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## DEVELOPMENTAL NICHE STRUCTURE IN THE GREGARINE ASSEMBLAGE PARASITIZING *TENEBRIO MOLITOR*

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**ABSTRACT:** The exogenous developmental niche spaces of *Gregarina cuneata* and *Gregarina polymorpha*, parasites restricted to larval *Tenebrio molitor*, and *Gregarina niphandrodes*, a parasite restricted to adult *T. molitor*, were determined along temperature and humidity axes and associated with parasite niche space on the host resource axis. Gregarine gametocysts were incubated at controlled humidity (0, 10, and 20 mm Hg vapor pressure deficit) at 20, 25, 30, and 35 C to determine the environmental limits to survival and sporulation. Although the environmental conditions that permit gametocyst development overlap, the gregarine parasite restricted to adult *T. molitor* utilizes a subset of sporulation and survival conditions that is incompatible with the developmental needs of the gregarines restricted to larval *T. molitor*. Likewise, the gregarine parasites that are restricted to larval *T. molitor* survive and sporulate under a subset of environmental conditions that are incompatible with the developmental needs of the gregarine restricted to adult *T. molitor*. *Gregarina niphandrodes* survived and sporulated under extended environmental conditions characterized by lower humidity and temperature. In contrast, *G. cuneata* and *G. polymorpha* survived and sporulated under extended environmental conditions at the upper end of the temperature scale. The pattern of interspecific variation in the environmental tolerances of the exogenous gregarine stages is analogous to the pattern of interspecific variation in host stadium specificity observed in the corresponding endogenous gregarine stages.

Parasites that form stable systems with only 1 or a very few host species are said to be host specific (Kennedy, 1975). A high degree of host specificity can be inferred from taxonomic literature concerning the genus *Gregarina*. The strength of this inference is reflected in the most recent review of Septatorina in which Levine (1979) noted the apparent homoxenous nature of the species within the genus as a justification for the use of host species as a taxonomic character. However, host specificity in the eugregarines seldom has been defined experimentally. Patil et al. (1985) addressed the question of eugregarine host specificity using gregarines of 9 species of *Stylocephalus*, *Xiphocephalus*, and *Cryptocephalus* in cross-infection experiments with 8 species of tenebrionid beetles. Although exsporulation was reported in 5 heterologous host–parasite combinations, parasite establishment and growth were observed only in homologous combinations.

Extreme host specificity within the eugregarine parasites of insects may extend to ontogenetic stages of a single host species. Clopton et al. (1992) demonstrated stadium specificity in the gregarine assemblage parasitizing *Tenebrio molitor* using controlled, reciprocal, experimental cross-infections. In this case, adult and larval beetles constituted different hosts and thus different habi-

tats, at least in laboratory colonies. Host stadium specificity in the gregarine assemblage parasitizing *T. molitor* is believed to be mediated by the interaction of a potential host and the sporozoite; that is, extreme host specificity is a functional feature of endogenous parasitic stages. Other indications of extreme host specificity also may be present in the exogenous stages of the gregarine life cycle. In a complex life cycle, the suite of characteristics that delimits niche space may vary among ontogenetic stages.

Most gregarines utilize a direct life cycle. Briefly, infective oocysts are consumed and exsporulate in the insect gut. Free sporozoites migrate to the mid-gut epithelium where they undergo first an intracellular and then an extracellular growth phase. Gamonts form reproductive associations and, when mature, undergo syzygy to form single gametocysts that are passed to the environment in the feces. Sexual recombination and asexual multiplication are completed in the exogenous gametocyst. Mature gametocysts sporulate in the environment to release oocysts and continue the infective cycle. Allegre (1948) and Levine (1985) provided more complete reviews of the gregarine life cycle.

The gregarines infecting *Tenebrio molitor* constitute a feasible experimental system for gametocyst studies because the gametocysts of these species are readily separated using structural features. Lipa (1967) described the gametocysts of *Gregarina cuneata* as follows, “Cysts oval up to 600 micrometers in diameter”; however, his ac-

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companying figures clearly illustrate *Gregarina polymorpha*. In single parasite species infections, the gametocysts of *G. polymorpha* are ovoid and approximately 400  $\mu\text{m}$  in diameter, whereas the gametocysts of *G. cuneata* are round and approximately 245  $\mu\text{m}$  in diameter (Reichenow and Wülker, 1929; Mackinnon and Hawes, 1961). In general, the gametocysts of *G. polymorpha* appear singly, whereas the gametocysts of *G. cuneata* are shed in grapelike clusters.

Ambient temperature has been identified as a factor influencing the rate of gregarine gametocyst development (Patil et al., 1983). Anecdotal observations suggest that in addition to temperature, water balance is a primary abiotic factor limiting gametocyst maturation and development. The environmental requirements for gametocyst development may differ among species in the gregarine assemblage parasitizing *T. molitor*, and the nature of this variation may reflect host specificity. This study explores these possibilities by quantifying the effects of temperature and humidity, over a controlled range, on gametocyst development in the gregarine assemblage parasitizing *T. molitor*.

## MATERIALS AND METHODS

### Gametocyst collection and parasite maintenance

*Tenebrio molitor* colonies were maintained on wheat bran and potato slices in 30.9-L plastic boxes. The wheat bran substrate was covered with burlap that was moistened daily. Three gregarine species were manipulated: *G. cuneata* and *G. polymorpha* from *T. molitor* larvae, and *Gregarina niphandrodes* from *T. molitor* adults. Multiple gregarine species infections are common in larval *T. molitor*. The gametocysts from multiple parasite species infections were sorted on the basis of gametocyst structure. Gametocysts were collected from both adult and larval *T. molitor* by placing 500–3,000 insects in a plastic box with moist paper towels overnight. Feces were examined the next morning. Gametocysts were freed by softening frass in basic saline solution, sorted by parasite species, surface sterilized in 0.01% neutral-buffered formalin, and pipetted in lots of 10 gametocysts to circles of black construction paper (6 mm diameter). The black background improved visibility of oocyst chains. Gametocysts were kept in separate filter paper-lined petri dishes according to parasite species and incubated at controlled temperature and humidity.

### Temperature and humidity control

Temperature and humidity were controlled using a series of Plexiglas humidity chambers inside a FREAS 815 low temperature incubator. Constant humidity was established and maintained using a modified apparatus similar to that of Perring et al. (1984). Aquarium pumps provided 2 air flow lines. One line bubbled through distilled water, producing a "wet" air stream; the other

line passed through a series of silica gel desiccating columns, producing a "dry" air stream. Experimental humidities were established by regulating the flow of the wet and dry air streams into each humidity chamber using a simple gang-valve system. Temperature and humidity within each chamber were monitored with a solid-state digital hygrometer/thermometer.

Humidities reported are vapor pressure deficits measured in millimeters of mercury (VPD). VPD is the difference between the actual vapor pressure of water in air and the saturation vapor pressure of water in air at the same temperature (Platt and Griffiths, 1964). Experiments were conducted at 0 (saturated  $\text{H}_2\text{O}$  vapor), 10 (median  $\text{H}_2\text{O}$  vapor), and 20 (low  $\text{H}_2\text{O}$  vapor) mm Hg VPD at 20, 25, 30, and 35 C. Low  $\text{H}_2\text{O}$  vapor tests at 20 C were conducted at 17.5 mm Hg, the maximum aqueous VPD possible at that temperature (Anonymous, 1986).

### Experimental protocol

The experimental design was devised to investigate 2 development processes in the exogenous gregarine gametocyst: survival and sporulation (oocyst chain extrusion). Sporulation at any given temperature/humidity combination was tested with a controlled incubation bioassay. Survival was tested using a reversal bioassay in which gametocysts were incubated at the experimental temperature/humidity for the duration of normal development, transferred to a high humidity incubation chamber, and observed for subsequent sporulation.

In each experimental replication, 60 gametocysts from each parasite species were incubated at controlled temperature and humidity for 100 hr. The condition of each gametocyst (sporulated, stable, or desiccated) was observed and recorded every 25 hr. After 50 hr of incubation (normal development time for sporulation [Clopton et al., 1991]), the reversal bioassay groups were transferred to the 0 VPD chamber. All gametocysts were removed and examined every 25 hr during the 100-hr experiment.

The data are derived from 3 replications for each of 12 experimental temperature/humidity combinations. A total of 2,160 gametocysts (720 gametocysts/parasite species) were manipulated.

## RESULTS

The percentages of gametocysts of *G. niphandrodes*, *G. cuneata*, and *G. polymorpha* sporulating under various temperatures and humidities are depicted in Figures 1–3. In all parasite species tested, temperature and humidity directly affected gametocyst development and extreme temperature or VPD limited gametocyst sporulation. Gametocyst sporulation rates in all 3 gregarine species were greatest at high humidity (0 mm Hg VPD). Low humidity (20 mm Hg VPD) generally depressed gametocyst sporulation in *G. niphandrodes* and precluded sporulation in *G. cuneata* and *G. polymorpha*. Low humidity in combination with low temperature (20 C) also precluded gametocyst sporulation in *G.*

*niphandrodes*. High temperature (35 C) precluded gametocyst sporulation in *G. niphandrodes* at median humidity (10 mm Hg VPD) and in all 3 species at low humidity. Gametocysts of *G. cuneata* and *G. polymorpha* were more tolerant of high temperature at high humidity than gametocysts of *G. niphandrodes* (63, 66, and 3% sporulation, respectively); however, gametocyst sporulation in *G. cuneata* and *G. polymorpha* was depressed at high temperature and median humidity. Low temperature precluded sporulation in *G. cuneata* and *G. polymorpha* at all humidities. Gametocysts of *G. niphandrodes* sporulated at low temperature only in combination with median or high humidity.

The percentage of gametocyst survival for *G. niphandrodes*, *G. cuneata*, and *G. polymorpha*, measured by sporulation under high humidity after initial incubation at various humidities and temperatures, is depicted in Figures 4–6. Gametocyst survival in all 3 gregarine species was greatest after incubation at median or high humidity and generally depressed under low humidity. Although gametocyst survival in *G. cuneata* and *G. polymorpha* was depressed by high temperature incubation, survival was not precluded. The gametocysts of these species were more tolerant of high temperature incubation at all humidities than gametocysts of *G. niphandrodes*. Incubation at low or median humidity in combination with high temperature precluded *G. niphandrodes* gametocyst survival. Incubation under low humidity at 20 C and 25 C precluded survival in *G. cuneata* and *G. polymorpha*. Survival was precluded or dramatically reduced in *G. cuneata* and *G. polymorpha* by low temperature incubation under all humidities tested.

Although these data are useful to determine the optimal temperature and humidity conditions for gametocyst development in *G. niphandrodes*, *G. cuneata*, and *G. polymorpha*, they are most informative when used to compare absolute, rather than relative, responses among parasite species.

Figure 7 depicts the environmental conditions that permit sporulation of the gametocysts of all 3 parasite species. *Gregarina niphandrodes*, the parasite of adult *T. molitor*, sporulated under drier conditions at 25 and 30 C. Its tolerance to low humidity decreased at higher or lower temperatures. *Gregarina cuneata* and *G. polymorpha*, the parasites of larval *T. molitor*, sporulated between 25 and 35 C. Under no condition tested

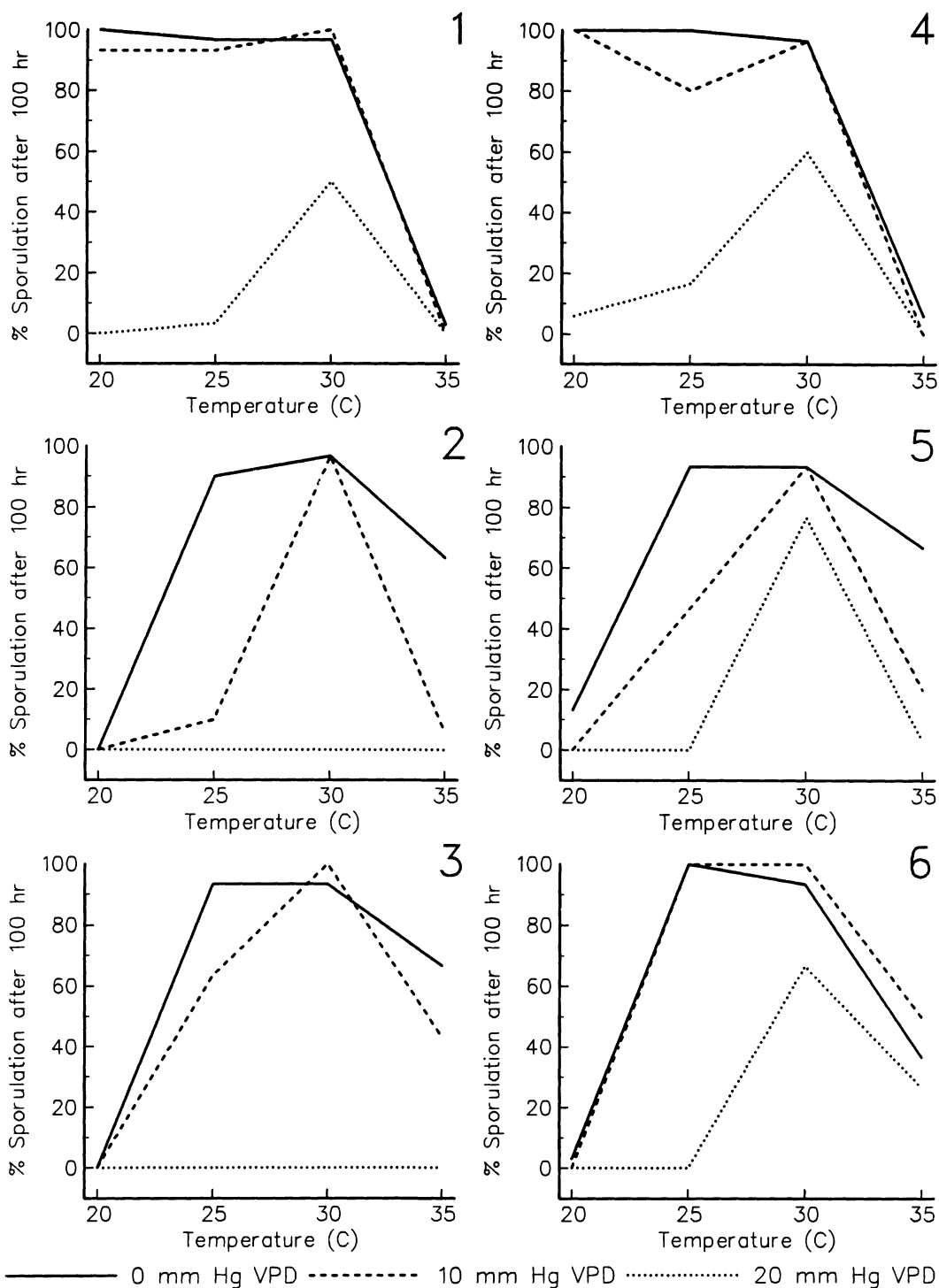
did they sporulate under vapor pressure deficits in excess of 10 mm Hg.

Figure 8 depicts the environmental conditions that permit survival of the gametocysts of all 3 species. *Gregarina niphandrodes* gametocysts could survive at humidities too low to facilitate sporulation: their survival tolerance to high VPD extended beyond sporulation limits at lower temperatures. Likewise, *G. cuneata* and *G. polymorpha* gametocysts survived at humidities that were too low to facilitate sporulation. In contrast to the gametocysts of *G. niphandrodes*, the survival tolerance of *G. cuneata* and *G. polymorpha* gametocysts to high VPD was extended beyond sporulation limits at higher temperatures. The set of environmental conditions that permit survival are similar to, but wider than, the environmental conditions that permit sporulation.

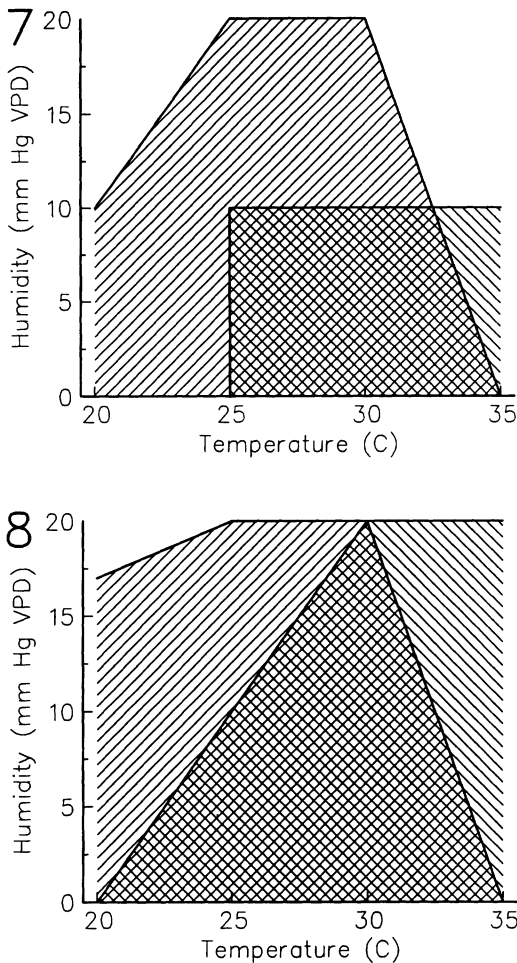
## DISCUSSION

Ferro and Chapman (1979) demonstrated that some measure of the effects of vapor flux, i.e., the exchange of water vapor between an animal and the environment, is required to establish humidity as a causal factor in the response of an organism to environmental changes. Vapor pressure deficit, rather than relative humidity, was chosen as the humidity measure for this study. VPD is a temperature-independent measure of the “drying power of the air” (a phenomenon of biological interest), and it measures the potential for water vapor exchange between an organism and the environment (Ferro and Chapman, 1979; Perring et al., 1984). VPD is the difference between the actual vapor pressure of water in air and the saturation vapor pressure of water in air at the same temperature (Platt and Griffiths, 1964). As VPD increases, the drying power of the air increases; that is, vapor pressure deficit and humidity are inversely related. In contrast, relative humidity is a function of temperature; constant relative humidity does not provide a directly comparable measure of the biological effects of ambient humidity over a temperature gradient. Thus the advantage of VPD over relative humidity is that biologically meaningful constant humidities can be measured over a temperature gradient in an effort to demonstrate the causal interactions of temperature and humidity on biological processes.

The sporulation and survival responses of *G. niphandrodes*, *G. cuneata*, and *G. polymorpha* gametocysts were directly affected by both temperature and humidity. For all 3 species, extreme



FIGURES 1-6. Gametocyst sporulation (1-3) and survival (4-6) as functions of temperature (20, 25, 30, 35 C) and humidity (0, 10, 20 mm Hg vapor pressure deficit [VPD]) for 3 species of *Gregarina*. 1. *Gregarina niphandrodes*. 2. *Gregarina cuneata*. 3. *Gregarina polymorpha*. 4. *Gregarina niphandrodes*. 5. *Gregarina cuneata*. 6. *Gregarina polymorpha*.



FIGURES 7, 8. Relative gametocyst sporulation and survival as functions of temperature (20, 25, 30, 35 °C) and humidity (0, 10, 20 mm Hg vapor pressure deficit [VPD]) for 3 species of *Gregarina*. *Gregarina niphandrodes*, //;//; *Gregarina niphandrodes* and *Gregarina polymorpha*, \\\;\\; *Gregarina niphandrodes*, *Gregarina niphandrodes*, and *Gregarina polymorpha*, xoxox. 7. Gametocyst sporulation. 8. Gametocyst survival.

temperature or humidity could act as a single limiting factor for gametocyst development. The temperature results are similar to those obtained by Patil et al. (1983) for *Gregarina bidari* and *Gregarina opatroidea* gametocysts. However, the effect of subsaturation humidity, alone or in combination with temperature, on gametocyst development in these latter species is unknown. In comparison to the developmental temperature ranges reported here for gametocysts of *Gregarina* species, Patil et al. (1983) reported broader developmental temperature ranges for the gametocysts of *Stylocephalus depressicus*,

*Stylocephalus pseudoblapsis*, *Stylocephalus punctulatus*, *Xiphocephalus gonocephali*, and *Xiphocephalus reitterae*. Narrower developmental temperature ranges were reported for *Cystocephalus rhytonotus*, *Cystocephalus devdhari*, and *Leidyana gnyanagangai*. In all known cases, less variation in developmental temperature tolerance has been observed for congeneric species than has been observed between species of different genera. That is, gregarine gametocyst developmental temperature tolerance appears to vary in a systematic way consistent with currently understood taxonomic relationships.

The absolute sporulation and survival responses of *G. niphandrodes*, *G. cuneata*, and *G. polymorpha* gametocysts indicate a shared set of environmental conditions for sporulation and survival. Although the environmental conditions that permit gametocyst development overlap, the gregarine parasite restricted to adult *T. molitor* utilizes a subset of sporulation and survival conditions that is incompatible with the developmental requirements of the gregarines restricted to larval *T. molitor*. Likewise, the gregarine parasites that are restricted to larval *T. molitor* survive and sporulate under a subset of environmental conditions that are incompatible with the developmental requirements of the gregarine restricted to adult *T. molitor*. *Gregarina niphandrodes* survived and sporulated under extended environmental conditions characterized by lower humidity and temperature. In contrast, *G. cuneata* and *G. polymorpha* survived and sporulated under extended environmental conditions at the upper end of the temperature scale. Thus, the pattern of interspecific variation in the environmental tolerances of the exogenous gregarine stages is analogous to the pattern of interspecific variation in host stadium specificity observed in the corresponding endogenous life cycle stages.

Functional survival and sporulation responses can delimit the niche breadths of *G. niphandrodes*, *G. cuneata*, and *G. polymorpha* in Hutchinsonian space. Figure 9 depicts the developmental niche areas for the gametocysts of all 3 gregarine species, using humidity (VPD) as the resource set at a constant temperature of 25 °C. Dispersal and transmission of gregarine oocysts are functions of the overlap of the niche spaces of host and parasite. Although dispersal is a passive function of host movement and behavior, transmission is dependent upon both host feeding and suitable environmental conditions for

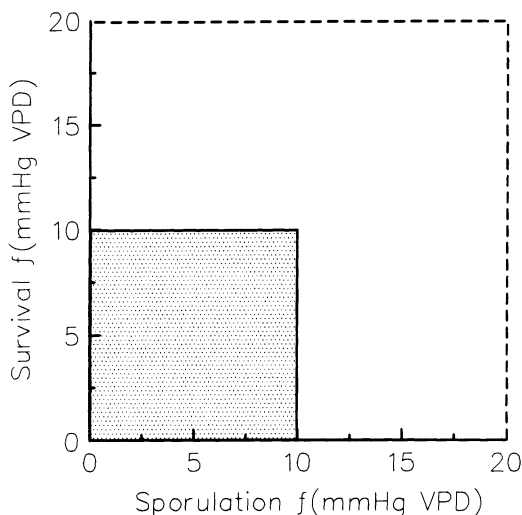


FIGURE 9. Gametocyst developmental niche area, as a function of survival and development on the resource set humidity (mm Hg vapor pressure deficit [VPD]) at 25 C, for 3 species of *Gregarina*. *Gregarina niphandrodes*, ---; *Gregarina cuneata* and *Gregarina polymorpha*, —; overlap of *Gregarina niphandrodes* with *Gregarina cuneata* and *Gregarina polymorpha*, ■.

gametocyst survival and sporulation. Thus, dispersal and transmission in a variable environment are limited by the survival and sporulation tolerances of the gametocyst. In effect, the habitat is partitioned among gregarine species by its differential suitability for gametocyst development. The difference among the developmental niche areas of the exogenous stages of *G. niphandrodes*, *G. cuneata*, and *G. polymorpha* (Fig. 9) indicates the potential for habitat partitioning among these 2 groups under various humidities at 25 C.

Gregarine gametocyst development is also subject to temperature influence and restriction. The temperature and humidity restrictions on the survival and sporulation of gregarine gametocysts can be represented in 3-dimensional Hutchinsonian niche space as a series of humidity-based developmental niche areas distributed along a temperature gradient. The enclosed developmental niche volume describes the conditions that will permit dispersal in the gametocyst stage (and subsequent transmission) as limited by temperature and humidity. The nature of shared and expanded developmental niches is apparent when the developmental niche volumes for the gametocysts of all 3 gregarine species are drawn in concomitant space (Fig. 10). All 3 parasite species share a common development niche volume congruent with the preferred tempera-

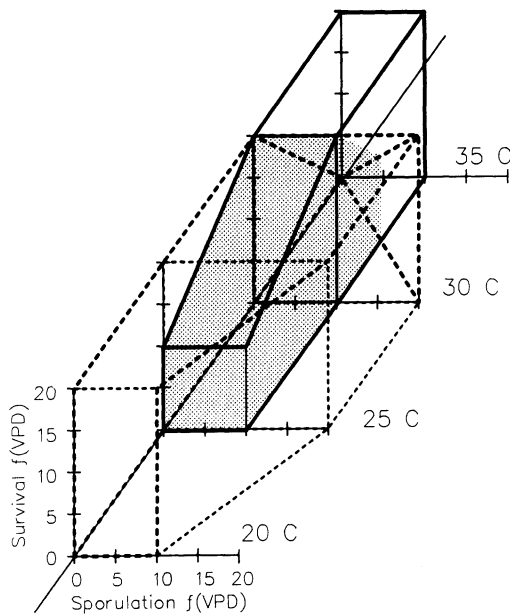


FIGURE 10. Gametocyst developmental niche volume, as a function of survival and development on the resource set humidity (mm Hg Vapor pressure deficit [VPD]) between 20 and 35 C, for 3 species of *Gregarina*. *Gregarina niphandrodes*, ---; *Gregarina cuneata* and *Gregarina polymorpha*, —; overlap of *Gregarina niphandrodes* with *Gregarina cuneata* and *Gregarina polymorpha*, ■.

ture range overlap of larval and adult *T. molitor* at all humidities (Mellanby, 1932; Howard, 1955; Punzo and Mutchmor, 1978, 1980). However, *G. cuneata* and *G. polymorpha* also share a development niche volume incompatible with *G. niphandrodes*. This volume is a function of the increased survival and sporulation tolerances of these parasites to higher temperatures and corresponds to the expanded thermal niche of larval *T. molitor* (especially younger larval instars) (Buxton, 1930; Pielou and Gunn, 1940; Punzo and Mutchmor, 1978, 1980). Likewise, *G. niphandrodes* retains a development niche volume incompatible with *G. cuneata* and *G. polymorpha*. This volume is a function of the higher overall survival and sporulation tolerances of this parasite to lower humidities between 20 and 30 C and corresponds to the expanded niche of adult *T. molitor* at low temperature and humidity (Mellanby, 1932; Pielou and Gunn, 1940; Howard, 1955; Punzo and Mutchmor, 1978, 1980; Punzo and Huff, 1989).

The observed conditions for gametocyst development correspond to the niche volumes of host stadia. The niche of *T. molitor*, as defined

by temperature and humidity, is subdivided into an intermediate area that supports all stadia, an area at upper temperatures that supports larval stadia but not the adult stadium, and an area at lower temperature and humidity that supports the adult stadium but not larval stadia. Low humidity tolerance is a function of the production of metabolic water from ingested food and, when provided with a sufficient food supply, adult and larval *T. molitor* can survive under relatively xeric conditions (Buxton, 1930, 1932). Temperature tolerance in late larval instars and adult stages is mediated by the potential for evaporative cooling (Buxton, 1930; Mellanby, 1932; Pielou and Gunn, 1940). The potential for evaporative cooling, as a function of VPD, does not satisfy the requirements of larger late instar larvae and adults at high temperatures and humidities (Mellanby, 1932; Punzo and Mutchmor, 1978, 1980; Punzo and Huff, 1989). This limitation becomes pronounced with decreasing surface area: volume ratios. Conversely, low temperature and humidity markedly increase the mortality of smaller early instar larvae (Punzo and Mutchmor, 1980). This phenomenon may be a result of reduced enzymatic rates. The results reported here are of biological significance mainly because temperature and humidity are not uniform in stored grain products and may vary due to the presence of localized insect populations (Ernst and Mutchmor, 1969). In addition molds may raise the temperature of a stored grain pocket up to 60 C and temperature gradients of 20 C/m are not uncommon (Surtees, 1964, 1965).

Niche structure usually is defined as a function of the overall tolerances of a life cycle. This study addresses the niche structure as a function of individual life cycle processes and reveals restrictions that are not apparent when life cycle processes are considered in combination over different life cycle stages. For example, MacDougall (1942) experimentally determined that the lethal temperature threshold for the oocysts of *G. polymorpha* was in the range of 60–64 C (some oocyst survival was observed at temperatures as high as 96 C). But, the extent to which the temperature tolerance of *G. polymorpha* oocysts affects the dispersal and transmission of the parasite in the host environment is mediated directly by the survival and developmental requirements of the gametocyst.

Host specificity has been discussed frequently as an ecological, largely host-mediated, phenom-

enon (Holmes, 1976, 1979, 1990; Freeland, 1983; Aho, 1990). Interactions between infective stages and their environments and the overlap of infective stages and host feeding ranges have been recognized as factors that restrict host utilization (e.g., Kennedy, 1975). Although adult and larval *T. molitor* appear to occupy different physical strata in a laboratory colony, interspecific differences in host utilization by *G. niphandrodes*, *G. cuneata*, and *G. polymorpha* do not appear to be a result of nonoverlapping host distributions or competitive exclusion. Evidence presented by Clopton et al. (1992) indicates that host stadium specificity is not a function of host escape in time or space, but of interaction at the host–parasite interface. Observed differences in the life history and site specificity of the endogenous stages of *G. cuneata* and *G. polymorpha* indicate no competition between these species (Ruhnke and Janovy, 1990a, 1990b).

Gregarine development niches reflect the niche spaces of host stadia. The congruence of exogenous and endogenous restrictions suggests that these development niches are representative of adaptation or historical constraint that may have played a role in the colonization of the parasites' respective host stadia; historical host-capture events may have been mediated by overlap of the host niche and the exogenous development niche of the parasite. The existence of survival conditions that extend far beyond sporulation conditions suggests the importance of the gametocyst wall in gregarine radiation. The gametocyst wall is a phenotypic character that is continually tested against the environment. Changes in the humidity and temperature tolerances of the gametocyst wall have the potential to alter the development niche of a gregarine radically and subsequently to alter niche overlap with potential host stadia or species.

The observed nature of life history variation in the gregarine assemblage parasitizing *T. molitor*, as partitioned among host stadia, may be a result of host capture (Chabaud, 1981) or coaccommodation (Brooks, 1979); however, the relative evolutionary importance of the exogenous and endogenous life cycle stages in the rise of specificity is unclear. Based on the data presented here and by Clopton et al. (1992), we hypothesize that, at least in the case of the gregarine assemblage parasitizing *T. molitor*, host stadium specificity is a historical restriction. The inability of the members of the *T. molitor* gregarine complex to establish when artificially introduced in a het-



erologous host stadium suggests that adaptation of the host-parasite interface enforces endogenous host stadium specificity. Interspecific differences in developmental niche structure suggest that cooccurrence of exogenous parasitic stages and their associated host stadia is mediated by the environmental tolerances of the gregarine gametocyst.

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