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# Unwelcome Guests – Coextinction of Parasites

***This is a guest article, kindly contributed by Luke Beall, a master's student of environmental science based at Duquesne University in Pittsburgh, Pennsylvania. Luke's focuses include conservation biology, ecology, and evolution, with a particular passion for rewilding. He be found on [Twitter](#).***

Parasite is a word with near-universally negative connotations in daily society. The

very existence of a symbiotic organism which depends, for much or all of its life history, on leeching nourishment and shelter from an unwilling host is an uncomfortable concept for many people. The word even sees use as a derogatory term for one who exploits others without giving anything in return.

In biology, parasitism is a form of symbiosis, a close association between species, in which one species (the parasite) exploits another (the host) for its own benefit. This aspect of harm is what separates parasitism from other symbioses, such as commensalism, in which one species sees gains while other isn't affected. Most parasites depend entirely on their hosts for nourishment and/or habitat, and so they become intimately tied in an evolutionary context. This host dependence often leads to extreme adaptations and body plans tailored to surviving on – or in – another organism's body.

While seeming extreme, parasitism is hardly unique; in fact, it's an extremely common lifestyle. Parasitic specializations are known in everything from unicellular bacteria to complex plants, fungi, and animals. Some studies have cited that the number of parasite species may be more than four-times that of free-living ones, which would make parasitism the dominant lifestyle on Earth (1, 2).

Less widely-known are the ecological consequences of parasites. While the parasite-host relationship is easily simplified as "parasite benefits, host suffers", the degree of their presence in an ecosystem and their greater impact is a complex affair. There is much that is not yet known, but parasites have been demonstrated to be of vital importance in shaping ecosystem interactions (2, 3). In a broad sense, parasitism is a form of predation, in which parasites exert negative regulatory pressures on their hosts. Through these pressures, parasites may influence their population dynamics and competition levels, increase connections and stability within a food web, and act as important participants in energy flow through the ecosystem (2, 3). Apart from these benefits, parasitic organisms can also make up a significant proportion of biomass in a community as well as act as prey themselves (1, 2, 3).

The life history of parasitic animals puts them in a unique position regarding evolutionary persistence and conservation. Their dependence on a specific host or

set of hosts means they are susceptible to the same risk factors, and if their hosts go extinct, the parasites follow suit (1, 2, 3, 4). As such, a slew of parasites is known to have gone extinct during the Holocene, and many are unlikely to ever be discovered on account of the extinction of their hosts and the general paucity of fossil parasite preservation (5, 6). Coextinction or co-endangerment of species along with their mutualistic or commensal partners in recent millennia is a well-documented, recurrent phenomenon, and parasitic relationships are subject to the same risks, if not more directly (5, 6, 7, 8). Crashes in a host's population may result in severe genetic bottlenecks among their parasites; parasites are now thought to be some of the most endangered groups on Earth (7). However, due to their difficult-to-study, inconspicuous nature, their status as invertebrates, and potentially the public's aversion to them, this endangerment and extinction attract much less attention than that of other groups (1).

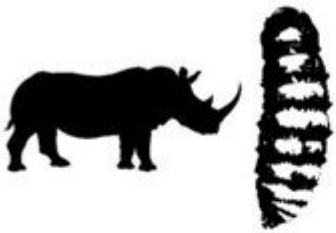

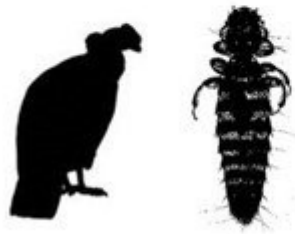

|                    | Host conserved  | Host extinct   |
|--------------------|---|--|
| Parasite conserved |  <p>Ideal circumstances: both are saved<br/>Charismatic megafauna with vital highly-specific parasites</p> |  <p>Reintroduction into alternative hosts<br/>OR<br/>Rediscovery after host extinction</p> |
| Parasite extinct   |  <p>Current conservation paradigm<br/>Parasite a human health risk or otherwise unsuitable candidate</p>   |  <p>Current paradigm when host conservation proves unsuccessful</p>                        |

Fig 1. Potential outcomes for parasite conservation (clockwise from top left). Black rhinoceros (*Diceros*

*bicornis*) and botfly *Gyrostigma rhinocerontis*. Band-tailed pigeon (*Patagioenas fasciata*) and louse *Columbicola extinctus*. Huia (*Heteralocha acutirostris*) and louse *Rallicola extinctus*. California condor (*Gymnogyps californianus*) and louse *Colpocephalum californici*. From Dougherty et al. (2015).

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Befitting the sparseness of parasite fossil remains, most extinctions are known from the Holocene, and fall under two main categories. They are here known as 1) true coextinctions and 2) conservation-induced extinctions. True coextinctions include cases in which the host becomes extinct and the parasite(s) follows suit (1, 6). Conservation-induced extinction is a phenomenon unique to parasites, in which a host species becomes extinct in the wild, resulting in the only remaining population existing in human care (6). As part of standard veterinary practices to increase survivability, parasites are removed, presumably without consideration of their own conservation status (1, 4, 6). Even in the event parasite removal doesn't occur or isn't entirely successful, parasites seem to have reduced fitness in captivity. Here, host individuals are prone to overgroom themselves and one another, and dispersal is more difficult, especially for parasites of solitary host species that don't often mingle with conspecifics (8).

Some instances of conservation-induced extinction are especially direct and discrete, particularly those associated with host species that became totally extinct in the wild, such as the California condor (Figure 1) and Guam rail. In each of these cases, the last remnants of the wild population were captured in a rescue operation, resulting in every last existing individual of the species being treated for their parasites (6).

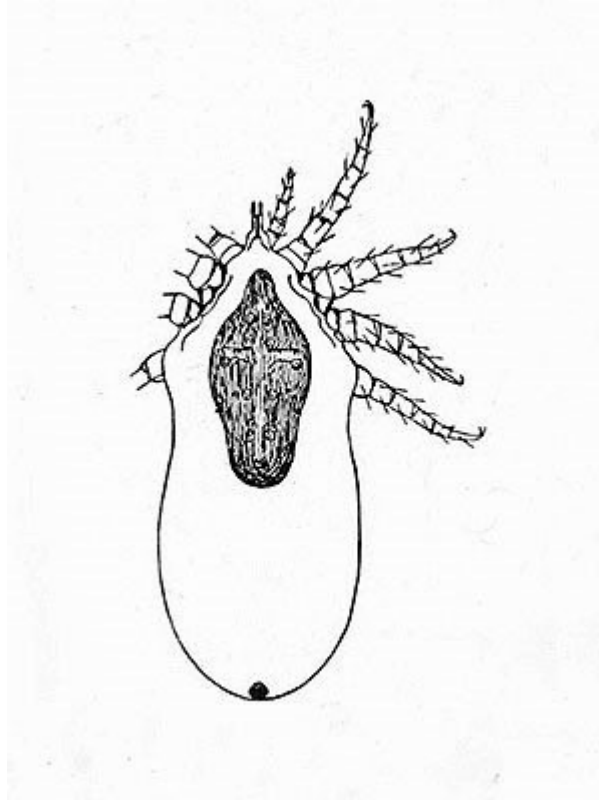
| Species | Host | Fate |
|---------|------|------|
|---------|------|------|

| <b>Psocodea (lice)</b>             |   |   |
|------------------------------------|---|---|
| <i>Colpocephalum californici</i>   | California condor ( <i>Gymnogyps californianus</i> )                            | Conservation-induced extinction (1987) <sup>6, 12</sup>                         |
| <i>Austromenopon confine</i>       | Slender-billed curlew ( <i>Numenius tenuirostris</i> )                          | Both host and parasites possibly extinct <sup>6</sup>                           |
| <i>Cummingsiella breviclypeata</i> |   |   |
| <i>Psittacobrosus bechsteini</i>   | Cuban macaw ( <i>Ara tricolor</i> )   | Co-extinct (~1860s) <sup>6</sup>  |
| <i>Acutifrons caracarensis</i>     | Guadalupe caracara ( <i>Caracara lutosa</i> )                                   | Co-extinct (~1900) <sup>6</sup>   |
| <i>Coloceras hemiphagae</i>        | Norfolk pigeon ( <i>Hemiphaga novaeseelandiae spadicea</i> )                    | Co-extinct (1901) <sup>6</sup>  |
| <i>Coloceras restinctus</i>        |   | Co-extinct (1901) <sup>6</sup>  |
| <i>Philopteroides xenicus</i>      | Bushwren ( <i>Xenicus longipes</i> )  | Co-extinct (1972) <sup>6</sup>  |
| <i>Rallicola pilgrimi</i>          | Little spotted kiwi ( <i>Apteryx owenii</i> )                                   | Conservation-induced extinction (~1938) <sup>6</sup>                            |
| <i>Rallicola extinctus</i>         | Huia ( <i>Heteralocha acutirostris</i> )  | Co-extinct (1907) <sup>6</sup>  |
| <i>Rallicola guami</i>             | Guam rail ( <i>Gallirallus owstoni</i> )  | Conservation-induced extinction (~1982) <sup>6</sup>                            |
| <i>Rallicola piageti</i>           | New Caledonian rail ( <i>Cabalus lafresnayanus</i> )                            | Both host and parasite possibly extinct <sup>6</sup>                            |
| <i>Linognathus petasmatius</i>     | Scimitar oryx ( <i>Oryx dammah</i> )<br>OR addax ( <i>Addax nasomaculatus</i> ) | Conservation-induced extinction (~1988) -OR- critically endangered <sup>6</sup> |
| <i>Felicola isodoroi</i>           | Iberian lynx ( <i>Lynx pardinus</i> )   | Conservation-induced extinction (~2001) <sup>8</sup>                            |
| <i>Longimenopon dominicanum</i>    | Guadalupe storm-petrel ( <i>Hydrobates macrodactylus</i> )                      | Co-extinct (~1912) <sup>6</sup>   |
| <i>Saemundssonina jamaicensis</i>  | Jamaican petrel ( <i>Pterodroma caribbaea</i> )                                 | Both host and parasite possibly extinct <sup>6</sup>                            |
| <b>Mecoptera (fleas, etc.)</b>     |   |   |
| <i>Xenopsylla nesiotus</i>         | Maclear's rat ( <i>Rattus macleari</i> )  | Co-extinct (1903) <sup>13, 14</sup>   |

| <b>Amphipoda (amphipods)</b>         |   |  |
|--------------------------------------|---|--|
| <i>Cyamus rhytinae</i>               | Steller's sea cow<br>( <i>Hydrodamalis gigas</i> )            | Co-extinct (1768) if valid <sup>15</sup>                     |
| <b>Ixodida (ticks)</b>               |   |  |
| <i>Ixodes nitens</i>                 | Maclear's rat ( <i>Rattus macleari</i> )                      | Co-extinct (1903) <sup>5, 14</sup>                           |
| <b>Mesostigmata (mites)</b>          |   |  |
| <i>Halarachne americana</i>          | Caribbean monk seal<br>( <i>Neomonachus tropicalis</i> )      | Co-extinct (1952) <sup>16, 17</sup>                          |
| <b>Sarcoptiformes (mites)</b>        |   |  |
| <i>Diplaegidia gladiator</i>         | Passenger pigeon ( <i>Ectopistes migratorius</i> )            | Co-extinct (1914) <sup>16</sup>                              |
| <i>Compressalges nipponiae</i>       | Crested ibis ( <i>Nipponia nippon</i> )                       | Conservation-induced extinction<br>(late 1900s) <sup>6</sup> |
| <i>Coraciacarus muellermotzfeldi</i> | Huia ( <i>Heteralocha acutirostris</i> )                      | Co-extinct (1907) <sup>18</sup>                              |
| <i>Genoprotolichus simplex</i>       | Carolina parakeet ( <i>Conuropsis carolinensis</i> )          | Co-extinct (1918) <sup>9</sup>                               |
| <i>Lopharalichus beckeri</i>         |   |  |
| <i>Neorhytidelasma conuropsis</i>    |   |  |
| <i>Chiasmalgas carolinensis</i>      |   |  |
| <i>Fainalgas gracilitarsus</i>       |   |  |
| <i>Protonyssus proctorae</i>         |   |  |
| <i>Pterotrogus principalis</i>       | Ivory-billed woodpecker<br>( <i>Campephilus principalis</i> ) | Co-extinct (1900s) <sup>19</sup>                             |
| <b>Nematoda (roundworms)</b>         |   |  |
| <i>Agamofilaria oxyura</i>           | Shasta ground sloth<br>( <i>Nothrotheriops shastensis</i> )   | Co-extinct (11,000 years BP) <sup>23</sup>                   |
| <i>Strongyloides shastensis</i>      |   |  |

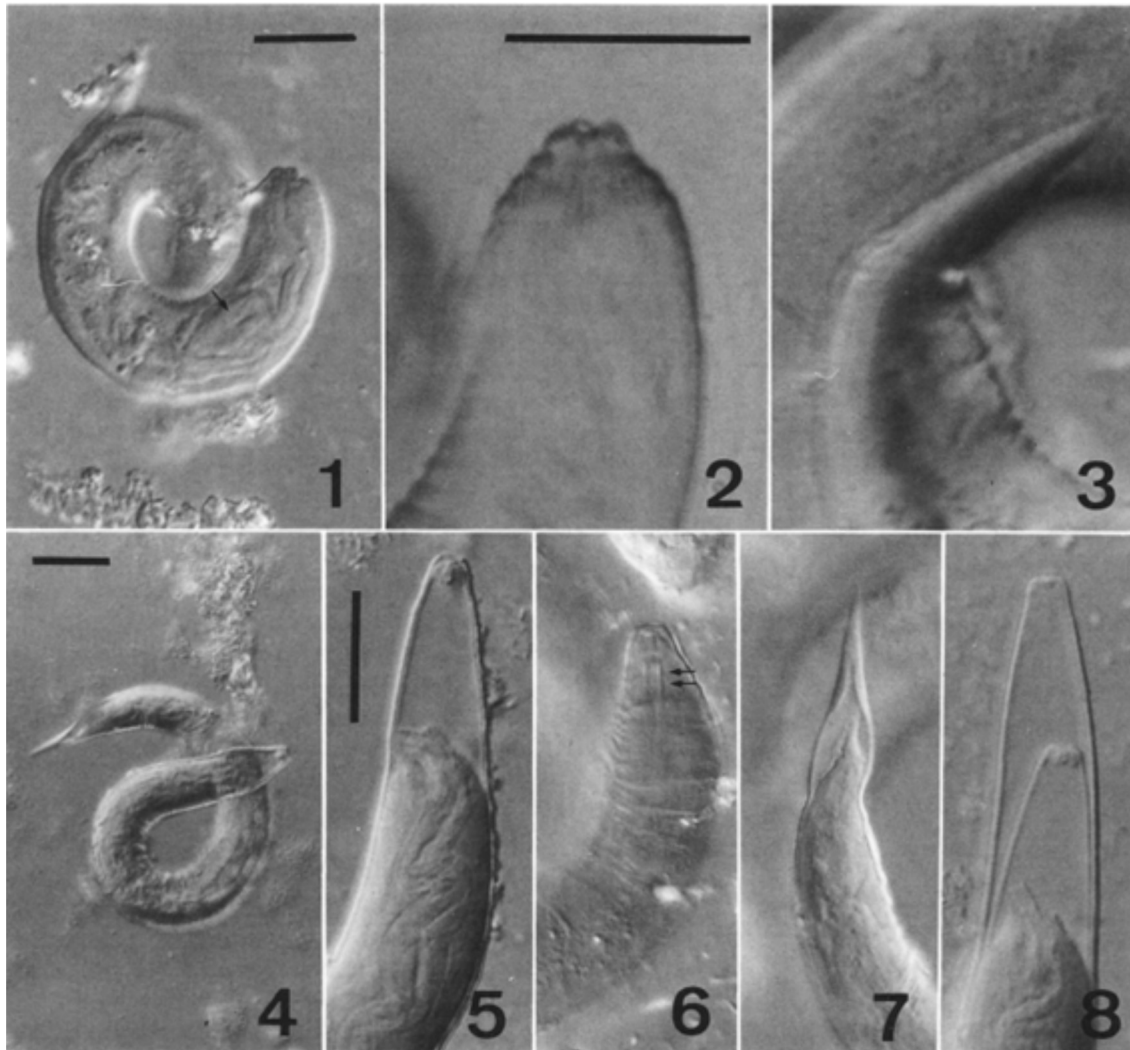
Table 1. Species, host, and fate of various extinct Holocene parasite species. Species that are only parasitic for stages of their life cycle (such as flies and mussels) are excluded.

It would seem that existing knowledge of recently-extinct parasites has some inherent biases. For one, they are almost entirely ectoparasites, living on the outside of their hosts. This is likely due to their ease of discovery to humans, who may happen upon them while inspecting a living host as well as carcasses or pelts, as opposed to inside-dwelling endoparasites, which are more secretive (1). Additionally, they are all specialized towards a single host. Host specificity correlates positively with risk of extinction, as more generalized parasites can rely on other potential host species if one becomes rare or absent. For example, the vast majority of known, recently-coextinct parasites are lice, insects of the order Psocodea (6). Lice have higher degrees of host specificity than other ectoparasites (see Figure 2) such as fleas, ticks, and mites, and are more obvious to observers than endoparasites like flatworms, nematodes, and horsehair worms. Lastly, the likelihood of a parasite to be known depends heavily on how well their host is known. For example, though extinct for over a century, the Carolina parakeet is known to have been home to at least six species of feather mites, thanks to an abundance of well-preserved museum specimens (9). Compare to long-extinct Pleistocene megafauna known only from a few fossils; it is almost certain that many of these specimens were home to their own parasite biota, yet their discovery is a much less likely event. A handful of exceptional cases of preserved dung from Pleistocene species have bypassed these biases, revealing ancient endoparasites (see Figure 3).



*fig 2. Female *Halarachne americana*, a mite only known from the nasal passages of the Caribbean monk seal (extinct 1952). Lice commonly display a high degree of host specificity, as illustrated by this species and its two living close relatives, which are also only known from the noses of a single seal species each (21). From Banks (1904).*





*Fig 3.* Micrographs of nematode remains recovered from dessicated dung of the Shasta ground sloth (*Nothrotheriops shastensis*). Upper row depicts *Agamofilaria oxyura*, lower row depicts *Strongyloides shastensis*. The growth stage of these worms indicate they were young parasites excreted by the sloths, not a free-living species that happened across the dung. From Schmidt et al. (1992).

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Regardless of life history or taxonomy, most parasites are highly cryptic, with some species only having been known from a single individual, and many more being unknown entirely (1). Some species were only discovered post-extinction, recovered from preserved museum specimens of their hosts, such as the feather mites known

from the Carolina parakeet (9). Others have been shrouded in confusion as to their taxonomy or host preference.

For example, *Columbicola extinctus* and *Campanulotes defectus* are two chewing lice species once thought to be unique to the extinct passenger pigeon (*Ectopistes migratorius*). However, the first was rediscovered on the living band-tailed pigeon (*Patagioenas fasciata*), while the other was found to be synonymous with an extant louse on the common bronzewing (*Phaps chalcoptera*) (6, 10). Conversely, the true host of the African louse species *Linognathus petasmatius* is unknown.

Disagreement exists as to whether the known specimens were recovered from scimitar oryx (*Oryx dammah*) or addax (*Addax nasomaculatus*). If the oryx is the host, the louse would've been eliminated when the oryx was rendered extinct in the wild, while if it is the addax, the louse is – in fact – extant, though critically-endangered along with its antelope host (6).

While the discipline of parasitology is well-established, parasite conservation is very much in its infancy. For many years, the diversity and ecological benefits of parasites were largely ignored, likely due to our own feelings of revulsion towards them and/or a lack of concrete data concerning their benefits (1, 4, 5, 6). Since the 1990s, however, discussion of parasites as organisms worthy of conservation has steadily increased, and some workers have drafted up action plans to protect them, many of which simply piggybacking off of the already-existing conservation of their endangered hosts (1, 11, 12). While few, if any, practical efforts to conserve endangered parasites have taken place, a paradigm shift in that direction seems to be underway. Parasites' highly-specialized nature and host dependency combined with their obscurity and unpopularity makes them especially vulnerable to anthropogenic extinction (7). When considering their direct and indirect contributions to biodiversity, their roles in food webs, and their tremendous potential for study, the continuing loss of these species makes clear an unsettling truth; their absence may be felt more strongly than their presence.

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