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HOST-MEDIATED SITE SEGREGATION OF ECTOPARASITES: AN INDIVIDUAL-BASED SIMULATION STUDY

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ABSTRACT: Site segregation of coexisting ectoparasite species may result either from a direct interaction such as resource competition between them or from a host-mediated interaction. Here we present an individual-based model for the coevolution of 1 host and 2 parasite species to study this latter hypothesis. Parasite species are generalists at the start of the simulation and develop site specificities under the following assumptions. Parasite populations are not subject to resource limitations but are limited directly by host defense as predation. Hosts have 2 sites that need different defensive abilities to reduce their parasite burden. Parasites need to exhibit different evasive abilities to survive on different sites. Host grooming selects parasites for an increasing capability for evasion, whereas parasites select hosts for an increasing efficiency of grooming. Two trade-offs are incorporated into the model: one between host defensive abilities on the 2 sites, and another between parasite evasive abilities on the 2 sites. We conclude that, under these assumptions, the optimization of host defense and parasite evasion strategies may select ectoparasites for site segregation and this may stabilize the coexistence of parasite species.

Most ectoparasite species are specialized upon certain areas of the host's body surface. Specificities of different ectoparasite species living on the same host species tend to segregate toward different sites. Site segregation is supposed to play a major role in the organization of parasite coexistence patterns (Marshall, 1981). It may result from resource competition between coexisting ectoparasite species and can be interpreted as a realization of character displacement caused by competition for limited resources (Clay, 1949; Marshall, 1981). Evidence is often scarce or absent, however, to support the assumption that parasite multiplication within an individual host is limited by the availability of resources like nutrients or space (Price, 1980). Most species seemingly do not face resource limitation, but still they exhibit site segregation. Some authors use the terms "apparent competition" and "negative interaction" in cases where selection pressure causing site segregation remains undefined (Halvorsen, 1976). An alternative approach is to describe site segregation of ectoparasites as a host-mediated interaction. Grooming partially serves to control ectoparasites (Marshall, 1981; Hart, 1997), and experimental manipulation of grooming abilities provided direct evidence that ectoparasite numbers were limited primarily by host defense in birds (Clayton, 1990, 1991) as well as in mammals (Mooring et al., 1996). Host grooming acts as predation from the ectoparasites' point of view and may select them to locate different topographic regions of the host's body as refugia. This concept originates from Nelson and Murray (1971) and is closely related to the Resource Tracking Hypothesis by Kethley and Johnston (1975), where similar argumentation is used to draw the conclusion that ectoparasite speciation patterns track host species characterized by similar topographies.

Here, we aim to study the interactions within the simplest possible system, i.e., using 1 host and 2 parasite species. Hosts exert selection pressure upon parasites and parasites exert selection pressure upon hosts in the model, thereby establishing a coevolutionary system in the sense of Ehrlich and Raven (1964). There is no direct interaction like resource limitation between the parasite species in the model. Both of them are generalists at the start and then develop site specificities due to selection pressure exerted by the hosts. The model is used to identify some conditions that influence the chances of site segregation and to study their effects on the stability of parasite coexistence.

Ischnoceran lice (Phthiraptera: Ischnocera) and their avian hosts are chosen as model taxa because many aspects of the natural history of their interaction broadly agree with our model presumptions. Experimental tests on the bird–louse interaction have already shown that lice negatively influence mating success (Clayton, 1990), metabolic rate (Booth et al., 1993), and long-term survivorship (Brown et al., 1995) of their hosts, supporting the view that lousiness decreases lifetime reproductive success in birds, which is represented by a positive correlation between the effectiveness of host defense and host reproductive success in the present model. Lice are selected by 2 kinds of host grooming. Scratching by the feet is oriented on the head and preening by the bill is oriented to all other body parts in most birds. Ischnoceran lice living on the head have a characteristic body shape markedly different from that of the lice living on other body parts of the host; thus, parasite body shape is likely to have evasive value (Marshall, 1981). This is illustrated by a negative trade-off in parasite evasive abilities on the 2 sites. Another negative trade-off represents an interaction between host defensive abilities on the 2 sites. Indeed, the time devoted to grooming behavior is constrained by other activities, and grooming time is allocated between scratching and preening (Cotgreave and Clayton, 1994). Birds with beaks unsuitable for preening are known to compensate for this relative disadvantage by increasing the proportion of scratching (Clayton and Cotgreave, 1993), also indicating a kind of negative trade-off between these 2 types of grooming.

The site-specific occurrence of lice may be derived from 2 factors. First, host defense is site specific (Rózsa, 1993) and ectoparasites may be effectively groomed off from all sites they are not adapted to. Second, lice apparently have their own site preferences. Stenram (1956) published early experiments to show that *Columbicola columbae* uses temperature gradients as cues for spatial orientation. Nelson and Murray (1971) concluded that the 4 louse species they studied utilized the same part of the plumage as food resource but moved to different body parts to take refuge. Cohen et al. (1991) isotope-labeled Amblyceran lice to track their considerably long movements

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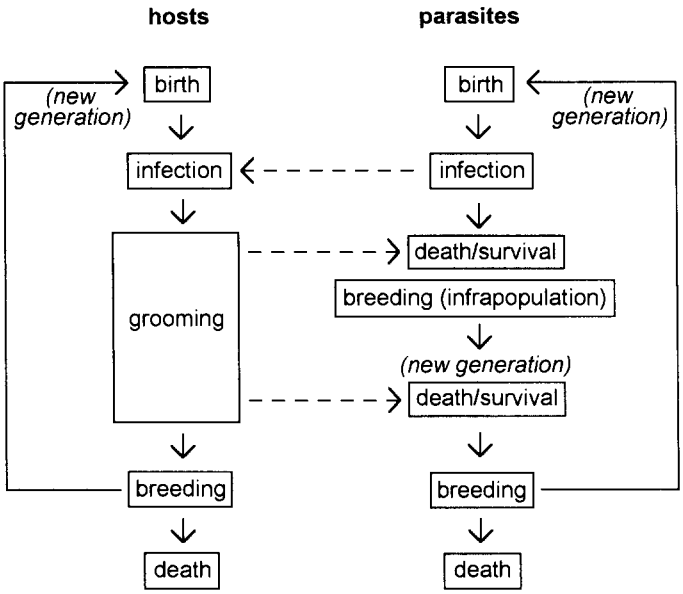

FIGURE 1. Life cycles of hosts and parasites in the model.

within the plumage of swans. These results support the view that lice are capable for orientation and active movements toward preferred sites within the plumage. In our model, both site-specific host defenses and parasite site preferences act to yield in a site-specific occurrence of parasites.

For sake of model simplicity, the 2 sites are regarded as parasite habitats of equal value with respect to nutrients as well as to host defense. Furthermore, the 2 parasite species are assumed to be equally pathogenic; thus, given equal densities, hosts are not selected for an enhanced defense against any of them. In other aspects, the model reflects some general features of host–parasite interactions. It assumes that parasite life cycles are shorter than the host life cycle, uses realistic mutation rates, and allows parasites to exhibit an aggregated distribution among hosts (Crofton, 1971). As environmental constraints may limit host defenses in natural host–parasite systems (Mooring and Hart, 1995), host defense is limited in our model too.

MATERIALS AND METHODS

Individual-based modeling is used because major aspects of host–parasite interactions and particularly the interaction between host defense and parasite evasion is best interpreted at this level (Judson, 1994). A model with 1 host and 2 parasite species is constructed with the following assumptions. First, parasite population growth is not subject to resource limitation but limited directly by host defense as predation. Second, hosts have 2 sites that need different defensive abilities to keep them free of parasites. Third, parasites need to exhibit different evasive abilities to survive on different sites. Fourth, both the defensive abilities of the hosts and the evasive abilities of the parasites are quantitative traits determined by polygenic inheritance. Fifth, host grooming selects parasites for an increasing capability for evasion, whereas parasites select hosts for an increasing efficiency of grooming. Finally, parasite transmission is horizontal. A diagram of the model with the life cycles of the hosts and parasites is presented in Figure 1.

Genetic representation

Defensive capabilities of hosts at the 2 sites are modeled as 2 polygenic traits, each of them affected by 100 genes with 2 allelic forms (0 or +). Alleles + increase defensive capability at the corresponding site, whereas alleles 0 have no effect on it. Thus, host genotypes are represented by 2 scores ranging from 0 to 100 (corresponding to the number of + alleles), denoted by $s_i^{(h)}$ ($i = 1, 2$). Phenotypes, i.e., actual abilities to defend sites against parasites, are calculated from these scores assuming a trade-off between the 2 capabilities as described below. No environmental variance is assumed.

The genetic background of the evasive capabilities of parasites is represented in the same way, using 2 scores, denoted by $s_i^{(p)}$ ($i = 1, 2$), and a trade-off.

Trade-offs are linkages between the defensive (evasive) abilities at different sites. For hosts, improving defense at one site and that at the other site are conflicting requirements. Also for parasites, improving evasive ability at one site and that at the other site are conflicting requirements. These are microevolutionary trade-offs as they affect the response of the population to selection (Stearns, 1992). They are represented by real numbers $t^{(h)}$ and $t^{(p)}$ between 0 to 1 in the model. The defensive abilities of hosts and the evasive abilities of parasites, $a_i^{(h)}$ and $a_i^{(p)}$ at site i ($i = 1, 2$) are expressed as

$$a_i^{(h)} = s_i^{(h)} - t^{(h)} s_{3-i}^{(h)} \quad \text{and}$$

$$a_i^{(p)} = s_i^{(p)} - t^{(p)} s_{3-i}^{(p)}$$

where $s_i^{(h)}$ and $s_i^{(p)}$ denote the above genotype scores. In the simulation, 4 levels such as no, weak, strong, and very strong were considered for both host and parasite trade-off, represented by $t^{(h)}$ and/or $t^{(p)}$ values 0, 0.25, 0.5, and 0.75, respectively.

Birth and infection

Generations are disjoint for both hosts and parasites, and they are synchronized between hosts and parasites. In the course of a host generation, 2 parasite generations take place. Host population growth is not modeled; in each generation the same number of offspring (100) is created. After birth, each newborn host is infected with a number of parasites (in most simulations, the number follows a uniform distribution between 20 to 25) randomly chosen from the pool of newborn parasites (including both parasite species). Thus, the model mimics horizontal transmission of parasites, i.e., transmission is not influenced by genetic relatedness among hosts. It also follows from this mechanism that the average size of the parasite assemblage (including both species) will remain constant over time, i.e., each parasite species can increase its share only to the detriment of the other one.

Host grooming

Host grooming is modeled by 50 "attacks" on randomly chosen individual parasites living on that host. The outcome of each attack is taken to be a random event where the probability of host success, i.e., eliminating the parasite, is modeled by an increasing function S of the difference between the host's defensive ability and the parasite's evasive ability at that site where the parasite is located. In formula

$$\text{probab(host success)} = S[a_i^{(h)} - a_i^{(p)}] = \left\{1 + \exp\left[-\frac{a_i^{(h)} - a_i^{(p)}}{u}\right]\right\}^{-1}$$

where $a_i^{(h)}$ and $a_i^{(p)}$ are the defensive/evasive abilities of the host/parasite at site i, calculated from their scores and the trade-offs. Function S is known as the logistic function; its graph (the so-called sigmoid curve) is shown in Figure 2 for those values of its parameter u that were used in the simulation. Parameter u controls the selection advantage of having a + allele compared to a 0 allele. The smaller the u, the greater the selection pressure on parasites (and indirectly on hosts too).

Each individual parasite is assumed to be located at the site it is better adapted to, i.e., at site i if $s_i > s_{3-i}$ (in case of equal scores, the site is chosen randomly with equal probabilities). The reason for this simplification is that, although it would be more realistic to model site specificity and site preference independently, selection would most probably favor those individual parasites in which site specificity and site preference correlates, i.e., which prefer that site that they are better adapted to.

Reproduction and inheritance

Host fitness is modeled by a decreasing function F of the number of parasites that survive host grooming:

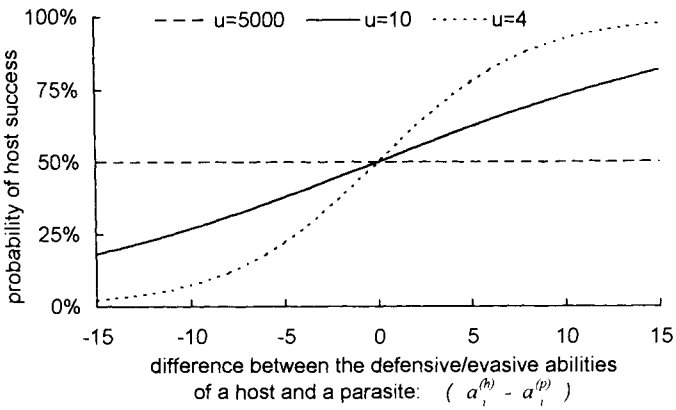

FIGURE 2. Probability of host success in grooming.

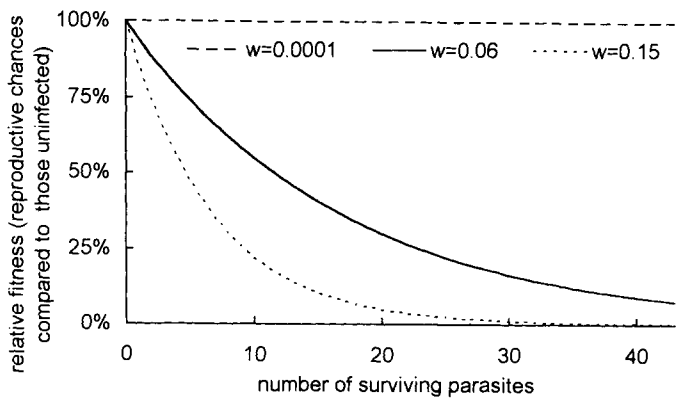

FIGURE 3. Relative host fitness defined by the number of parasites that survived grooming.

$$F(n) = \exp(-wn),$$

where n denotes the number of surviving parasites and w determines the shape of the function. Higher w represents higher selection pressure on hosts and can be interpreted as increased parasite pathogenicity. Figure 3 shows the graph of F for those values of w that were used in the simulation. Host reproduction is based on random mating with mating chances proportional to the fitness; that is, the more parasites that survive grooming, the less is the host's relative reproductive success.

For each parasite species, reproduction is based on random mating of surviving parasites (from any host and site). The gene pools of the 2 parasite species are isolated by a reproductive barrier, and no hybridization occurs. As parasite transmission is facilitated by host sexual activity, the reproductive chances of a parasite are taken to be proportional also to the fitness of its host. This establishes a negative feedback on parasite specialization, providing that high specialization of parasites compared to that of their host will reduce their reproduction chances.

The defensive and evasive abilities of hosts and parasites are modeled as quantitative traits of diploid individuals reproducing themselves sexually. As the inheritance of a quantitative trait is usually characterized by the normal distribution (Rédei, 1982), the offspring score is set up in the model as a random value with an approximate normal (actually binomial) distribution within the range between the parental scores. Offspring scores s_1 and s_2 are determined independently of each other. Mutations in both hosts and parasites are generated randomly with a mutation rate of 5×10^{-4} per gene per generation, which is roughly comparable to the mutation rates in eukaryotes (Rédei, 1982). Multiple mutations within the same individual are not considered.

To represent the difference between the lengths of the life-cycles of hosts and parasites, a parasite breeding phase is inserted into the middle of the grooming period, that is, after half of the attacks occurred. All parasites having survived the first half of grooming are involved in this breeding phase that takes place separately within isolated infrapopulations. Breeding chances are equal here, independently of host fitness, and growth rate is 2.5 for both parasite species.

Simulation experiments

Simulations started with generalist host and parasite species (except Experiment 4), i.e., with scores 49, 50, and 51 taken with equal probabilities for each individual at both sites. The process continued up to 300 generations or until 1 of the parasite species went extinct. Indicators, e.g., the population mean scores, were recorded in every 10th generation. A simulation run consisted of 200 replications of this process to generate a statistically evaluable amount of data. A simulation experiment included several runs varying some parameter values. The following experiments were made.

Experiment 1 was a screening experiment in which all combinations of 3, 4, 6, and 10 for u with 0.06, 0.10, 0.15, and 0.20 for w were considered, each with no, weak, and strong trade-off levels. Its aim was to provide information for the choice of parameters in the following experiments.

Experiment 2 was designed to analyze the influence of the trade-offs on some characteristics of the coevolution. All 9 possible combinations of *no, weak,* and *strong* levels for host and parasite trade-off were considered. They were analyzed for 3 combinations of u and w, namely for ($u = 4$, $w = 0.15$), ($u = 10$, $w = 0.06$), and a control, ($u = 5000$, $w = 0.0001$), representing no selection pressure. For the last 2, very strong trade-offs were also considered.

Experiment 3 was designed to explore how the results would change with increased population sizes. Host population size was increased to 200 with everything else unchanged. This experiment was carried out for ($u = 4$, $w = 0.15$), ($u = 10$, $w = 0.06$), and ($u = 5000$, $w = 0.0001$), with both trade-offs being *weak.*

Experiment 4 was aimed to mimic coevolution after a host population is invaded by 2 parasite species being already specialized at the start of the simulation. The 2 possible initial configurations for parasite specialization, i.e., specialization on the same site vs. segregation, were compared in this experiment. It was made for ($u = 10$, $w = 0.06$) and ($u = 4$, $w = 0.15$) with both trade-offs being weak. Initial specialization of parasites was represented by the same population mean scores as those experienced in the 200th generation of Experiment 2, that is, 50 and 55 for ($u = 10$, $w = 0.06$) and 47 and 62 for ($u = 4$, $w = 0.15$).

Sensitivity analysis

To determine whether the performance of the model is influenced by fixed parameters, the following sensitivity analyses were made. The number of genes was decreased to 20 (both for hosts and parasites). The intensity of infection was decreased to a (uniformly distributed) number between 15 and 20 and increased to a (uniformly distributed) number between 25 and 30. The number of attacks in grooming was decreased to 40 and increased to 60. The mutation rate was decreased to half (2.5×10^{-4}) and increased to 2-fold (10^{-3}) the original rate. The growth rate in the infrapopulation breeding of parasites was decreased to 2 and increased to 3. These analyses were carried out only for $u = 4$, $w = 0.15$ with weak trade-offs.

Computer program

The model was implemented by a computer program written in BASIC. Program length was about 500 lines. Typical simulation runs with 200 replications required 25–50 hr of computer time on a 66-MHz 486 PC. The program can be obtained from the first author.

Statistical analysis

Simulated data were analyzed with respect to the site specialization and site segregation of parasites, the persistence of coexistence, the parasite abundance, and the distribution of parasites. Because random simulation was applied, all these characteristics were random variables. Their measurement was made as follows.

For an individual, site specialization is related to the difference between its 2 scores. For a species, it is related to the difference between the population mean scores. As simulations started with generalist parasite species, the difference between the population mean scores in the 200th generation (denoted by d_{200}) was chosen to quantify the tendency toward site specialization. In the results, the estimated mean and stan-

dard deviation of d_{200} are reported, both calculated from the 200 replications in each simulation run.

Site segregation is experienced when 2 coexisting and specialized parasite species are specialized to different sites. Simulation can be used to estimate the probability of site segregation at any given time point, say at the 100th or 200th generation, by taking the proportion of those replicates in which site segregation occurs among those that show specialization. As we found that both the persistence and the degree of specialization depended considerably on model parameters, we did not use a fixed time point, rather we chose that time point in each simulation in which the empirical probability of persistence was 10%. Thus, in each simulation, the most persistent 10% of the replicates were analyzed with respect to site segregation. (Working with 200 replications, it gave a sample size of 20, which was sufficient for statistical analysis.) In most cases, the time point derived this way was between the 150th and the 300th generation. Site segregation was regarded as the dominant way of coexistence compared to specialization to the same site if the experienced probability of site segregation was significantly greater than 0.5, since (because of the assumed symmetry between the 2 sites as well as between the 2 parasite species) the 2 species have a probability of 0.5 to specialize to different sites by chance. In this analysis, parasite species were considered as specialized if d_{200} values were greater than 2 for both of them.

The persistence of coexistence was measured by the probability that parasite coexistence lasted for at least 200 generations (denoted by p_{200}). We had 2 reasons to use this measure instead of the direct measurement of the time span. First, a probability is easier to handle statistically than a time variable with an unknown distribution that even depends on other model parameters; and second, this measurement reflects better the long-term behavior of the system than the average time span. The estimation of p_{200} was based on the 200 replications in each simulation run.

For each parasite species, mean abundance was measured by the average number of parasites that survived host grooming. Parasite aggregation was quantified by the exponent k of the negative binomial distribution fitted to data. It was estimated using the maximum likelihood method of Bliss and Fisher (1953). The distribution of parasites was compared to the negative binomial distribution by Pearson's chi-square test. Comparison of proportions or probabilities was made by exact binomial test. Effects of the trade-offs were analyzed applying multifactor analysis of variance and, for the abundance and the negative binomial exponent k where the normality assumption did not hold, the Kruskal–Wallis rank test, using STATGRAPHICS 6.0.

RESULTS

Experiment 1

As this experiment was a preliminary screening to choose parameter values for further experiments, results are rather descriptive without any statistical testing at this point.

Site specialization of parasites depended strongly on the selection pressure on parasites (u) and much less on the selection pressure on hosts (w) in the domain under study. Higher selection pressure on parasites (smaller u values) as well as on hosts (higher w values) led to more pronounced site specialization, with a maximum of mean d_{200} = 20.3 (SD = 1.6) for u = 3, w = 0.20, no trade-offs.

Site segregation was the dominant way of parasite coexistence for $u < 10$ even with no trade-offs, whereas at least weak trade-offs were necessary for the site segregation to be dominant for u = 10. Site segregation did not seem to depend on the selection pressure on hosts (w) in this domain.

Persistence of coexistence was influenced strongly by the selection pressure on parasites (u), namely higher selection pressure (smaller u values) resulted in longer persistence. It was, however, in interaction with the trade-offs, namely for low selection pressure (large u) strong trade-offs provided the longest persistence, whereas for higher selection pressure (smaller u) weak trade-offs did. The influence of the selection pressure on hosts (w) was weak, w = 0.15 provided the longest persistence. Values of p_{200} varied between 4% (for u = 10, w = 0.20, no trade-offs) and 59% (for u = 3, w = 0.15, weak trade-offs).

Mean abundance of parasites was affected by all of u, w, and the trade-offs. Higher selection pressure on parasites (smaller u values) as well as lower selection pressure on hosts (higher w values) yielded in an increase of parasite abundance. Stronger trade-offs also resulted in higher mean abundance.

On the basis of these results, 2 (u, w) combinations were chosen for further analysis, such as u = 10, w = 0.06, representing low selection pressure and u = 4, w = 0.15, representing high selection pressure. An additional combination, u = 5,000, w = 0.0001, representing no selection pressure, was also introduced as a control.

Experiment 2

Site specialization of parasites could not be observed at no selection pressure, mean d_{200} varied between 0.6 and 0.9 (SD = 0.7–0.9), with no significant trade-off effects ($P > 0.10$). At low selection pressure, parasite trade-off affected specialization positively ($P < 0.001$, d_{200} = 4.3, 5.7, 6.9, SD = 1.4), whereas host trade-off affected it negatively (P = 0.002, d_{200} = 5.9, 5.5, 5.1, SD = 1.4). Similarly, at high selection pressure, parasite trade-off had a positive effect on specialization ($P < 0.001$, d_{200} = 11.0, 13.6, 15.0, SD = 1.3), whereas host trade-off had a negative effect on it ($P < 0.001$, d_{200} = 17.7, 14.3, 10.2, SD = 1.3).

Site segregation of parasites could not be analyzed at no selection pressure because no parasite specialization occurred. At low selection pressure, site segregation was found to be the dominant way of parasite coexistence for all trade-off combinations ($P < 0.05$) except for no trade-offs, where neither segregation nor specialization to the same site was dominant. At high selection pressure, segregation was dominant for all trade-off combinations ($P < 0.001$). An additional analysis was made with u = 15, w = 0.04, which is between no and low selection pressure, and with no, weak, strong, and very strong trade-offs. Site segregation proved to be dominant for strong (P = 0.041) and for very strong (P = 0.008) trade-offs. Neither segregation nor specialization to the same site was dominant in the case of no and weak trade-offs.

Persistence of coexistence, measured by p_{200}, varied between 14% and 22% (mean value = 19%) at no selection pressure, without any significant effect of the trade-offs ($P > 0.10$). At low selection pressure, p_{200} varied between 9% and 15% (mean value = 11%), again without any significant trade-off effect ($P > 0.10$). At high selection pressure p_{200} varied as 7%, 34%, 27% according to no, weak, and strong host trade-off levels (highly significant association, $P < 0.001$). Parasite trade-off had no significant effect ($P > 0.10$) on the persistence of coexistence.

In analyzing the effects of trade-offs on parasite abundance and on the negative binomial exponent k, medians were used instead of means and the Kruskal–Wallis rank test was applied instead of ANOVA because both variables followed a rather skewed distribution. Because it is typical in this model under site segregation that there is a frequent and a rare parasite species (see Discussion), to check whether trade-offs affect them

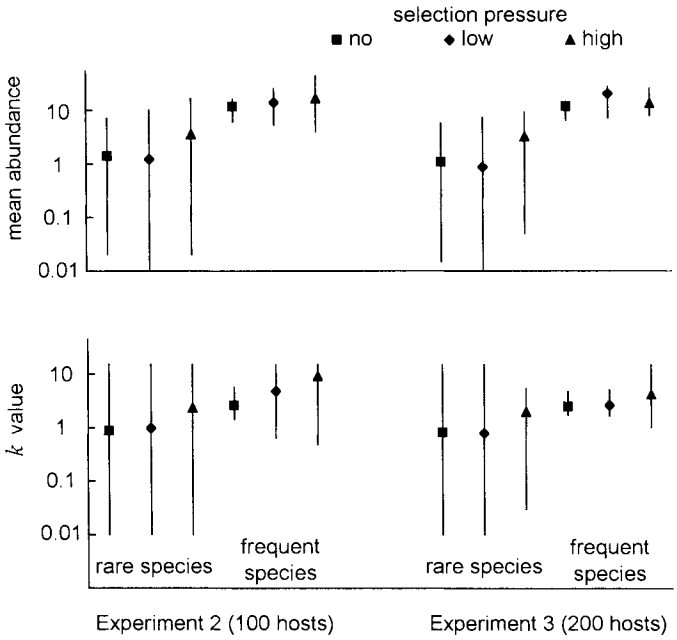

FIGURE 4. Minimum, maximum, and median values of mean abundance and the negative binomial exponent k (200th generation).

differently these analyses were made for the frequent and the rare species separately. Results show that trade-offs affect both of them in the same way. The dependence of parasite abundance and k (both measured in the 200th generation) on the selection pressure and the trade-offs is summarized in Figure 4 and Table I.

The fit of the negative binomial model to the simulated data was evaluated at no, low, and high selection pressure with no and weak trade-offs. In each case, chi-square tests were made for 10 samples of size 100. The negative binomial model was found to fit well to data ($P > 0.05$) for 50–90% of the samples.

Experiment 3

Enlarging host population size increased the persistence but in other respects did not bring changes in the results. At no selection pressure p_{200} was 33% and no specialization occurred ($d_{200} = 0.6$, SD = 0.8). Segregation could not be analyzed because of the lack of specialization. At low selection pressure, p_{200} was 30%, parasite specialization could be observed with $d_{200} = 6.2$ (SD = 0.9), and site segregation emerged as the dominant way of parasite coexistence ($P < 0.001$). At high selection pressure, p_{200} was 79%, parasite specialization could be observed with $d_{200} = 15.3$ (SD = 0.9), and site segregation was dominant again ($P < 0.001$). Mean abundance of parasites and average values of the negative binomial exponent k are presented in Figure 4. Fit of the negative binomial model was tested for 10 samples of size 100 in each case. The negative binomial model was found to fit well to data ($P > 0.05$) for 60–100% of the samples.

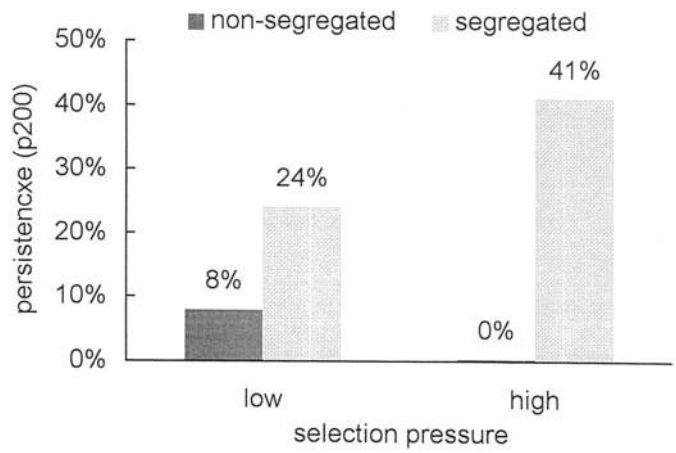

FIGURE 5. Persistence measured by p_{200} in Experiment 4.

Experiment 4

Persistence of coexistence was significantly greater ($P < 0.001$) under site segregation at low as well as at high selection pressure (Fig. 5). Site segregation clearly increased the stability of coexistence of the 2 parasite species. At low selection pressure, the degree of site specialization, d_{200}, was 9 (SD = 1.0) under segregation and 11 (SD = 1.3) when parasites were specialized on the same site (difference is significant at $P < 0.001$). At high selection pressure, d_{200} was 25 (SD = 1.2) under segregation (not available under specialization to the same site, because no replicates survived till the 200th generation). Parasite abundance as well as k values varied in the same range as in the previous experiments (median of the mean abundance:

TABLE I. Effects of the trade-offs on the quantity and distribution of parasites (Experiment 2, 200th generation). For all significant effects, stronger trade-off is associated with higher abundance and less aggregation (higher k).

Selection pressure	Rare parasite species*		Frequent parasite species*†	
	Mean abundance	k‡	Mean abundance	k‡
No	—	—	—	—
Low	—	—	$t^{(h)}$ ($P = 0.003$) $t^{(p)}$ ($P = 0.001$)	$t^{(h)}$ ($P < 0.001$)§ $t^{(p)}$ ($P = 0.001$)
High	$t^{(h)}$ ($P < 0.001$)§	$t^{(h)}$ ($P < 0.001$)§	$t^{(h)}$ ($P < 0.001$)§ $t^{(p)}$ ($P < 0.001$)	$t^{(h)}$ ($P < 0.001$)§ $t^{(p)}$ ($P < 0.001$)

* $t^{(h)}$ = host trade-off.
† $t^{(p)}$ = parasite trade-off.
‡ Dispersion index of negative binomial model.
§ Effect remains significant ($P < 0.05$) even if strong trade-offs are excluded.

from 0.63 to 18.45; median of k: from 1 to 10.08). The majority (80–90%) of parasite distributions exhibited a good fit to the negative binomial model.

Sensitivity analysis

In general, whereas persistence and specificity showed some variability, site segregation remained highly dominant ($P < 0.001$) and parasite distribution remained more or less aggregated (the median of k varied between 1.8 and 7.4) throughout these analyses. Decreasing the number of genes to 20 reduced both the persistence (p_{200} = 30%) and the specificity (d_{200} = 8.1, SD = 0.6). Decreasing the intensity of infection reduced the persistence to p_{200} = 15% and increased the specificity (d_{200} = 16.6, SD = 1.4), whereas effects of its increasing were the opposite (p_{200} = 41%, d_{200} = 11.8, SD = 1.1). Decreasing the number of attacks in grooming decreased both the persistence (p_{200} = 23%) and the specificity (d_{200} = 10.8, SD = 1.1). Its increasing augmented the persistence (p_{200} = 38%) and increased the specificity (d_{200} = 17.3, SD = 1.4). Decreasing the mutation rate decreased both the persistence (p_{200} = 17%) and the specificity (d_{200} = 11.8, SD = 1.1), whereas its increasing had the opposite effect (p_{200} = 63%, d_{200} = 18.2, SD = 1.3). Decreasing the growth rate in the infrapopulation breeding of parasites decreased the persistence (p_{200} = 23%), whereas its increasing had no effect on it (p_{200} = 35%). Specificity was not influenced by changing the growth rate (d_{200} = 14.5–14.8, SD = 1.4).

DISCUSSION

Model on host defense regulated parasite assemblage

Specialization toward enemy-free space is a well known hypothesis to explain responses of prey populations facing intense predation (Berdegue et al., 1996) or host populations under parasitoid pressure (Holt and Lawton, 1993). It has already been claimed to yield apparent competition (Holt and Lawton, 1993) and to induce host specificity in phytophagous arthropods (Bernays and Graham, 1988). Our present model of a host defense regulated parasite assemblage is basically an interpretation of this hypothesis for the case of 2 coexisting ectoparasite species facing host grooming, which acts as predation. An advantage of the proposed model is that it allows one to investigate microevolutionary processes that are impossible to study experimentally in the field because of the long time period required and offers a possibility to exclude the influence of other potential factors, e.g., resource limitation. Though this model mimics a small and unstructured host population, analyzing its behavior may lead to more realistic models based on a host metapopulation structure.

A considerable proportion of our simulation runs ended by the extinction of 1 parasite species, which suggests that high extinction rates are characteristic of the process. This view is also supported by early arguments of Clay (1949) who regarded extinction of colonizing louse populations as a common alternative to site specialization. An advantage of individual-based models in general, as compared to traditional differential equation models, is that they tend to treat extinction in a more realistic manner (Uchmanski and Grimm, 1996). Extinction rates during the emergence of site specialization are undetectable when the outcome of the process, i.e., site specificity of surviving species, is studied empirically.

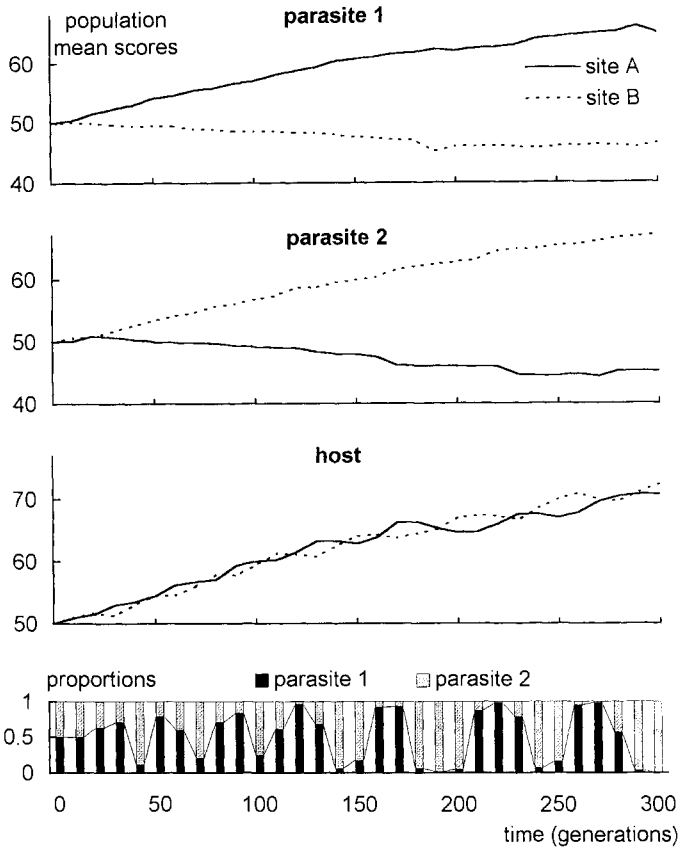

FIGURE 6. "Arms race" between the simulated host and ectoparasite species (high selection pressure, weak trade-offs). The 2 parasite species specialize toward site-specific evasive abilities at different sites, whereas the host species evolves to improve its defensive abilities at both sites. However, hosts show alternating differences in defensive abilities between the 2 sites, which coincide with cyclic changes in the proportions of the 2 species.

When both virtual parasite species survived, they engaged in a coevolutionary "arms race" with the host population and with each other (Fig. 6). Segregation toward different sites as refugia apparently caused the host population to reduce its speed of specialization, and this was paralleled by an increased stability of parasite species coexistence. System complexity increased during these simulations in 2 senses. First, the frequency distribution of parasites changed from a uniform distribution to an aggregated one and, second, generalist parasite species developed site specificities and tended to segregate their specificities toward different sites. Thus, a macroevolutionary trade-off emerged between the 2 parasite species, i.e., a trade-off between 2 traits at the species level when both traits are fixed within species (Stearns, 1992). The spontaneous increase of system complexity is a known feature of some models in evolutionary biology (Dawkins, 1986).

The influence of selection pressures and trade-offs on parasite coexistence

The present study focused on 3 major aspects of the coexistence of the 2 ectoparasite species, i.e., site specialization of generalist species, site segregation of specialized species, and finally the persistence of this assemblage. Site specialization

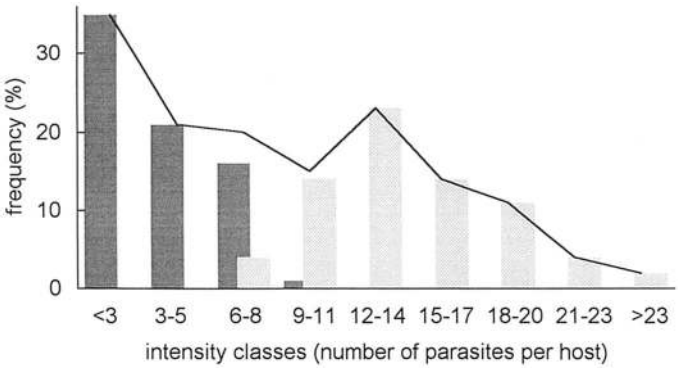

FIGURE 7. The frequency distribution of a particular parasite species (200th generation, high selection pressure, weak trade-offs), calculated from 72 simulation replicates. The resulted bimodal distribution (line) is a mixture of 2 unimodal components, one representing those replicates in which the parasite species was rare (dark columns) and another representing those in which it was frequent (light columns).

was positively influenced by the selection pressure exerted on parasites. The degree of parasite trade-off affected it positively, whereas host trade-off exhibited an opposite effect.

The emerging site specificities of 2 coexisting ectoparasite species may exhibit a positive interaction (a tendency to specialize to the same site), a negative interaction (a tendency to segregate), or no interaction (independent specialization). Significant positive interactions did not occur within the domain of the present study. Significant negative interactions were found for high selection pressure independently of the trade-offs and for low selection pressure with strong trade-offs. For low selection pressure with no or weak trade-offs, no interaction could be proven.

In particular, the results of Experiment 4 support the view that site segregation stabilizes the coexistence of the 2 ectoparasite species in the model. This finding is in full accordance with early observational evidence given by Clay (1949), who argued that site segregation might increase parasite species richness.

Abundance and frequency distribution of parasites

Simulations resulted in parasite abundance values comparable to those of louse species of passerine hosts (Rózsa, 1997). Under site segregation, it was typical in the model that there was a frequent and a rare parasite species. In the long run, the 2 parasite species alternated being the frequent and the rare one, with short transition phases between these 2 states. These cycles were related to the alternating differences in host defensive abilities between the 2 sites (Fig. 6). Because simulations started with generalist parasites, a parasite species had equal chances to become frequent or rare at a given time point. Thus parasite abundance, if estimated from several simulation replicates, exhibited a bimodal distribution as shown in Figure 7. Considering a single replicate, 1 of the component distributions was obtained, depending on whether the parasite species happened to be the frequent or the rare one.

The medians of the negative binomial exponent k of the simulated parasite populations were greater than most of those experienced in case studies on avian lice (see Rékási et al. [1997] for a recent review), indicating that aggregation tended to be relatively weak in our model. This was presumably due to some model features, namely the panmictic structure of the host population and the horizontal transmission of parasites assuming uniform infection. Some population studies on lice of colonial birds (Fowler and Miller, 1984; Fowler and Shaw, 1989) or polygynous species (Stewart et al., 1996) documented aggregation indices roughly comparable with the present ones. Both colonial breeding (Rózsa et al., 1996) and polygyny are likely to facilitate horizontal transmission of lice.

Parasite distribution interacts with parasite abundance in this model. Highly aggregated distributions cannot emerge in the case of high parasite abundance because abundance is limited (taking both species together, the maximal number of parasites per host after grooming is 63, i.e., the maximum intensity of infection, 25, multiplied by the growth rate in the infrapopulation parasite breeding, 2.5). As strong trade-offs resulted in particularly high parasite abundance, analyses on aggregation were repeated after excluding this trade-off level. Some changes in the results are summarized in Table I.

Improving our knowledge of many quantitative aspects of louse life histories, such as offspring numbers, generation times, and mortality rates, could allow us to use more realistic estimates of these measures in the future.

Scale and generality

It is important to recognize that interactions among coexisting parasite species can occur on different temporal and spatial scales. The present model covers interactions on the level of parasite infrapopulations because considerable amount of empirical evidence suggests the lack of resource limitation at this particular level for a number of ectoparasite taxa. We have not addressed the consequences of increasing the scale to the community level, so potential effects of many other factors, such as partially different host specificities, are not discussed here. The time scale considered in the present study is a period of a few hundred host generations. Presuming that mutation rates and selection pressures are high, this time scale allows us to examine microevolutionary processes by simulation. On the other hand, factors acting on a much shorter time scale (like epidemics) or on a much longer one (like speciation) were not considered.

Because the processes illustrated in our model take place during a considerably long period of time, it seems to be rather hard to test the present results in the field. In general, our results predict that proportions of coexisting parasite species undergo periodic changes (which are much slower than fluctuations caused by epidemics), and that these changes coincide with microevolutionary changes in the hosts' time and energy allocation among different defense mechanisms (Fig. 6). Furthermore, one could also test whether avian species that are capable of both preening and scratching harbor more diverse ectoparasite assemblages than those that either cannot effectively scratch (like swifts) or cannot effectively preen themselves (like long-beaked birds).

Our present results coincide with recent concerns that many parasite communities do not possess resource limitations within the host individuals. Rohde (1977, 1979, 1991) repeatedly emphasized that site specificity in monogeneans is not caused by competition for limited resources, whereas Lotz et al. (1995)

described and modeled recruitment-driven parasite communities. There seems to be a shift in parasite ecology from traditional resource competition models to models of low density populations living in resource-rich habitats. We do feel that generalized versions of models on host defense-regulated parasite assemblages might probably be applied to interpret the coexistence patterns of many other parasites and pathogens, such as helminths, bacteria or even viruses, and that this is a challenging new field open for innovative speculation.

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