hierarchy, writing that the chicken hawk “lives by devouring birds of so much greater value than itself that the law of the survival of the fittest should be enforced by lead until these villains, from being the commonest of their generally useful tribe, adorn museum cases only.” (314-315)

5. Assumptions About Parasites: Two Case Studies

On its own, this brief survey of the history of the terms ‘parasite’ and ‘predator’ is suggestive: it would be surprising if the values associated with these terms (e.g., powerful/important vs. weak/unimportant) played no roles whatever in scientists’ thinking about parasites and predators. Like the divergent societal values associated with sex and power that promulgated the reign of the “king bee,” the divergent values associated with predators and parasites probably had some impact on scientists’ appreciation of parasites’ ecological significance. However, the impacts of these values are clearer when we consider specific assumptions about parasites. In what follows, we turn to two case studies: one about the assumption that parasites are ecologically insignificant; the other about parasites being unworthy of conservation. In each case, we argue that societal values played some role in explaining why earlier scientists opted not to explore hypotheses that framed parasites as powerful/important – and thus as ecosystem assets.

5.1. Parasites as Weak and Unimportant Dependents

From the 19th century birth of evolutionary biology until well into the 20th century, parasites were seen as biologically degenerate, ecologically marginal and evolutionarily anomalous... [This atmosphere] casts a pall over parasite evolution and affects the questions we tend to ask. (Jackson 2015, S1)

Elton was the first to categorize trophic patterns in feeding relationships in his pyramid of numbers: “Eltonian pyramids,” the ancestors of the more familiar trophic pyramids in ecological textbooks today (Sukhdeo 2010). Like many early 20th-century ecologists, Elton was influenced by the capitalism of his day, claiming that “the carnivores ... live on capital and the [parasites] on income,” where living “on capital and not on income [is] an almost ideal existence” (Elton 1927, 71, 138). Echoing centuries of associating powerful, wealthy men with carnivores, Elton’s pyramid placed carnivores at the peak of the pyramid, mirroring “the philosophy that had prevailed in Washington since 1921 ... [that] government was to provide prosperity for those who lived and worked at the top of the economic pyramid” (presidential speechwriter Samuel Rosenman, 1952, 62).

Elton himself recognized the limits of this model – acknowledging, for instance, that carnivore numbers are (at least partially) controlled by parasites. However, mere pages after acknowledging the similarity of predators and parasites, he still concluded (without providing evidence) that “many ectoparasites have no very important direct effects upon the food-cycle [and] it is for this reason that parasites can very often be ignored in practice” (Elton 1927, 81). While predators, much like those at the top of the economic pyramid, were considered too important to be ignored, parasites, much like the marginalized people with whom they were historically associated, could (and would) be neglected (Lafferty et al. 2006; Sukhdeo 2012).

As mentioned earlier, ecology’s perspective on parasites began to shift due to a series of critical publications in the 1970s and 1980s. Modern trophic pyramids and food webs may

even place parasites at *the very top* (Rafaelli 2002; Sukhdeo 2010), and parasites are now known to serve many powerful roles in ecosystems: generating host population cycles (Dobson and Hudson 1992; Hudson et al. 1998), making prey vulnerable to predation (Hudson et al. 1992), affecting the structure or connectivity of food webs (Marcogliese and Cone 1997; Lafferty et al. 2006; Lafferty et al. 2008), direct or indirect ecosystem engineering (Thomas et al. 1999; Pascal et al. 2020), changing temporal ecosystem dynamics and biogeochemical cycling (Preston et al. 2016), initiating trophic cascades (Holdo et al. 2009; Buck and Ripple 2017; Monk et al. 2022), contributing to biomass and secondary productivity (sometimes more than the top predators; Kuris et al. 2008), and more (Price et al. 1986; Thomas et al. 2005b; Hudson et al. 2006; Hatcher and Dunn 2011; Hatcher et al. 2012).

In addition, parasites can be important players in evolutionary ecology. Contrary to the “traditional, but untested, assumption that anti-parasite responses are weak relative to anti-predator responses” (Rohr et al. 2009, 447), parasites drive numerous changes in host behavior through the evolution of anti-parasite responses (Bush and Clayton 2018) and through direct and indirect manipulation (Moore et al. 2005; Hughes et al. 2012). Indeed, parasite-induced changes in host behavior may be more numerous and frequent than anti-predator behaviors (Daversa et al. 2021). After decades of ignoring the possible powerful roles of parasites in natural selection (Vickerman 2009; often in favor of predators, Haldane 1949), recent research shows parasites drive speciation and diversity, mediate gene transfer among species, and may have played a role in the evolution of sex and sociality (Schmid-Hempel 1998; Poulin 2007; Jokela 2009; Auld et al. 2016; Brunner and Eizaguirre 2016; Yang et al. 2016; Turko et al. 2017; Poulin 2021).

The morphological simplicity of many animal parasites, and their physiological reliance on their hosts, generated assumptions of negatively-valenced dependency; parasites were positioned as ‘having regressed’ evolutionarily to a simplified and weak state (see quote by zoologist Lankester in supplementary table 1; Vickerman 2009), precluding a transition back to free-living lifestyles (Dollo 1893; Cruickshank and Paterson 2006). In a review of fifteen parasitology textbooks, “only four texts allowed the possibility that reversals of parasitism [back to a free-living state] might be possible, but all cautioned that it is unlikely to occur” for parasites (Cruickshank and Paterson 2006, 511). However, recent evidence has shown that parasites can become free-living species again and there are likely more examples than the few discovered so far (Siddal et al. 1993; Dorris et al. 2002; Klimov and O’Connor 2013; Xu et al. 2016). Parasites are also more complex than initially assumed, with highly specialized genetic and morphological adaptations for host manipulation and survival, suggesting parasites are not ‘regressed’ but rather innovative (Auld and Tinsley 2015; Hughes et al. 2012; Hurford and Day 2013; Jackson 2015; Jackson et al. 2016; Carvalho Cabral 2019; Yang 2019). Parasites are now known to shape ecosystems and exert powerful selective pressures on their hosts despite long-held assumptions to the contrary. It seems plausible, then, that our realizing these facts was hampered by a predisposition to view parasites as *definitionally* weak, unimportant, dependent, and heritably simplified.

5.2. Parasites as Categorically Threatening

Parasitism as a way of life is usually confounded with a status: a parasite, at any density, is automatically considered as a pest, because wildlife is a valuable resource for man. (Pérez et al. 2006, 2034)

There has been a similar transition regarding the management of parasites. To be worthy of conservation – i.e., of status as a protected ‘natural resource’ or asset – the services an organism provides must outweigh the perceived burdens they impose on humans (Clutton-Brock 1995).

A large literature exists about how and when predators went from mostly ‘threat’ to mostly ‘asset’ over the course of the 20th century (Dunlap 1988; Kruuk 2002; Bergstrom 2017). Two factors appear to have been particularly important: first, the actual diminishing threat posed by predators to industrial settler-colonialist societies due to successful predator control and the industrialization of habitat; second, predators’ role as a recreational and economic asset for powerful men (like United States President Theodore Roosevelt; Dunlap 1988; Johnson 2002).

By contrast, veterinary/medical parasitologists presented parasites as a substantial threat to health and comfort at home and abroad (Cox 1993; 2002; Morris 2011; Sarasohn 2021) leading to, for example, militarized tropical medicine (Lederman 2005; Keller 2006; Mitman and Erickson 2010). Parasites also posed major challenges to colonial projects, such as the construction of the Panama Canal where the threat of mosquito-borne parasites led to ecologically ruinous control strategies such as ‘oiling’ sources of standing water (“the greatest liberty man has ever taken with nature,” according to Englishman James Bryce, quoted in Haskin 1913, 20; Moore 2017; Lindsay-Polard 2003).³

Conservation has never been an impartial enterprise, even when it has appealed to values that support such an orientation. Most 19th and early 20th century conservation efforts were directed toward species that had some easily discernible value for human beings (Stork and Lyal 1993; Singer 2009). Michael Soulé, the founding father of conservation biology, attempted to correct this by arguing that biodiversity ought to be valued in itself (1985). While this idea helped many species with no obvious value for humans, it did not seem to benefit parasites. Parasites were categorically either assumed to be unimportant (as previously described), and thus not worthy of consideration (completely absent from 42% of conservation textbooks), or represented as threats to human conservation interests (31% of all textbooks; Nichols and Gomez 2011). Only 15% of conservation textbooks in 2011 contained at least one sentence positively describing the conservation value of parasites (Nichols and Gómez 2011). This near-universal absence of positive perceptions of parasites in the conservation literature prevented “a paradigm shift in the perception and valuation of parasites ... similar to that of apex predators in the mid-20th century” (Dougherty et al. 2016, 724).

Despite being more speciose than predators (Price 1980; Poulin and Morand 2004), and despite their enhanced vulnerability due to the threat of co-extinction with their hosts (Koh et al. 2004; Strona 2015; Thompson et al. 2017), parasites were ‘missing’ in conservation: neglected in studies of extinction and left out of reintroduction efforts, translocation considerations, and theoretical de-extinction conversations (Moir et al. 2012; Jørgensen 2015; Northover et al. 2018; Selbach et al. 2018). Humans have driven some parasites to extinction or endangered their intermediate hosts without conducting risk assessments, including during wildlife conservation efforts and in direct contradiction of taxonomically unbiased biodiversity goals (e.g., condor lice on California condors, about which more below; Gompper and Williams 1998; Kristensen and Brown 1999; Colwell et al. 2009; Dunn 2009; Pizzi et al. 2009; Mihalca et al. 2011; Pérez et al. 2013; MacKenzie and Pert 2018; Milotic et al. 2020).

Moreover, when parasite conservation began to gain traction among some researchers, it met resistance from many others who, in the absence of acknowledged ecological roles for parasites, latched on to the narratives of threat imported from medical/veterinary parasitology. Windsor (1995, 1) notes that “informing most people, even most biologists, that parasites are going extinct is sure to bring a response such as ‘good riddance’... [E]ven those who specialize in the study of parasites tend to regard them with controlled disdain.” Indeed, the uncertainty

3. Given the ample evidence of negative value associations with the term ‘pest’ (see, e.g., McWilliams 2008; Biehler 2013; Sarasohn 2021), our argument would only be strengthened by considering the tendency to classify parasites as pests. For the sake of space, however, we set this issue aside.

surrounding the actual threat level posed by most parasites led to a tendency to exaggerate the threat that all parasites pose to wildlife. For instance, among the IUCN endangered species reports that listed parasites/disease as a “major threat,” approximately 70% provided no evidence to back up the claim (Smith et al. 2006). Stringer and Linklater (2014, 935) offer three historical examples of the “overestimation of the threat ... of parasites within an ecological community,” and McCallum (2012, 2829) states that “attributing prehistoric extinctions to infectious disease has become almost a cottage industry in the last two decades,” before demonstrating that the evidence for such claims is rarely convincing.

Despite this magnified perception of their threat, parasites/disease are only listed as a contributing factor in 8% of endangered species cases, even including the 70% of cases with no supporting evidence (Smith et al. 2006). Parasites are estimated to contribute to the decline of less than 1–4% of species; moreover, they are rarely the sole threat (Wilcove et al. 1998; Yingming and Wilcove 2005; Smith et al. 2006; Heard et al. 2013). Instead, they usually act as the last straw for species on the edge of extinction, already threatened by habitat loss, invasive species, overexploitation, and climate change (Wilcove et al. 1998; Smith et al. 2006; Sodhi et al. 2009; Smith et al. 2009; Heard et al. 2013). Host-specific parasites may even be threatened with extinction more rapidly than their hosts, potentially serving as early indicators of biodiversity decline (Koh et al. 2004; Hechinger et al. 2007; Lafferty and Kuris 2009; but see Strona et al. 2013).

Of course, some parasites contribute significantly to local population declines, failed reintroductions, or even historical and current extinctions. The threat level posed by a specific parasite can be very high, especially when the parasite is non-native or the host population is genetically homogeneous (de Castro and Bolker 2005; Ewen et al. 2012; McCallum 2012; MacPhee and Greenwood 2013; Heard et al. 2013). But predators can also pose severe threats, and in similar cases (Doherty et al. 2015). It is thus crucial to find evidence to guide each species's categorization as ‘asset’ or ‘threat’ in its unique context (if these categorizations are determined to actually be helpful at all). In any case, changing the default “parasite = threat” assumption will prevent the mismanagement of parasite biodiversity – e.g., the use of broad-action anti-parasite treatments in wildlife communities (Pedersen and Fenton 2015).

Lingering assumptions of parasites as threats have been slowly revised over the past 15 years, allowing an increased focus on active parasite conservation that positions parasites as important and positive components of biodiversity in their own right. Estimates of parasite extinction rates are accumulating, global and specific conservation guidelines have been proposed (and in a few cases, implemented), calls are mounting for cataloging diversity, and there is research starting on the factors that make specific parasites more or less vulnerable to extinction and more or less threatening to host biodiversity (Dobson et al. 2008; Lafferty 2012; Gómez and Nichols 2013; IUCN/SSC 2013; Brown et al. 2017; Carlson et al. 2017; Cizauskas et al. 2017; Thompson et al. 2017; Wait et al. 2017; Okamura et al. 2018; Kwak et al. 2019, 2020; Carlson et al. 2020a, 2020b; Moir and Brennan 2020). However, absent the values that seem to have shaped thinking about parasites, these revisions to conservation strategies and priorities (and the extinction of some parasite species, such as the Condor louse) may never have been necessary.

6. The Importance of Attending to Values

Parasitology ... has been forced to address a number of stereotypes, prejudices, and common misconceptions which surround the objects of its research ... theories which at the time were considered indisputable, but which have long been disproved. (Jajszczok 2015, 67)

We have argued that societal values associated with the terms ‘predator’ and ‘parasite’ were uncritically imported into ecology. We contend that these values partially explain both the appeal and durability of erroneous assumptions about parasites relative to predators, even though both are ecologically similar classes of consumer organisms. The values associated with predators made it easier to appreciate their ecological importance and conservation value; by contrast, the values associated with parasites made it harder to do the same.

Of course, it is not possible to quantify exactly how much harder these values made it for ecologists to appreciate the ecological importance and conservation value of parasites. In part, this is because there is no obvious metric by which to make the comparison. For instance, we can’t show that these values set back appreciation of parasites by a specific number of years. However, we think a strong case can be made that the contributions of values associated with parasites were not entirely trivial. The first part of that case involves demonstrating that ecologists persisted in their beliefs about parasites long after ample evidence became available to contradict those beliefs. At that point, it becomes necessary to seek potential cultural explanations for belief persistence. One component of scientific culture is the values associated with the concepts that scientists employ. The rest of that case involves showing that a cultural explanation of the neglect of parasites would be inadequate were it *not* to cite the relevant value associations. Imagine, for example, a cultural explanation that just appealed to “within-paradigm” scientific conservatism as the mechanism for the neglect of parasites. Such an explanation would miss the mechanisms by which conservatism is implemented – e.g., particular ways of understanding parasites that are informed by values – as would other explanations that attempt to avoid this level of granularity.

In any case, insofar as the value associations hypothesis is correct, it raises two important questions. One of them concerns whether there were or are any other costs of having these values shaping parasite ecology. The second focuses on moving forward: are there ways to mitigate any impacts of negative values being associated with parasites?

6.1. *Broader Costs*

We’ve focused on one way that science can be set back when scientists aren’t sufficiently critical about the way that social values inform theory. However, as has been well-documented in other contexts, the direction of influence can go the other way too: society pays costs when scientific theories lend themselves to misinterpretation and misuse. Here, we’ll briefly consider some of the ways this has happened with parasites.

Prior to the scientific adoption of ‘parasite’ to describe an entire category of plants in the 17th century (Gullestad 2011), the invective was aimed exclusively at individual persons. Following the scientific adaption of the term for categorical usage, the social ‘parasite’ expanded to label whole categories of undesirable people (Musolff 2016). Conceptions of parasites’ properties were also evolving. Before the advent of parasitology in the 19th century, biological parasites were believed to spontaneously generate within a host’s body (Gullestad 2011). After the development of 19th and 20th-century medical and veterinary parasitology, new concepts became associated with both biological and social parasitism: contagiousness, physical invasion by a foreign entity, and bodily resource exploitation/host dependency. Moreover, the advent of medical/veterinary parasitology – and the race to eliminate numerous parasites across the globe in the late 19th to early 20th century – naturalized the idea that parasites were to be eliminated, all at a time when natural history and biological research were increasingly reaching the public (Musolff 2016; Inda 2000; Gullestad 2011; Osborne 2017).

Jointly, these developments made it natural to describe whole categories of humans as “para-

sites” – the downtrodden and oppressed. They too could then be framed as having “contagious” and socially undesirable traits, as foreign (at least in the sense of “not like us,” though often literally of other nationalities), and as objectionably dependent. Minimally, such individuals are unimportant to the social order; worse, they are threats. And just as physical disgust is often directed toward animal parasites, moral disgust is often directed toward human “parasites,” who can be understood as ‘worthless’ and ‘depraved’ (Haslam et al. 2011).

It’s no surprise, therefore, that the label of ‘parasite’ is often used against already vulnerable people. Parasite metaphors are aimed at people of color, the poor, and the disabled, especially when these populations can be represented as invaders, weak, dependent, degenerate/impaired, or disgusting – as, e.g., in the case of immigrants (especially women), those who receive state welfare, transgender people, or disabled people (or intersectional identities that cross these numerous axes of oppression; Markel and Stern 2002; Musolff 2016; Waśniewska 2017; HoSang & Lowndes 2019). Sometimes, these metaphors have even been advanced casually by parasitologists (e.g., ‘welfare state’ in Stunkard 1954, ‘illegal aliens’ in Drisdelle 2010). All these groups have been described as ‘parasites’ or ‘leeches’ by hate groups, and even by politicians (Hogan and Haltinner 2015; Pring 2017; Brufke 2018, Gander 2018). This appears to be an effective strategy: one study found that participants exposed to the metaphor of “countries as bodies” were more concerned with the threat of physical contamination and had more negative attitudes towards immigrants (Landau et al. 2009). This language is used to legitimize discriminatory views, actions, and policies as both natural and necessary: after all, parasites are either (at best) unimportant or (at worst) threatening to the maintenance of a ‘healthy’ ecosystem or body; so, the relevant groups must be excluded or eradicated.

To be clear, we are not claiming that the choices of early ecologists are responsible for xenophobia, classism, or the systematic devaluation of the economically marginalized. Instead, we’re making the modest point that scientific theories are not simply attempts to understand or make predictions about their ostensible subject matter: in addition, they create new metaphors using the natural world that society may use to make claims about the social world, whether for good or ill. And insofar as scientific theories are already informed by social values, this means that there is some risk of a vicious loop, where negative values shape science that shapes society that shapes science, and so on. With respect to the rhetorical utility of the language of parasitism, those looking to preserve key hierarchies and systems of oppression would, no doubt, find other ways to make their case. Still, the case was probably easier to make because that language invokes the aura of science and a supposed ‘natural’ order.

Put differently, every hegemonic dichotomy – e.g., citizen/alien, man/woman, human/animal – takes work to maintain. Scientific theories can help prop up these hegemonic structures when scientists fail to interrogate the values that those theories inherited from the societal context in which they were developed, thereby creating tools that lend themselves to the preservation of such orders. The contribution may be small, but it’s a contribution nonetheless – one to which self-critical scientists have reason to attend.

6.2. *Moving Forward*

Suppose that we accept that societal values played some non-negligible role in the development of parasite ecology, with some effects lingering to the present day. One encouraging thought is that societal values are not destiny: ecology has made significant strides toward correcting the record on parasites without any major changes in the broader societal value associations with these animals. As ecologists developed increasingly powerful tools – theoretical, methodological, and physical – for understanding the roles and value of parasites, scientific thinking began

shifting, even if that change took time and is not yet complete.

Still, in managing societal values in science, we shouldn't rely entirely on somewhat chancy scientific developments as a strategy for self-correction. Better, we submit, to pursue two strategies: first, taking some preventive medicine in hopes of avoiding such risks in the future; second, considering how we might leverage other cultural values to counteract problematic cultural associations that are already in place.

On the preventive side, there may be value in considering frameworks that blur the lines between scientists, the societies in which they live, and the objects of their inquiries. The naturalcultural framework, for instance, proposes that "nature and culture are so tightly interwoven that they cannot be separated," implying that our understanding of even ostensibly objective phenomena, like ecological relationships, "are both biophysically and socially formed" (Malone and Ovenden 2017, 1; MacCormack and Strathern 1980). This approach invites us to be especially sensitive when our ostensibly objective descriptions of phenomena have served as natural metaphors for human behaviors and societies across cultures and millennia (Yamamoto 2000; Palmatier 1995; Talebinejad and Dastjerdi 2009; Haslam et al. 2011; Liu 2013; Urton 1985). Culture is visible in animal ecology in the way it lends itself to constructing both interspecific (human/animal) and intraspecific (human/human) divisions (MacCormack and Strathern 1980). This construction ultimately depends on the premise of a clean separation between the culturally-located human 'self' observing the naturally-located animal 'other'. Rejecting this separation means acknowledging that ecological research is not done by objective humans outside of and above nature, but rather subjective humans embedded within a unified natureculture.

In practice, this involves thinking carefully and critically about *why* certain terms seem useful for describing and theorizing about some phenomenon, why certain metaphors or particular turns of phrase seem so intuitive or insightful. What assumptions come along with that language, and how well do they fit with what the evidence actually supports? What are the costs of a given way of characterizing a particular role in an ecosystem, whatever the benefits may be? Asking these questions is the first step toward naming the influence of culture on the study of nature, bringing out the relationship between our positionality and the practice of science, from the questions we ask to the theories we construct.

Preventive measures aside, what can we do about existing values associated with parasites, such as the view that they aren't important enough to conserve? The proposal here is to identify positive societal values that can counteract any negative associations with parasites. We can appreciate the idea by revisiting an example that we mentioned earlier: namely, the case of *Colpocephalum californici* (Psocodea: Menoponidae), the California Condor's host-specific louse that was wiped out in the 1980s in an effort to save the condors. Barrett and Fischer (2023) explore the various dimensions of *C. californici*'s importance as a species, including the information it held about its host's ecology (Adler et al. 2011) and evolutionary history (Whiteman and Parker 2005), its contributions to biodiversity and ecosystem complexity (Norton 1988), its aesthetic value (Parsons 2007), its potential value to future generations, and its intrinsic value. Once we appreciate these dimensions of *C. californici*'s value, we have ways of resisting the assumption that delousing the California condor was a costless conservation action. By articulating and communicating such values, we may be able to undo some of the negative impacts these other values we have described have on ecological parasitology and the parasites themselves. And insofar as we can do this, the Condor louse example suggests a general blueprint for navigating negative cultural associations in science: first, explicitly identifying those negative values; second, highlighting the many implications of more positive values for the case in question.

7. Conclusion

It takes work to retrofit parasites into a century of ecological research that ignored them; in some cases, it is difficult enough that some researchers have argued that we must start anew (e.g. food web theory; Sukhdeo 2010). Moreover, when societal values are uncritically incorporated into scientific theories, they can lend themselves to unfortunate social uses. Credit is due to the many researchers who have questioned prevailing societal and cognitive biases about roles of parasites in ecological systems when confronted with contradictory evidence. However, it would have been far better – for researchers, for conservation, and for parasites themselves – had earlier generations of ecologists been more aware, more reflective, and more critical of the values that informed the way these organisms were viewed and studied.

Scientists have some responsibility to be critical of the concepts they borrow and question the values associated with them. This process can be facilitated by reconfiguring our conception of the relationship between the inquirer, society, and the object of inquiry (e.g., the naturalcultural framework). We can also search for other values that can counteract objectionable consequences of past theoretical choices. Via such strategies, progress can be maintained and accelerated into the future.

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ISSN 2475-3025