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TROPHIC INTERACTIONS: SIMILARITY OF PARASITIC CASTRATORS TO PARASITOIDS

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ABSTRACT

An analysis of life history features of insect parasitoids and crustacean parasitic castrators suggests that these are similar trophic phenomena, distinct from parasitism and predation. A parasitoid consumes only one host during its lifetime; parasitic castrators cause the reproductive death of only one host. Since population densities of many insect species are regulated by parasitoids, parasitic castrators may also play an important role in host population regulation.

Parasitoids of insects and parasitic castrators of crustaceans

(1) in single infections always kill the host; whereas lone parasites do not affect host viability; and predators kill many prey;

(2) do not cause increasing pathology or increasing likelihood of mortality in multiple infections; whereas parasites often have an additive impact;

(3) do not cause increasing damage in mixed species infections; whereas mixed parasite infections often have interactive negative effects;

(4) usually have mechanisms to reduce or eliminate multiple infections; whereas multiple infections are common features of parasite systems;

(5) also show reduced frequencies of mixed species infections; whereas such infections are common among parasite species;

(6) are often taxonomically closely related to their hosts; whereas parasites rarely are and predators vary in this respect;

(7) are often less than one order to a few orders of magnitude smaller (by weight) than their hosts; whereas parasites are several to many orders of magnitude smaller; and predators range from similar-sized to several orders of magnitude larger than their prey;

(8) show strong positive size correlations with their hosts; whereas parasites show no size correlation with their hosts; and only relatively small predators are sometimes correlated by size with their prey;

(9) frequently are killed or castrated by obligate hyperparasitoids and hypercastrators; whereas parasites rarely have hyperparasites;

(10) sometimes act as facultative hyperparasitoids or hypercastrators; whereas parasites very rarely act so;

(11) parasitoids and often castrators most commonly attack very young hosts; whereas parasitism and predation are very variable with respect to age of the host (prey); and

(12) often cause precocious host development; whereas parasites rarely affect host maturation processes.

Some insect parasitoids castrate their hosts before killing them; some crustaceans are ultimately consumed by their castrators.

Parasitoid and castrator systems not involving insect or crustacean hosts are briefly reviewed. These trophic interactions may be more widespread than is generally considered. Hydatid cyst disease is regarded as the only parasitoid affliction of humans.

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INTRODUCTION

PARASITIC castration may be regarded as a specialized mode of predation. In the general case, each castrator causes the reproductive death of one and only one host. Viewed in this sense, the population consequences of parasitic castration may be remarkably analogous to those of the parasitoid insects. Parasitoid insects undergo their larval development within the eggs, larvae, pupae, or adults of other insects, almost invariably consuming the host in the process (see Douthett, 1959, for an excellent review). A single parasitoid is thus responsible for the consumption of one and only one host during its lifetime.

The role of insect parasitoids in regulating host abundance has been demonstrated in many laboratory and field studies (Varley, 1947; Huffaker and Kennett, 1966; Van den Bosch, Schlinger, Lagace, and Hall, 1966; and many others). A minority view holds that insect parasitoids are of limited importance in the population regulation of insect hosts (Andrewartha and Birch, 1954).

The basis of the significant part played by the entomophagous parasitoids in the control of host populations lies in the efficient searching ability of the parasitoids at low host densities and in the density-dependent response of the parasitoids to increasing host numbers. If parasitic castrators of Crustacea operate in a like manner, then parasitic castration is implicated as an extremely important part of the system of population regulation for crustacean species.

Regulation of crustacean populations by parasitic castration has not been studied. Only a few host species have been sampled well enough to allow accurate density estimates. In none of these have the population dynamics of the parasitic castrators and their hosts been studied concomitantly to establish a correlation between host and parasite density changes. Investigation of density-dependent mechanisms in host-parasite interactions involving parasitic castration must await access to suitable laboratory systems. Unfortunately, the life histories of both the crustacean hosts and their parasites are sufficiently complex not to have permitted routine rearing of more than one generation in the laboratory.

Despite the inadequacy of knowledge regard-

ing the effect of parasitic castration on host populations, I hypothesize that if castrators are efficient density-dependent predators consuming one prey per individual, as do insect parasitoids, then there should be many analogous features evident when parasitic castrators of crustaceans are compared with insect parasitoids. Some of these parallel features are likely to be of great importance in the biology of these parasite-host (predator-prey) systems. The hypothesis that parasitic castrators may have an impact on their hosts' populations comparable to that demonstrated for insect parasitoids is tested by the comparison of similarities of the two systems (Table 1). The differences between castrators and parasitoids as a class of trophic interactions, when compared with either true parasites (such as monogeneans, adult digeneans and cestodes, many nematodes, most protozoans, or fish copepods), or predators (such as many insects, vertebrates, prosobranch gastropods, spiders, turbellarians, or coelenterates) are also indicated in Table 1. The parasite-host trophic relationship between populations of larval digeneans and cestodes and their intermediate hosts are seen in almost all respects to be similar to that of either the castrator or parasitoid system or both. These relationships will be analyzed elsewhere (Kuris, in prep.). One should bear in mind that when large categories of animals are treated in such terse fashion, exceptions to every generalization may be brought forth. Still, the generalities do fit the large majority of each group of interactions.

COMPARISON OF CRUSTACEAN CASTRATORS, INSECT
PARASITIDS, TYPICAL PARASITES, AND GENERALIZED
PREDATORS

This section is a documentation and discussion of Table 1. To prevent the vast literature from overwhelming a work of this sort, I have resorted to the frequent citation of recent reviews and monographs for the ample literature on insect parasitoids. Exceptional studies, cases which the reviewer did not seem to endorse, and cases where my own interpretation of the work in question disagrees with that of the reviewer are cited from the primary literature. As for the castration literature, which has not been well reviewed and for which my generalizations may consequently be subject to question,

I have provided more abundant citations. Scientific nomenclature has been updated in many places, but I have no pretension of having satisfied a consensus of modern specialists in the range of organisms brought into this discussion. My use of suprageneric taxa is uneven and is intended merely to permit readers of diverse interests to place unfamiliar organisms. The terse comments regarding generalized predators and typical parasites are my own, but I regard them as being widely held opinions if parasitoids and castrators are excluded from those categories. Section numbering below follows that of Table 1.

1. *Outcome of a Single Act*

Infection by one parasitoid almost invariably results in the death of the host (Doutt, 1959). Parasitic castration results in the reproductive death of the host. Sometimes a host may outlive the castrator and recover its reproductive capabilities (Caullery, 1908; Miyashita, 1941; Pike, 1960; Kuris, in prep.). Such post-castration broods are often small with regard to size-specific fecundity curves (Pike, 1960; Kuris, in prep.) and likely do not have much impact on the rate of increase of host populations, as Cole (1954) argues. A single typical parasite causes no reduction in host viability; a lone predator consumes many prey.

2. *Summation Effects: Multiple Infection by a Single Species*

Multiple infection (the *superparasitism* of entomologists) by most parasitoid species usually does not produce any additive effect in pathogenicity to the individual host. Rarely, multiple infection results in premature destruction of the host (Dogiel, Polyanski, and Kheisin, 1962). Multiple infection by parasitic castrators neither speeds up castration effects nor produces additional deleterious effects (Veillet, 1945; Hartnoll, 1967; Kuris, in prep.). Multiple parasitism by generalized parasites is frequently important and may lead to a reduction in host viability.

3. *Summation Effects: Mixed Species Infections*

There are usually no additive aspects in terms of host viability and pathology when hosts are

simultaneously infected by two species of parasitoids. Occasionally both parasitoids perish owing to unsuccessful competition or host over-exploitation (Salt, 1961). For parasitic castrators no increase in castration of the hosts is indicated for mixed species infections (Reverberi, 1943; review, Veillet, 1945). Mixed species infection of typical parasites frequently causes an increase in their effects upon the host.

4. *Density-Dependent or Regulatory Effects upon the Host Population*

Density-dependence has been demonstrated in some cases involving insect parasitoids. The manner of control and its importance have sometimes been contested. I suspect this effect applies likewise to parasitic castrators of Crustacea.

There is insufficient evidence to permit generalization in this matter in respect to typical parasites; it is likely that the effect is variable. Because of the over-dispersion of parasites within host populations, the death of heavily infected hosts, and the higher reproductive potential of parasites, the regulation of host population size is considered to be an essential feature of parasitism by Crofton (1971) (larval *Acanthocephala* are used as examples). Although Crofton (1971) does show how over-dispersed parasite populations will lead to some host mortality, the percentage of such heavily infected hosts likely to die increases slowly with increases in mean parasite density. This is an inherent property of approximately negative binomial host-parasite frequency distributions generated by parasitologically realistic factors (see Crofton, 1971). Crofton also fails to distinguish parasitoids and castrators from typical parasites. His frequency distribution analysis applies only to the latter organisms. Parasites at low densities do not lower the fitness of their hosts. Density-dependence has been demonstrated for many generalized predators.

5. *Outcome of Multiple (Single-Species) Infections in Respect to the Parasite (Predator)*

Multiple infection rarely occurs, and less often succeeds among solitary insect parasitoids (Salt, 1961; Force and Messenger, 1964; Burnett, 1967; and many others). Usually only one parasitoid adult emerges per infection. Ord-

TABLE 1

A summarized comparison of the biological features of insect parasitoids, crustacean parasitic castrators, typical parasites, and generalized predators

BIOLOGICAL FEATURE	INSECT PARASITIDS	PARASITIC CASTRATORS	TYPICAL PARASITES	GENERALIZED PREDATORS
1. Outcome of a single act	results in death of the host	results in reproductive death of the host	no reduction in host viability	a single predator consumes many prey
2. Summation effects: superinfection by single species	usually none	always none	frequently important, leading to a reduction in host viability	does not apply
3. Summation effects: mixed infections	usually none	none indicated	frequent	does not apply
4. Density-dependent effects on host populations	demonstrated in many cases	suspected herein	variable	variable, demonstrated in many cases
5. Superinfection as it affects parasite (predator)	usually only one parasitoid emerges (except gregarious species)	usually rarer than expected; often only two parasitic isopods may mature per host	multiple infections common	does not apply
6. Outcome of mixed-species infections	usually only one survives; first to arrive commonly destroys later animals	often less frequent than expected; in one case the second arrival causes the death of the first castrator	many mixed infections normally coexist	does not apply
7. Density of parasite (predator) relative to host	at high densities parasitoid is implicated as a host population control agent; low and high densities common	commonly very low occasionally high	variable, often high	almost invariably low
8. Taxonomic relationship between host (prey) and parasite (predator)	12% of all insect species are parasitoids of other insects; sometimes host and parasitoid are in same family	3% of all crustacean species are castrators of others crustaceans; a number of castrators and hosts belong to the same order, and in one example, to the same family	very rare within same phylum	variable
9. Other taxa affecting hosts in like manner	mermithid nematodes, nematomorphs	coccidians, digenetic trematodes, metacercariae, dinoflagellates, nematomorphs, ellobiopsids, fecampid turbellarians, fungi, cestodes	does not apply	does not apply

TABLE 1 (continued)

BIOLOGICAL FEATURE	INSECT PARASITOIDS	PARASITIC CASTRATORS	TYPICAL PARASITES	GENERALIZED PREDATORS
10. Host (prey) specificity	most are moderately host-specific; some species with low or high specificity	typically highly specific; a few have low or moderate degrees of specificity	variable; often highly specific	variable; often very unselective in terms of prey species
11. Size of mature parasite (predator) stage in relation to size of the mature host (prey) stage	parasitoid often less than one order of magnitude smaller than host	castrator often less than one order of magnitude smaller than host	parasite several orders of magnitude smaller than host	ranges from predator similar in size to prey to predator several orders of magnitude larger than prey
12. Correlation of size of individual parasite with individual host	positive correlation demonstrated	positive correlation demonstrated	no correlation except in cases involving intermediate hosts	typically not correlated; sometimes a positive correlation
13. Obligate hyperparasites	frequent; usually Hymenoptera	many reported; usually Isopoda	rare; Microsporida most often reported; usually involving intermediate host of the primary parasite	does not apply
14. Facultative hyperparasites	many cases known	a few examples known	very rare	does not apply
15. Host (prey) age at infection	usually early in life, some intermediate, few in adult	many early in life, some restricted to adults, others variable	variable	variable
16. Host maturity	parasitoid may induce premature pupation	a few species cause host precocity or hyperfeminization	rarely if ever effects host maturation	does not apply

narily, the initial oviposition results in emergence. Subsequent larvae are killed by combat or are physiologically suppressed (Messenger, 1964). Salt (1961) has regarded these happenings as the logical outcome for systems having a fixed food supply (the host). Some species regularly permit the emergence of larvae from more than one oviposition (i.e., they are gregarious) (King and Rafai, 1970). In both gregarious and nongregarious species, mechanisms exist whereby the frequency of multiple oviposition is so strongly reduced (King and Rafai, 1970) that multiple infection is felt to be unimportant in the field populations of solitary species (Force and Messenger, 1964). In a few well-studied species multiple infection is unknown (Force and Messenger, 1964).

Multiple infections are usually much rarer than randomly expected for most entoniscids, bopyrids, and sacculinids (Veillet, 1945; Altès, 1962; Hartnoll, 1967; and others) and for a dinoflagellate (*Blastulidium contortum*) (Chatton, 1920; Cattle, 1948). The presence of one parasite prevents concurrent establishment of subsequent infective stages encountered (Giard, 1888). In systems in which more than one parasite may infect a given host, maturation is often limited to only two adults (Shiino, 1942; Veillet, 1945; Kuris, 1971). At least for the bopyrids and entoniscids, the upper limit of two coincides with the maximum number of sites based on the morphological configurations of host and parasite. Gregarious species are known, and include most of the parasitic din-

oflagellates (Chatton, 1920) and some sacculinids (Hartnoll, 1967). Polyembryony, resulting in the production of many progeny from a single infection, is a regular feature of the life cycle of certain chalcid wasps (Askew, 1971) and some Rhizocephala (Veillet, 1945; Hartnoll, 1967; Bocquet-Védrine and Parent, 1973).

Among typical parasites many examples of multiple infection are known, at least some of which are due to simultaneous acquisition of more than one parasite (such as by way of ingestion of an intermediate host harboring several intermediate infective stages). Multiple infection is sometimes limited by already established parasites (premunition) or host responses. Polyembryony occurs in many helminths (see review of parthenogenesis by Cable, 1971). Many of his examples are drawn from the insect-parasitizing nematodes and larval digeneans, both of which are herein implicated as parasitoids and castrators respectively.

Multiple attack by generalized predators is rare, but does occur, for example, among social Carnivora and Primates.

6. Outcome of Mixed-Species Infections

(A mixed-species infection is the *symparasitism* of Dogiel, Polyanski, and Kheisin, 1962; the *superparasitism* of Noble and Noble, 1964; the *multiparasitism* of entomologists—see Askew, 1971).

Among insect parasitoids, typically (i.e., solitary parasitoids), only one individual of one species can survive to emergence. Usually the first to arrive destroys the subsequent arrivals (Fisher, 1962). Rarely, both may survive, or both perish because of host overexploitation (Salt, 1961). Mixed infections of parasitic castrators of Crustacea are often found to be less frequent than expected on the basis of random infective behavior patterns (Chatton, 1920; Reinhard and Buckeridge, 1950; data from Bourdon, 1960; Altès, 1962). Sometimes mixed infections are more numerous than expected (Veillet, 1945; Bourdon, 1960). In at least one such case the second arrival often causes the death of the earlier castrator (Veillet, 1945). This interaction is akin to hyperparasitism. Mixed infections may also occur randomly (Altès, 1962).

Many mixed infections of typical parasites normally coexist. Nematode species flocks

(Schad, 1963; Petter, 1966) have been described. Sometimes competition does result in unexpectedly low frequencies of mixed infections. Mixed-species predator attacks on individual prey organisms rarely occur.

7. Density of Parasite (Predator) Relative to Host (Prey)

Both very low (less than 2% infected) and high densities (25–90+%) are commonly recorded (e.g., Price, 1970). Huffaker (1971) notes that to exert a controlling influence on host populations, the parasitoid must have a high density relative to its host: Densities of many castrators of crustaceans are very low (Bourdon, 1960, 1963, 1964). Occasionally, both with regard to season (Gifford, 1934) and locality (Veillet, 1945; Bourdon, 1963; Hartnoll, 1967; Heath, 1971; Born, pers. commun.) the percentage of infection may range from 25 to 75 per cent. Some populations of the entoniscid isopod, *Portunium conformis*, in the grapsid crab, *Hemigrapsus oregonensis*, reach infection levels of 92 per cent (Kuris, unpub.). Such castrated populations are most probably maintained by immigration from other localities.

Typical parasites have a wide range of densities per host. Often such densities are far higher than the densities reached by the majority of parasitoid and castrator populations. Patterns of infection of typical parasites lead to frequency distributions of the parasite load that approximate negative binomial expansions (Li and Hsu, 1951; Crofton, 1971; Pennycuik, 1971b). These result in very high absolute densities of parasites in the total population at a given percentage of infection, in comparison to either castrator or parasitoid populations.

Generalized predators almost invariably have low population densities compared to the densities of their prey, even when these systems are implicated in population control.

8. Taxonomic Relationship between Host (Prey) and Parasite (Predator)

An estimated 12 per cent of all insect species are parasitoids of other insects (calculated from information given in Askew, 1971). Sometimes hymenopterous parasitoids attack species belonging to the same family of parasitoids.

An estimated 3 per cent of all crustacean

species are castrators of other Crustacea (calculated from information given in Waterman and Chace, 1960). A number of instances of castration within the same order are known (Carayon, 1942; Bocquet-Védrine, 1961, 1967; Bourdon, 1967) and at least one example within the same family (Caroli, 1946; Catalano and Restivo, 1965).

For both the Insecta and the Crustacea, their respective parasitoid and castrator faunas are dominated by species of the same taxonomic class (see below for exceptions). Possibly these taxa are preadapted for this relationship. Parasitoids and castrators are very finely attuned to their hosts' life histories. Since key features of insect life histories, such as diapause and metamorphosis, are under the control of endocrine systems, it seems reasonable to expect that insect parasitoids can either "read" (e.g., Schoonhoven, 1962) or "direct" (e.g., Johnson, 1965) these systems. In like manner, molting of bopyrid isopods in synchrony with their hosts (Caroli, 1927; Tchernigovtzeff, 1960; pers. observ.) and the feminization of male hosts through effects on the androgenic gland (Veillet and Graf, 1958) probably represent "reading" and "direction" of crustacean hosts.

Generalized parasites very rarely parasitize hosts within the same phylum. The taxonomic relationship between generalized predators and their prey is variable.

9. Other Taxa Affecting Host in a Like Manner

Many mermithoid and steinernematid nematodes (Welch, 1965) and nematomorphs probably have a parasitoid effect upon their orthopteran hosts. For reasons as yet unknown, insects are very susceptible to one-on-one predation systems.

Non-crustacean parasitic castrators of Crustacea include the coccidian *Aggregata* (see Smith, 1905), digenean trematode metacercaria (Noble and Noble, 1964), dinoflagellates (Chatton, 1920; Cattley, 1948), Nematomorpha (Pérez, 1927; Born, 1967), the enigmatic Ellobiopsidae (Chatton, 1920; Fage, 1940; Wickstead, 1963; Hoffman and Yancey, 1966; Mauchline, 1966), fecampid turbellarians (Mouchet, 1931; Baylis, 1949; Christensen and Kannevorff, 1965; Kannevorff and Christensen, 1966), cestode procercooids (Mueller, 1966),

and fungi (Johnson, 1958). For unknown reasons, crustaceans are subject to castration by members of several different taxa.

Judgement as to whether many species of Microsporida belong in both of the above categories is reserved until relationships between the number of spores involved in transmission, reproduction within the host, pathology, and mortality are better understood. If the size of the initial inoculum does not determine the outcome of the infections, then I would consider the appropriate species to be parasitoids or castrators rather than parasites. Certainly for some species (Veber and Jasič, 1961) the pathology is dosage-dependent. For similar reasons, most Microsporida and other protozoan pathogens are omitted from Tables 1 to 3.

I stress the fact that these very diverse groups of organisms, especially the mermithids, nematomorphs, insect parasitoids, dinoflagellates, fecampids, copepods, isopods, and rhizocephalans, all share virtually every aspect of the detailed comparison summarized in Table 1. The exigencies of the parasitoid-castrator process seem to force narrow strategic limitations on parasitoids and castrators.

10. Host (Prey) Specificity

In the following discussion high host specificity means one or two closely related hosts exist; low host specificity means that dozens of hosts exist, often belonging to separate families.

Insect parasitoids are moderately host-specific, such specificity being primarily behaviorally and ecologically determined (Doutt, 1959). Some species, such as *Nasonia vitripennis* (Whiting, 1967), have a low degree of host-specificity.

Parasitic castrators are typically highly host-specific. Epicaridean isopods are classically regarded as strictly host-specific (Giard and Bonnier, 1887; Bonnier, 1900), although it is likely that much of this specificity is ecologically influenced. A few species have a low degree of host-specificity in the field; for example, *Hemiarthrus abdominalis* has been recorded from 22 hosts (Pike, 1960).

Typical parasites have variable degrees of host-specificity, but often are highly host-specific. Generalized predators also have varying degrees of prey-specificity, but are often very unselective in terms of prey species.

11. *Size (Weight) of the Mature Parasite (Predator) Stage in Relation to the Size of the Mature Host (Prey) Stage*

Insect parasitoids are from one to a few orders of magnitude smaller than their hosts—i.e., they are of relatively large size (Doutt, 1959). Parasitic castrators have a similar size range relative to their hosts. Typical parasites, in contrast, are several to many orders of magnitude smaller than their hosts. Generalized predators range in size from being about the same size as their prey to being several orders of magnitude larger than their prey.

12. *Correlation between the Size of the Individual Parasite (Predator) and Its Individual Host (Prey)*

The parasite-host (predator-prey) size correlation should be envisaged between animals at a similar stage in life history whenever discrete stages occur—e.g., only fourth instar parasitoid larvae should be compared with each other. The strongest correlations will of course be between host size and relatively mature stages of parasitoid or castrator. In the cases of parasitoids, castrators, and parasites it seems most reasonable to regard host size as the independent variable. Positive correlations result from parallel growth of both members of the interacting pair. For predator-prey systems, the predator's size is usually regarded as the independent variable as size of the prey usually involves some selection on the part of the predator.

Positive correlation between host and parasitoid size has been demonstrated (Askew, 1971). Host and castrator size are likewise typically positively correlated (Pike, 1960; Allen, 1966; Samuelsen, 1970; Kuris, 1971; by inference, Giard and Bonnier, 1887; Morris, 1948). Size of typical parasites is usually not correlated with host size, except in instances involving intermediate hosts. Prey are often not correlated with predator size (e.g. Galbraith, 1967; Moran and Fishelson, 1971). When positive correlations do occur (for a good example, see Menge, 1972), the correlation is usually weaker than that seen in the parasitoid or castrator systems (compare with Pike, 1960). Predator-prey systems with similar relative sizes (see Section 11 above) are those in which individual predator-prey size correlations are found.

13. *Hyperparasites (Obligate)*

Hyperparasitoids are frequently reported in insect parasitoid systems. They are usually hymenopterous species. Several examples are given in Askew (1971). These may play a role in disruption of the control of host populations by the primary parasitoids. Hypercastrators are known for a number of parasitic castrators. They are usually isopods—for example, liriopids on sacculinids (Pike, 1961), *Cabirops* on *Pseudione* (Carayon, 1942), *Gnomoniscus* on *Podascon* (Caullery, 1952), and perhaps the copepod *Paranicothoe* found in the empty brood pouch of bopyrid isopod hosts (Carton, 1970). Stromberg, however (pers. commun.), believes that, in general, the cryptoniscine isopods are true hyperparasites, not hypercastrators.

Interestingly, the only previous reference to the resemblance between parasitic castrators and insect parasitoids seems to be that of Pérez (1931), whose many contributions to crustacean biology have often been overlooked by later writers. Working with the hypercastrator, *Liriopsis pygmaea*, on *Peltogaster paguri*, a primary castrator of *Eupagurus bernhardus*, Pérez (1931) observed that the observed *Peltogaster* population was sterilized by an epidemic of the hypercastrator. He noted the similarity of the phenomenon to the effect of hyperparasitoids on insect primary parasitoids.

Hyperparasites of typical parasites are very rare, the most commonly reported being microsporidians (Dissanaike, 1957; Canning and Basch, 1968). It is significant that several of these microsporidians parasitize larval stages of helminths in the intermediate host (see below). The haplosporidian, *Urosporidium*, in microphallid metacercariae (Couch and Newman, 1969) fits this pattern.

14. *Hyperparasites (Facultative)*

Many hymenopterans are known to be either primary parasitoids or hyperparasitoids. Some species, upon completion of a hyperparasitic phase resulting in the destruction of the original primary parasitoid, complete their development as parasitoids of the original host (e.g., Price, 1970). In some arrhenotokous primary parasitic species, larval males, only, develop as hyperparasites, often conspecifically. Females, however, are only primary parasites (Doutt,

1959; Kennett, Huffaker, and Finney, 1966).

A few examples of facultative hypercastration are known. Caroli (1946) reports that the young bopyrid *Pseudione euxinica* spends the early part of its life on the bopyrid *Gyge branchialis*. Upon the death of *Gyge*, *P. euxinica* becomes a primary parasite of the host, *Upogebia littoralis*. The gradual destruction of a previously infecting sacculinid by entoniscids, coupled with the non-random prevalence of mixed infections of these species (Veillet, 1945; Miyashita, 1941) lends this situation some of the qualities of facultative hyperparasitism. Altès (1962) feels that *Cryptoniscus paguri*, a hypercastrator of *Septosaccus rodriquezi*, may sometimes be a parasite of the primary host, *Clibanarius erythropus*. The dwarf, hyperparasitic males that typically accompany female Epicaridea do not merit consideration here because there is no evidence that they harm the female. In fact, they may not feed at all. No examples of facultative hyperparasites are known, but the apparent ingestion of some protozoan parasites by digenetic trematodes (Dogiel, Polyanski, and Kheisin, 1962), may be judged as rare, comparable examples.

15. Age of Host at Time of Infection

Insect parasitoids usually infect their hosts early in life (Salt, 1963). Many egg and larval parasitoids are known. Pupal parasitoids are common, but adult-infecting parasitoids are infrequent (Doutt, 1959). Salt (1968) has proposed that invasion of young hosts leads to the acquisition of the proper surface "immunological passport." Infecting young animals gives the parasitoid time to act as a chronic destructor.

Among parasitic castrators, most bopyrids are considered to attack only young hosts (Carayon, 1943; Pike, 1960, 1961). A few species may be restricted to adult hosts (Pike, 1961). Sacculinids also seem to settle preferentially on juvenile hosts (Veillet, 1945). The time of infection by entoniscids appears to be relatively unrestricted by the age of the host (Veillet, 1945; Kuris, 1971). Salt's (1968) immunological passport theory is held to be applicable to castrators, too.

Typical parasites and generalized predators vary greatly with regard to the phase of the life history of the host attacked.

16. Host Maturity

Several insect parasitoids have been noted to induce premature pupation in their insect hosts (Varley and Butler, 1933). Among parasitic castrators, *Cryptoniscus pagurus* may cause precocious development of infested *Septosaccus rodriquezi* (Altès, 1962). Reinhard (1956) notes that hyperfeminization, the appearance of adult characteristics on small female hosts, is an oft-reported effect of sacculinization. Typical parasites rarely, if ever, cause precocious host maturity.

CASTRATORS OF INSECTS, PARASITOIDS OF CRUSTACEA

The functional similarity of parasitoid and castrator systems on their insect and crustacean host populations is further suggested by an interesting turnabout. Some insect species are subject to parasitic castration prior to their parasitoid-induced death (Table 2), and some crustaceans are essentially consumed by organisms which were initially merely castrators (Table 3).

Inspection of Table 2 shows that for most castrator-insect host systems, the cessation of reproductive activity is a prelude to death of the host following emergence of the parasitoid. In some systems, such as the nemestrinid-orthopteran system, the outcome of the parasite-host interaction is variable; sometimes the host survives, sometimes it does not. Some tylenchoid nematodes and most Strepsiptera are close to nonlethal castrators, the host's life span rarely being shortened. As the crustacean castrators control the host's reproductive system through the host's endocrine system (Veillet and Graf, 1958), so does the aphelenchoid nematode parasite of *Bombus*, *Sphaerularia bombi*, by causing degeneration of the corpora allata (Palm, 1948). Again in parallel with crustacean castrators, a single *Sphaerularia* elicits the full castration response, and the pathology is not additive with superinfection (Hattingen, 1956, from Welch, 1965). The reciprocal relationship, wherein crustaceans are killed through a parasitoid-like action (Table 3), also provides some insight. Like the vast majority of insect parasitoids, *Kromborgia*, a fecampid turbellarian, kills its host upon emergence of the adult worm. Although Kanneorff (1965) demonstrates that

the castration effect is of greater importance, this is, in part, a parasitoid-host relationship. The terrestrial success of the oniscoid isopods undoubtedly exposed them to infection by the

parasitoid insects. Examination of other terrestrial and semiterrestrial crustacean taxa may well provide more examples of insect parasitoids that affect crustaceans.

TABLE 2

Some organisms having a castrator effect on their insect hosts

CASTRATOR(S)	HOST(S)	REMARKS	REFERENCE
Cestoda			
Dilepidids	ants	castrate; many morphological effects; behave as social parasites; superinfection may cause an additive response	Plateaux, 1972
Nematoda			
Mermithids	ants	intercastes	Welch, 1965
Mermithids	chironomids, simuliids, others	intersexes; gonads affected; kill upon emergence	Welch, 1965
Many tylenchoids and aphelenchoids	Coleoptera, Lepidoptera, Diptera, Hymenoptera	reduce fecundity; rarely kill	Welch, 1965
<i>Heterotylenchus pavlovskii</i> (tylenchoid)	fleas	castrates; kills on emergence	Welch, 1965
Nematomorpha	Orthoptera	castrates; kills on emergence	Dorier, 1965
Insecta			
Strepsiptera	Hymenoptera, Hemiptera, some Thysanura, Orthoptera	castrates; usually doesn't kill hosts; males feminized, females masculinized	Askew, 1971
Hymenoptera some braconids	weevils	castrates; kills on emergence	Loan and Holdaway, 1961
Diptera nemestrinids, some calliphorids and muscids	Acridoidea	usually castrates before killing on emergence; some only reduce fecundity; lethal	Greathead, 1963

TABLE 3

Organisms having a parasitoid effect on their crustacean hosts

PARASITOID(S)	HOST(S)	REMARKS	REFERENCE
Fungus			
<i>Metschnikowia</i> (yeast)	Copepoda, Cladocera, <i>Artemia</i>	causes host's death	Fize, Manier, and Maurand, 1970
Turbellaria			
<i>Kronborgia amphipodica</i>	<i>Ampelisca macrocephala</i>	castration precedes death upon emergence	Christensen and Kannevorff, 1965
Diptera			
Tachinidae	terrestrial isopods	typical parasitoid effect	Askew, 1971

TABLE 4

Parasitoid-like phenomena involving hosts other than crustaceans and insects

PARASITOID	HOST(S)	REMARKS	REFERENCE
Microsporida <i>Pleistophora</i>	Nematoda <i>Metoncholaimus scissus</i>	host, marine; infection always terminal; authors suggest Microsporida-nematode infections are more common than previously expected	Hopper, Meyers, and Cefalu, 1970
<i>Perezia eurytremae</i>	Trematoda-Digenea	hyperparasitoid of larvae in snails	Canning and Basch, 1968
Haplosporida <i>Urosporidium crescens</i>	Trematoda-Digenea	hyperparasitoid of metacercariae in <i>Callinectes</i>	Couch and Newman, 1969
Platyhelminthes-Cestoda <i>Echinococcus</i>	Mammalia humans, voles, sheep, and other herbivores	hydatid cysts in intermediate hosts resulting from single infections typically reduce host viability	Rausch and Schiller, 1956; Schiller, 1966
Nematoda <i>Daubaylia</i>	Mollusca freshwater pulmonates	reproduces within host; causes some castration effects before killing host	Chernin, 1962
Nematomorpha	Arthropoda millipedes, centipedes, whip-scorpions	castrate host before killing upon emergence	Dorier, 1965; Sahli, 1972
Mollusca-Opisthobranchia <i>Phyllirhoe</i>	Coelenterata-Hydrozoa <i>Zanclaea</i>	medusa gradually consumed	Martin and Brinkmann, 1963
<i>Cephalopyge</i>	<i>Nanomia</i>	probably similar to <i>Phyllirhoe</i> , but may possibly consume more than one host to complete development	Sentz-Braconnot and Carré, 1966
Hymenoptera	Arthropoda ticks, mites, spiders, pseudo-scorpions	typical parasitoid process	Askew, 1971
Diptera tachinids phorids	centipedes millipedes	typical parasitoid process uncertain	Askew, 1971 Picard, 1930
sciomyzids	Mollusca freshwater and terrestrial	many species are predators, some are typical parasitoids; suggested as biocontrol agents	Berg, 1964; Bratt, Knutson, Foote, and Berg, 1969
Acarina <i>Histiotoma murchiei</i>	Annelida earthworm	an egg parasitoid	Oliver, 1962

TABLE 5

Parasitic castration-like phenomena involving hosts other than crustaceans or insects

CASTRATOR	HOST(S)	REMARKS	REFERENCE
Sporozoa	Annelida- Oligochaeta		
<i>Mackinnonia tubificis</i>	<i>Tubifex tubifex</i>	destroys gonad	Janiszewska, 1967
Microsporida	Sporozoa-Gregarinia		
<i>Nosema frenzelinae</i>	<i>Frenzelina conformis</i>	prevents sporogony after syzygy; pre-reproductive growth normal	Léger and Dubosq, 1909
<i>Pleistophora ovariae</i>	Pisces-Cyprinidae <i>Notemigonus crysoleucas</i>	partial castration; possibly enhances somatic growth	Summerfelt and Warner, 1970
Haplosporida	Cestoda		
<i>Urosporidium charletti</i>	<i>Catenotaenia dendritica</i>	hypercastrator	Dollfus, 1943
Ciliatea	Echinodermata- Asteroidea		
<i>Orchitophrya stellarum</i>	<i>Asterias rubens</i>	mostly in male hosts; may only be partial castration; possible role in population control	Vevers, 1951
Mesozoa	Echinodermata		
Orthonectida	Ophiuroidea	typically render host gonads nonfunctional	Giard, 1888; Caullery and Lavallée, 1912; Fontaine, 1968
Coelenterata-Anthozoa	Coelenterata- Hydrozoa		
<i>Peachia quinquecapitata</i>	<i>Phialidium</i>	a temporary castrator, sometimes a parasitoid; ectoparasitic, feeding on gonads of medusa; host may die after anemone leaves; gonads can regenerate	Spaulding, 1972
Turbellaria	Turbellaria		
<i>Oikiocolax plagiostomorum</i>	<i>Plagiostomum</i> sp.		Reisinger, 1930 (from Jennings, 1971)
Trematoda-Digenea	Gastropoda		
most sporocyst and redial stages		acute castration appears to be the rule; sometimes secondary sexual characteristics affected and behavioral changes; prolonged life or gigantism suggested for some infections; sometimes reduce host viability; mixed species infections rare—one species eliminates competitor either indirectly or through direct predation	Rothschild, 1941; Wright, 1966; Køie, 1969; Lim and Heyneman, 1972; Kuris, 1973.
<i>Bucephalus mytili</i> sporocysts	Bivalvia	destroys gonad, infected hosts larger	Breton, 1970
gymnophaline metacercariae	Brachiopoda <i>Glottidia pyramidata</i>	sometimes gonad destroyed	Paine, 1963

TABLE 5 (continued)

CASTRATOR	HOST(S)	REMARKS	REFERENCE
Cestoda pseudophyllid plerocercoids	Pisces Cyprinidae, <i>Gasterosteus</i>	destroy gonad; may reduce host viability; causes many behavioral changes	Arme and Owen, 1967; Arme, 1968; Penny-cuick, 1971a
Nematoda <i>Mammanidula asperocutis</i>	Mammalia <i>Sorex</i>	infect lactating mammarys, prevent nursing; high infection rates accompany high host density suggesting role in population regulation; a castrator in the sense that it eliminates host's reproductive capabilities	Okhotina and Nadochty, 1970
Annelida Myzostomida	Echinodermata Crinoidea	some species cause partial castration	Prenant, 1959
Mollusca-Gastropoda <i>Entoconcha mirabilis</i>	Holothuroidea	—	Giard, 1888
Crustacea-Copepoda monstrilloids <i>Xenocoeloma</i>	Annelida Syllidae <i>Polycirrus</i>	— fecundity reduced	Malaquin, 1901; Boquet, Boquet-Védrine, and l'Hardy, 1968
<i>Mytilicola</i>	Bivalvia <i>Mytilus</i>	gonad reduction	Mann, 1967
<i>Sarcotretes scopeli</i>	Pisces Myctophidae	prevents gonadal maturity; no effect on secondary sexual characters; parasitized animals slightly smaller than their age class	Gjøsaeter, 1971
Crustacea-Cirripedia Ascothoracica	Echinodermata Echinoidea, Asteroidea	destroys or greatly reduces gonads	Brattström, 1936; Achituv, 1970
<i>Anelasma squalicola</i>	Pisces-Elasmo-branchia <i>Etmopterus spinax</i>	hosts ovaries become inactive, testes probably functional; increased mortality of parasitized sharks	Hickling, 1963
Crustacea-Brachyura <i>Pinnotheres</i>	Bivalvia	castration and even sex reversal of infected hosts; female crab size correlated with host size	Hornell and Southwell, 1909; Awati and Rai, 1931; Atkins, 1926; Berner, 1952
Pisces <i>Jordanicus</i>	Holothuroidea	eats gonads; extent and permanence of effects uncertain	Trott, 1970

PARASITOID AND CASTRATOR SYSTEMS IN THE ANIMAL
KINGDOM

Even with the exclusion of larval trematodes, cestodes, and acanthocephalans (to be covered in detail in Kuris, in prep.), parasitoid systems (Table 4) and castrator systems (Table 5) operate on a surprisingly diverse list of host systems.

Parasitoids of non-insects are very poorly known, excepting the detailed studies on the Sciomyzidae by Berg (1964) and coworkers. Most of the interactions placed in Table 4 should be regarded as tentative. Of interest again, the specialized hymenopterous and dipterous parasitoids have invaded most non-insect terrestrial arthropod taxa. Again, the inclusion of protozoan infections in this list is speculative.

Castration effects seem to occur more frequently and in a greater taxonomic diversity of systems than do parasitoid effects. Table 5 provides a list of castrators ranging from Protozoa to Brachyura and Gastropoda, a list of hosts from Protozoa to Mammalia. *Orchitophyra* in *Asterias* and *Mammanidula* in *Sorex* have both been suggested as being involved in host population control (Vevers, 1951; Okhotina and Nadochy, 1970). Indeed, the mammary nematode infection rate appears to be density-dependent.

Larval trematodes commonly castrate (Kuris, 1973) and sometimes kill (Sturrock and Webbe, 1971) their snail hosts. The snail-trematode trophic interaction satisfies most of the biological features of parasitoid and castrator systems given in Table 1. The similarity of snail-trematode to insect pest-parasitoid trophic interactions has already been proposed (Kuris, 1973). Consequences of mixed species larval trematode infections (see reviews by Lim and Heyneman, 1972; Lie, 1973) are much like mixed parasitoid infections. Biological control of schistosomiasis through competitive exclusion by trematodes with redial generations is theoretically feasible (Kuris, 1973).

In some cases parasitic castration has been shown to be accompanied by prolonged life or gigantism of the host, or by both. This curious parasite-induced syndrome—castration, prolonged life, and gigantism—occurs in snails harboring certain larval trematodes (Rothschild, 1941), in male pea crabs infected with *Pinnotherion* (Mercier and Poisson, 1929), possi-

bly in minnows castrated by Microsporida (Summerfelt and Warner, 1970) and pelagic copepods castrated by *Blastulidium contortum* (Cattley, 1948; but not Chatton, 1920). If the “replacement” of the ovary by the parasite results in an energetically less expensive total system, as is suggested by data on *Hemigrapsus oregonensis* castrated by *Portunion conformis* (Kuris and Lawlor, in prep.) then gigantism or increased survivorship of parasitized hosts, or both, should not be unexpected. Summerfelt and Warner (1970) also take this viewpoint. If a castrator has a positive effect on its host's viability or growth (or both), the increased production of castrator offspring because of prolonged life and the strongly host size-specific fecundity schedules of many of the castrators would seem to be strong selective factors favoring the castration pathology. Rothschild (1938) recognized the selective advantage of large snail size to cercarial production. Castrators of intermediate hosts, where the transmission involves ingestion of that host by the definitive host, would not be expected to energetically “conserve” intermediate hosts. Walkey and Meakin (1970) indicate that larval *Schistocephalus* are quite costly to their stickleback hosts.

Arguments raised concerning the loss of the host's progeny to future parasite generations tacitly and unnecessarily invoke group selection. Mechanisms to reduce pathological effects characterize those parasites for which the pathology does not improve the survival or reproductive success of the parasites on hand.

Drastic modifications in host behavior sometimes accompany parasitization by parasitoids and castrators. Braconid parasitoids prevent diapause in some insect hosts (Varley and Butler, 1933). Sacculinized *Carcinus* behave as reproductive females, migrating to shallow water and showing egg-care behavior (Rasmussen, 1959). Ants harboring dicrocoelid tapeworm larvae act as social parasites, always requesting food from unparasitized workers (Plataeux, 1972). Sticklebacks carrying advanced cestode plerocercoids swim near the surface and are thus easy prey for birds (Arme and Owen, 1967). Poinar and van der Laan (1972) show that infected queen bumblebee “eternal seekers” do not complete their hibernation flight, but continue to fly low over the ground, stopping briefly to dig little pits in the soil and release *Sphaerularia* infective larvae. The classic

host behavioral modification is caused by the sporocyst of *Leucochloridium*, a brightly colored active form in snail tentacles—essentially a semaphore system to attract birds—the definitive hosts (Noble and Noble, 1964). In the latter three cases the host becomes little more than a parasitoid-guided missile system, operating to complete the life cycle of the parasitoid in a self-destructive act. Such gross modifications of host behavior rarely occur under the influence of true parasites.

A few interacting systems combine parasitic castration with the shortened host life span characteristic of parasitoids. The fecampid turbellarian, *Kronborgia*, causes such effects on its amphipod host (Kannevorff, 1965). Gordiaceans and mermithid nematodes also cause castration; death of the host follows upon the emergence of the parasite (Dorier, 1965; Théodoridès, 1965). The bizarre relationship between the parasitic barnacle, *Anelasma*, and its deep-sea shark host *Etmopterus* seems also to be of this nature. Hickling (1963) makes a good case for the premature demise of the parasitized host. The nematode *Daubaylia* produces some castration effects prior to overwhelming its snail host (Chernin, 1962). Possible differential mortality of parasitically castrated hosts is also suggested in the data of Gjøsæter (1971) for myctophids infected by the copepod, *Sarcotretes*.

In agreement with Kannevorff (1965), I regard castration of the host as having a more important effect on the host population than does the ultimate death of the afflicted host. Upon release of the worm, the host is old and often past the period when its contribution to the population's reproductive effort would be

significant. In these parasitized populations, prevention of reproduction in early breeding periods has a more suppressive effect on population than does the prevention of reproduction (by death) in later periods.

In brief, on the basis of the sharp resemblances between parasitic castrators and parasitoids outlined above, I conclude that castration phenomena may be important components of population regulation systems for many marine organisms. Malacostracan Crustacea are considered to be particularly subject to such castration systems. Parasitic crustaceans are often discovered to exert a castration effect on their hosts, crustacean or otherwise.

Further elucidation of the role of parasitic castrators in the regulation of crustacean host populations must await long-term density sampling programs for both host and castrator populations, or the domestication of suitable laboratory systems. The comparative analysis assembled here suggests that the regulatory role of castrators may be considerable.

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