Factors influencing the composition of mixed populations of a hemiclonal hybrid and its sexual host

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Abstract

Hemiclonal/hybridogenetic hybrids combine demographic superiority of asexuals and genetic diversity of sexuals, but their need for backcrossing with a parental species tightly couples them with this sexual host. How can systems like this persist in ecological and evolutionary time? Two discrete-time mathematical models describing the complex life cycle and mating system of hybridogenetic waterfrogs (*Rana esculenta*) identified four factors and their interactions as important. Although female mating preferences, in combination with differences in fecundity, determine species coexistence, differences in larval competitiveness seem to be more important for the hybrid's actual frequency. However, coexistence is possible even when host and hybrid are equally fecund and competitive. Dispersal and competition interact in their influence on species composition, but ecological and reproductive dispersal has opposing effects. In ecological terms our results explain the remarkable stability of observed species ratios over time within natural hybridogenetic populations, and indicate why the species composition can vary so widely between localities. In evolutionary terms they explain the old age of these and other hybridogenetic systems. They also suggest interesting consequences for other tightly coupled systems.

Introduction

Species coexistence is of great and continued ecological and evolutionary interest. Numerous studies are devoted to understanding the coexistence and coevolution of hosts with their parasites (e.g. Clayton, 1997), the competitiveness and long-term persistence of asexual organisms in a sexual world (e.g. Maynard Smith, 1978) and the ecological and evolutionary importance of interspecific hybrids (e.g. Arnold, 1997). Hybridogenetic systems combine aspects of all these examples. Hybridogens, which originally derived from interspecific hybridization (Vrijenhoek, 1989), premeiotically exclude one parental genome and transmit the nonrecombined other genome clonally to the gametes. For producing

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viable offspring, hybrids have to regain the excluded genome by backcrossing with the appropriate parental species (Schultz, 1969). Therefore, coexistence is indispensable for the sexually parasitic hybrid. Identifying conditions for stable coexistence and understanding the dynamics of these admittedly peculiar systems may yield the same kind of insight that unusual diseases have provided in unravelling the physiology of healthy organisms (Vrijenhoek, 1989).

With one sexually and one clonally inherited set of chromosomes, hybridogenetic (=hemiclonal) organisms lie between the extremes of asexual and sexual reproduction. Unisexual stick-insects (*Bacillus rossius-grandii*) and fish (*Poeciliopsis monacha-lucida*, *Tropidophoxinellus alburnoides*) approach the asexual end and bisexual waterfrogs (*Rana esculenta*) the sexual end (Dawley & Bogart, 1989; Bullini, 1994; Carmona *et al.*, 1997). Hybridogens combine, to some extent, the demographic superiority of asexuals, the genetic diversity of sexuals

and the high levels of somatic heterozygosity of hybrids (hybrid vigour or 'heterosis', Bullini, 1994). The latter often implies faster growth, larger final size and/or higher disease resistance. As an obligate sexual parasite, however, the hybrid is constrained in two ways. Firstly, it cannot reproduce too successfully because it risks driving itself extinct by outcompeting its host demographically. Secondly, reproductively active hybrids have to co-occur with the appropriate parental host(s) in the same habitat at least during reproduction. This also implies (partial) niche overlap of and competition between the offspring of both 'species', which is in the interest of neither of them. Moreover, as backcrosses usually exclusively produce hybrids the parental individuals involved lose all or part of their yearly reproductive output – assuming non-negligible fitness consequences for parental males in unisexual systems (Kawecki, 1988). The resulting interspecific conflict over mating should select for a high degree of assortative mating within the parental species. Hybridogenesis therefore not only implies competition for mates (or gametes) and limited resources, but also tightly couples population dynamics and evolution of sexual hosts and hybrids, as is typical for most host-parasite systems.

This study aims at understanding the ecological and evolutionary stability of hemiclonal mating systems. Why and how have these systems persisted, for example over 200 000 *Poeciliopsis* generations? (Vrijenhoek, 1993) Why does the species composition in some systems vary so widely between localities whereas remaining remarkably stable over time within them? (e.g. waterfrogs, Berger, 1977; *Poeciliopsis*, Moore, 1976) We address these questions here using mathematical models for organisms with overlapping generations, discrete breeding seasons, delayed maturation and a complex three-stage life cycle (cf. Hellriegel, 2000). In their details, the models describe the life cycle and mating system of the waterfrog complex (see below). This hybridogenetic system has three especially interesting features. The consequences of hemiclonal reproduction can be examined uncoupled from unisexuality. Demographic hybrid superiority varies as a result of different sex-ratios, and mating decisions result in easily detectable all-or-nothing fitness consequences. Based on results from experiments, field studies (see below) and mathematical models (e.g. Som *et al.*, 2000) we chose to investigate the influence of four factors on the dynamics and composition of mixed hybrid–host populations. In addition to (1) assortative mating and its interaction with (2) interspecific differences in fecundity which are considered in a recent model (Som *et al.*, 2000), we accounted for (3) interspecific differences in tadpole performance and for (4) dispersal between two breeding sites of different quality. In order to understand the relative influence of these four factors our models are subjected to analytical (see Appendix) and systematic numerical investigations. Although these models are adapted to the waterfrog complex, we argue that our results are also relevant to other tightly coupled systems.

Materials and methods

The hybridogenetic waterfog complex

The waterfrog *R. esculenta* (E) is originally a hybrid between the poolfrog *R. ridibunda* (R) and the lakefrog *R. lessonae* (L) (Berger, 1977). Mixed *R. lessonae*/*R. esculenta* (L/E) populations represent the most widespread system (Graf & Polls Pelaz, 1989). Their *R. lessonae* proportion varies between 5 and 95% (Blankenhorn, 1974; Berger, 1977). In a L/E system, hybrids of both sexes exclude the L-genome premeiotically, transmit the R-genome clonally and backcross with *R. lessonae* to regain the L-genome. Heterotypic matings produce hybrid offspring in a 1 : 1 sex ratio ($E^f \times L^m$) or daughters only ($L^f \times E^m$) (Graf & Polls Pelaz, 1989). This yields female-biased hybrid sex ratios varying among populations from 1 : 1.3 to 1 : 4 (Blankenhorn, 1974; Holenweg, 1999; G. Abt, unpublished observations). Homotypic matings result in *R. lessonae* ($L^f \times L^m$) or nonviable *R. ridibunda* tadpoles ($E^f \times E^m$) (Berger, 1977). Mating decisions of both species therefore have all-or-nothing fitness consequences (cf. Fig. 1b).

Although males mate repeatedly and exert no choice, females of both species choose *R. lessonae* males in 70% of binary choice experiments (Abt & Reyer, 1993; Engeler, 1994; Roesli & Reyer, 2000). Female preference can be overrun by male-male competition (Bergen *et al.*, 1997), but may be partly restored by cryptic choice through clutch size adjustment (Reyer *et al.*, 1999). Usually, *R. lessonae* clutches (c_L) are smaller, with fecundity ratios ($r_c = c_E/c_L$) ranging from 1.3 (G. Abt, unpublished observations) to 3.3 (Graf & Polls Pelaz, 1989). Interspecific larval competition seems to be asymmetric. Hybrid tadpoles are much less affected by experimentally increased densities of conspecific and heterospecific competitors (Semlitsch, 1993). Information on juvenile dispersal is lacking, but adult dispersal is species- and sex-specific (Holenweg, 1999).

The models

The two discrete-time models describe waterfrog population dynamics in an L/E system. Model A investigates the influence of female mating preferences, relative fecundities, and interspecific larval competition on population dynamics in an isolated habitat. Model B extends model A to study the influence of species- and habitat-specific adult dispersal between two different breeding sites. Dispersal is assumed to be density-independent and to entail no additional mortality. Both models assume the usual 1 : 1 sex ratio for *R. lessonae* ($L_A^m = L_A^f = 1/2\ L_A$), whereas *R. esculenta* males and females are modelled separately to track the
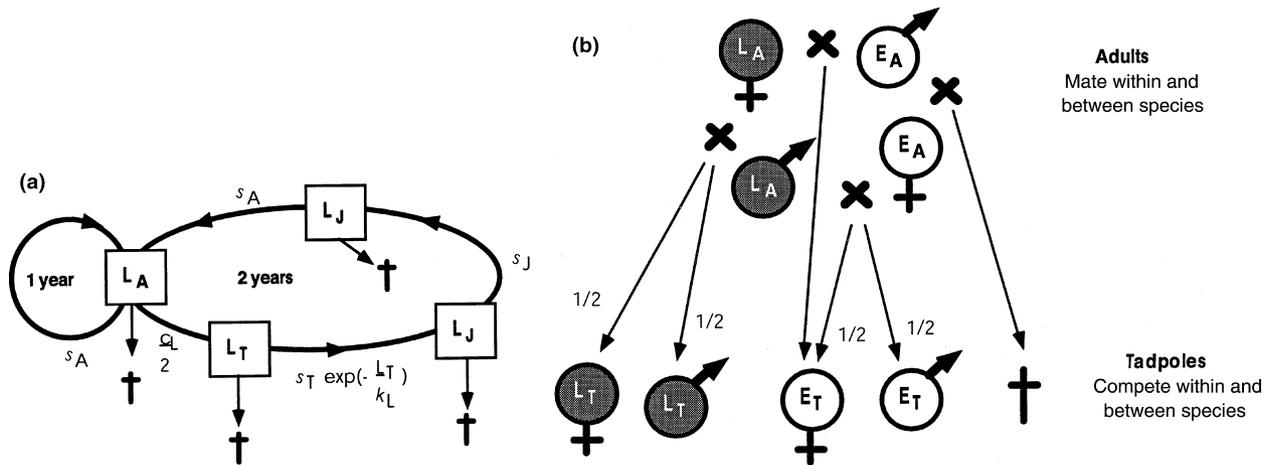
Fig. 1 (a) Simplified frog life cycle as described by the models. It consists of two major parts: the subadult stage from egg deposition until sexual maturity and the adult stage. Surviving adult frogs (s_A L_A) breed yearly. The resulting tadpoles (L_T) compete for limited resources ($\exp(-L_T/k_L)$) and develop into juveniles (L_J). Juveniles surviving their first and second year of life (s_J s_A L_J) mature and join the adult population. (b) Mating system of waterfrogs in the L/E system. While *R. lessonae* (L_A) reproduces normally, the hemiclonal hybrid *R. esculenta* (E_A) has to backcross with its sexual host to reproduce successfully. Host and hybrid dynamics are tightly coupled by interspecific matings and interspecific larval competition. The factors 1/2 indicate a 1 : 1 offspring sex ratio.

female bias ($E_A^m \le E_A^f$). All parameters are defined in Table 1.

The models are based on a simplified life cycle, which for *R. lessonae* is described by difference equation (1) (cf. Fig. 1a). The census is taken at the start of the yearly breeding season (t). The breeding population for the next year ($L_A(t + 1)$) consists of surviving adults (s_A $L_A(t)$) and of subadults reaching maturity. As sexual maturation of both sexes takes about two years (cf. Berger & Uzzell, 1980) the second term dates two time steps back ($t - 1$).

Table 1 List of functions and parameters (with typical values).

$L_{A(i)}$	Adults of the sexual host *R. lessonae* (in habitat *i*) [initial size = 50 males + 50 females]
$E_{A(i)}$	Adults of the hybrid *R. esculenta* (in habitat *i*) [initial size = 50 males + 50 females]
Species dependent	
m_{LL}	Preference of L-females for L-males
m_{EL}	Preference of E-females for L-males
M_L, M_E	Mating functions = male-frequency dependent proportions of females that mate
c_L, c_E	Number of L- and E-hatchlings per female and season
$r_c = c_E/c_L$	Clutch size ratio ($r_c = 1.3 = 1100/825$) (G. Abt, unpublished)
k_L, k_E	Strength of density effects on survival of L- and E-tadpoles ($k_E/k_L = 1.5 = 7500/5000$)
μ_L, μ_E	Dispersing fractions of L- and E-adults
Species independent	
s_T, s_J	Surviving fractions of tadpoles and first-year juveniles ($s_T = 0.3, s_J = 0.4$)
s_A	Surviving fractions of second-year juveniles and adults ($s_A = 0.3$)

$$L_A(t + 1) = s_A L_A(t) + s_A s_J s_T c_L$$
$$\times \exp\left[-\frac{s_T c_L}{2k_L}L_A(t - 1)\right]\frac{L_A(t - 1)}{2} \quad (1)$$

Although males may mate with several females, every female ($L_A^f = L_A/2$) is assumed to lay eggs only once a year. The species-specific fecundity parameter (c_L) incorporates mean clutch size per female and season, fertilization rate, and zygote survival. The resulting tadpoles (L_T) metamorphose and grow into first-year juveniles (L_J). Larval survival up to the completion of metamorphoses is assumed to have a density-independent component (s_T) and a density-dependent component. Following Wilbur (1996) we chose an exponential form of density-dependence (cf. Hellriegel, 2000). The strength of larval competition is determined by the species-specific parameter k_L. A proportion of first- and second-year juveniles survives (s_J and s_A, respectively) and joins the breeding population in the third year.

Models A and B assume this simplified life cycle for both species. For want of empirical data, we assume that both sexes and both species have identical stage-specific density-independent survival rates (s_T, s_J, s_A, cf. Table 1). The reproductive dependence of the hybrid couples the resulting difference equations through interspecific matings and interspecific larval competition. The latter implies that larval survival depends on the larval densities of both species (e.g. for *R. lessonae* $\exp[-(L_T + E_T^f + E_T^m)/k_L]$, eqn (3a)). Interspecific mating functions describe the probabilities that a female mates with an E- or L-male. These functions (M_L, M_E, see below) depend on the preferences of L- and E-females for L-males (m_{LL}, m_{EL}) and on the relative frequency of the

two male types (cf. Som *et al.*, 2000). Female preferences can range from total avoidance ($=0$) through random choice ($=1/2$) to total preference ($=1$). The proportion of L-females preferring and therefore mating with their own males is described by

$$M_L(t) = \frac{m_{LL}L_A(t)}{m_{LL}L_A(t) + 2(1 - m_{LL})E_A^m(t)},$$

whereas the proportion of L-females mating with E-males is

$$1 - M_L(t) = \frac{2(1 - m_{LL})E_A^m(t)}{m_{LL}L_A(t) + 2(1 - m_{LL})E_A^m(t)}.$$

Because of the $1:1$ sex ratio, a total preference of L-females for their own males ($m_{LL} = 1$) implies that all L-females reproduce successfully ($M_L = 1$). The same cannot be true for E-females showing a total preference for L-males ($m_{EL} = 1$). Their reproduction must still be proportional to the frequency of L-males in all males ($M_E = L_A^m/[L_A^m + E_A^m]$). Hybrid matings therefore depend on L-male frequency in a slightly different way than host matings. The proportion of E-females preferring and mating with L-males is given by

$$M_E(t) = \frac{m_{EL}L_A(t)}{L_A(t) + 2E_A^m(t)}$$

For $0 < m_{EL} < m_{LL}$ the proportion of E-females mating with L-males is smaller than that of L-females ($M_E < M_L$) and M_L increases faster than M_E with increasing frequency of L-males. With the reverse relation between m_{EL} and m_{LL} the two mating functions (M_E, M_L) can intersect.

Model A: Isolated habitat without dispersal

To ease accessibility we give a separate equation for each life stage although only juveniles and adults are present at each census.

(1) R. lessonae *subpopulation*

$$L_T(t) = s_T c_L \frac{m_{LL}L_A(t)}{m_{LL}L_A(t) + 2(1 - m_{LL})E_A^m(t)} \frac{L_A(t)}{2} \quad \text{tadpoles}$$
(2a)

$$L_J(t + 1) = s_J \exp\left[-\frac{L_T(t) + E_T^f(t) + E_T^m(t)}{k_L}\right] L_T(t)$$
(3a)
1st-year juveniles

$$L_A(t + 1) = s_A(L_A(t) + L_J(t)) \quad \text{adults}$$
(4a)

(2) R. esculenta *subpopulation*

$$E_T^f(t) = \frac{s_T c_E}{2} \frac{m_{EL}L_A(t)}{L_A(t) + 2E_A^m(t)} E_A^f(t)$$
$$+ s_T c_L \frac{2(1 - m_{LL})E_A^m(t)}{m_{LL}L_A(t) + 2(1 - m_{LL})E_A^m(t)} \frac{L_A(t)}{2}$$
tadpoles
(5a)

$$E_T^m(t) = \frac{s_T c_E}{2} \frac{m_{EL}L_A(t)}{L_A(t) + 2E_A^m(t)} E_A^f(t)$$
(6a)

$$E_J^f(t + 1) = s_J \exp\left[-\frac{L_T(t) + E_T^f(t) + E_T^m(t)}{k_E}\right] E_T^f(t)$$
(7a)
1st-year juveniles

$$E_J^m(t + 1) = s_J \exp\left[-\frac{L_T(t) + E_T^f(t) + E_T^m(t)}{k_E}\right] E_T^m(t)$$
(8a)

$$E_A^f(t + 1) = s_A(E_A^f(t) + E_J^f(t)) \quad \text{adults}$$
(9a)

$$E_A^m(t + 1) = s_A(E_A^m(t) + E_J^m(t))$$
(10a)

As a result of delayed maturation, previous year juveniles are added to the adult population (e.g. $L_J(t)$ not $L_J(t + 1)$ in eqn (3a)).

Model B: Two habitats connected by dispersal

In each generation, a constant species-specific fraction of the adult population leaves habitat i for habitat j (μ_{Li}, μ_{Ei}, $i,j = 1,2$ and $i \neq j$). For incorporating dispersal, eqns (2a), (3a) and (5a)–(8a) are extended by the additional index i, indicating tadpole, juvenile and adult numbers in the two habitats (e.g. for *R. lessonae* L_{Ti}, L_{Ji}, L_{Ai}, $i = 1,2$) with their site- and species-specific parameters determining the strength of larval competition (k_{Li}, k_{Ei}).

(1) R. lessonae *subpopulation*
Equation (4a) is replaced by

$$L_{Ai}(t + 1) = s_A\left[(1 - \mu_{Li})L_{Ai}(t) + \mu_{Lj}L_{Aj}(t) + L_{Ji}(t)\right].$$
adults
(4b)

(2) R. esculenta *subpopulation*

Equations (8a) and (9a) are replaced by

$$E_{Ai}^f(t + 1) = s_A\left[(1 - \mu_{Ei})E_{Ai}^f(t) + \mu_{Ej}E_{Aj}^f(t) + E_{Ji}^f(t)\right] \quad \text{adults}$$
(9b)

$$E_{Ai}^m(t + 1) = s_A\left[(1 - \mu_{Ei})E_{Ai}^m(t) + \mu_{Ej}E_{Aj}^m(t) + E_{Ji}^m(t)\right]$$
(10b)

Numerical solutions (Figs 2–5) were obtained with the software package RAMSES2.2 (Fischlin, 1991). Analytical results for a rescaled model version are presented in the Appendix.

Results

Isolated habitat without dispersal (model A)

Pure populations of the sexual host *R. lessonae* can reach a nonzero equilibrium size of

$$L_A^* = \frac{2k_L}{s_T c_L} \ln\left[\frac{s_A s_J s_T c_L}{2(1 - s_A)}\right].$$
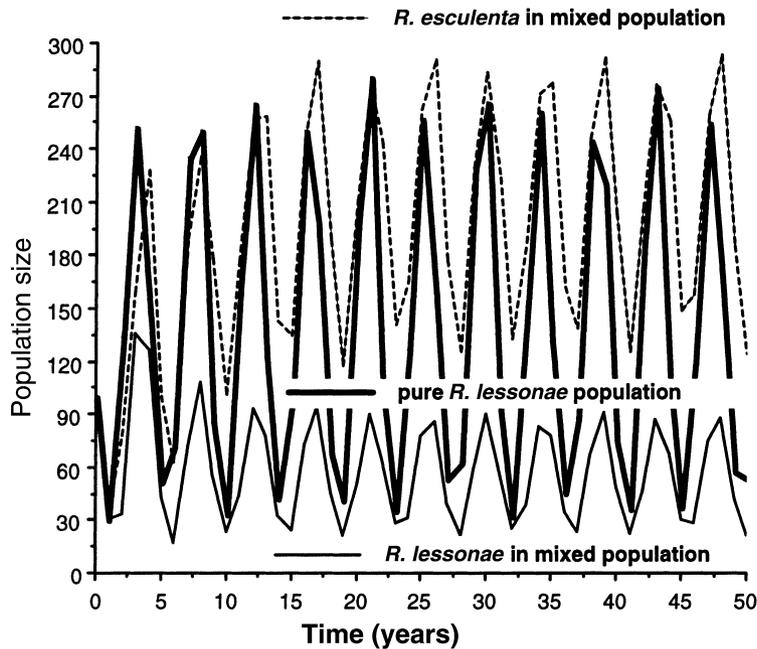
Fig. 2 Growth curves for *R. lessonae* when alone and when *R. esculenta* is also present. Here, the presence of hybrids lowers the host's mean population size and the height of its fluctuations. In the mixed population females of both species show nearly total preferences for *R. lessonae* males ($m_{LL} = m_{EL} = 0.95$); the values for the other parameters are given in Table 1.

The condition (A2) for this equilibrium to be stable (see Appendix) is easily fulfilled for the parameter values used here ($0.0198 < s_A$ or $2.34 < R_L$, see Table 1). Under the same condition the zero equilibrium is unstable so that the host can re-establish itself after extinction. Whether the hybrid *R. esculenta* can invade a host population which is at its non-zero equilibrium, depends on all survival rates, host clutch size, the fecundity ratio, the preference of hybrid females, and interspecific larval competition (cf. inequality (A4) in Appendix). If host and hybrid larvae are competitively equal, the invasion condition reduces to $1 < r_c m_{EL}$. That is, if hybrid females show a high preference for host males, hemiclonal hybrids can be much less than twice as fecund as their sexual hosts (cf. Maynard Smith, 1978) and still invade (e.g. for $m_{EL} = 0.7$, $r_c > 1.43$). Taken together these results imply that after extinction a new two-species system can arise by re-establishment of the host and subsequent invasion of the hybrid.

For the parameter values chosen here (see Table 1), the population size of *R. lessonae* alone fluctuates (Fig. 2) as observed in nature (Sjögren, 1991). When coexistence occurs, the hybrid's presence either slightly to moderately reduces the amplitude of the fluctuations in host population size (Fig. 2) or both species reach an equilibrium (stabilization). Whether the hybrid stabilizes the system dynamics and whether mixed populations are dominated by one species (defined here as 'contributing more than 60%') depends on all four factors of interest which we will further consider in the following sections.

Female preferences for host males

Mixed populations only occur if hybrid females and host males mate ($m_{EL} \neq 0$). Despite its demographic importance, the reverse mating combination ($L^f \times E^m$) alone cannot assure hybrid persistence. Hybrids go extinct because no further hybrid males are produced (cf. Fig. 1b).

Host and hybrid can coexist (grey area, Fig. 3a) even when they are equally fecund and competitive ($c_L = c_E$, $k_L = k_E$). The species ratio then depends on the female preferences only and the proportion of hosts is

$$\frac{L_A^*}{L_A^* + E_A^*} = \frac{2m_{EL} - m_{LL}[m_{LL} - m_{EL}(3 - m_{LL})]}{m_{LL}[1 - m_{LL} - m_{EL}(2 - m_{LL})]}.$$

However, pure host populations (black area, Fig. 3a) are more than twice as frequent as mixed populations

Fig. 3 Influence of fecundity ratio ($r_c = c_E/c_L$) and larval competitive abilities (k_L, k_E) on the percentage of *R. lessonae* (L) in an isolated mixed L/E population, for different combinations of female preferences for L-males (m_{LL}, m_{EL}). (a), (b) $k_L = k_E = 5000$. (c), (d) $k_E = 1.5 \times k_L$. In (a)–(d) a horizontal comparison between graphs demonstrates the effect of increased hybrid fecundity (under symmetric and asymmetric larval competition). A vertical comparison shows the influence of increased competitive ability of hybrid larvae (with equal and unequal fecundities). (e), (f) reveal the effect of a reversal in larval competitive abilities for $r_c = 1.3$ (cf. Fig. 4a,c): (e) $k_L = 1.5 \times k_E$ and (f) $k_L = 1.2 \times k_E$. Red lines: below solid line, population sizes and species ratio are stable, below broken line, the ratio varies by up to 10% (percentages then are means over the last 10 of 1000 years). In (a), (b) the species ratio is always stable. Black dot indicates the centre to facilitate comparisons between graphs.
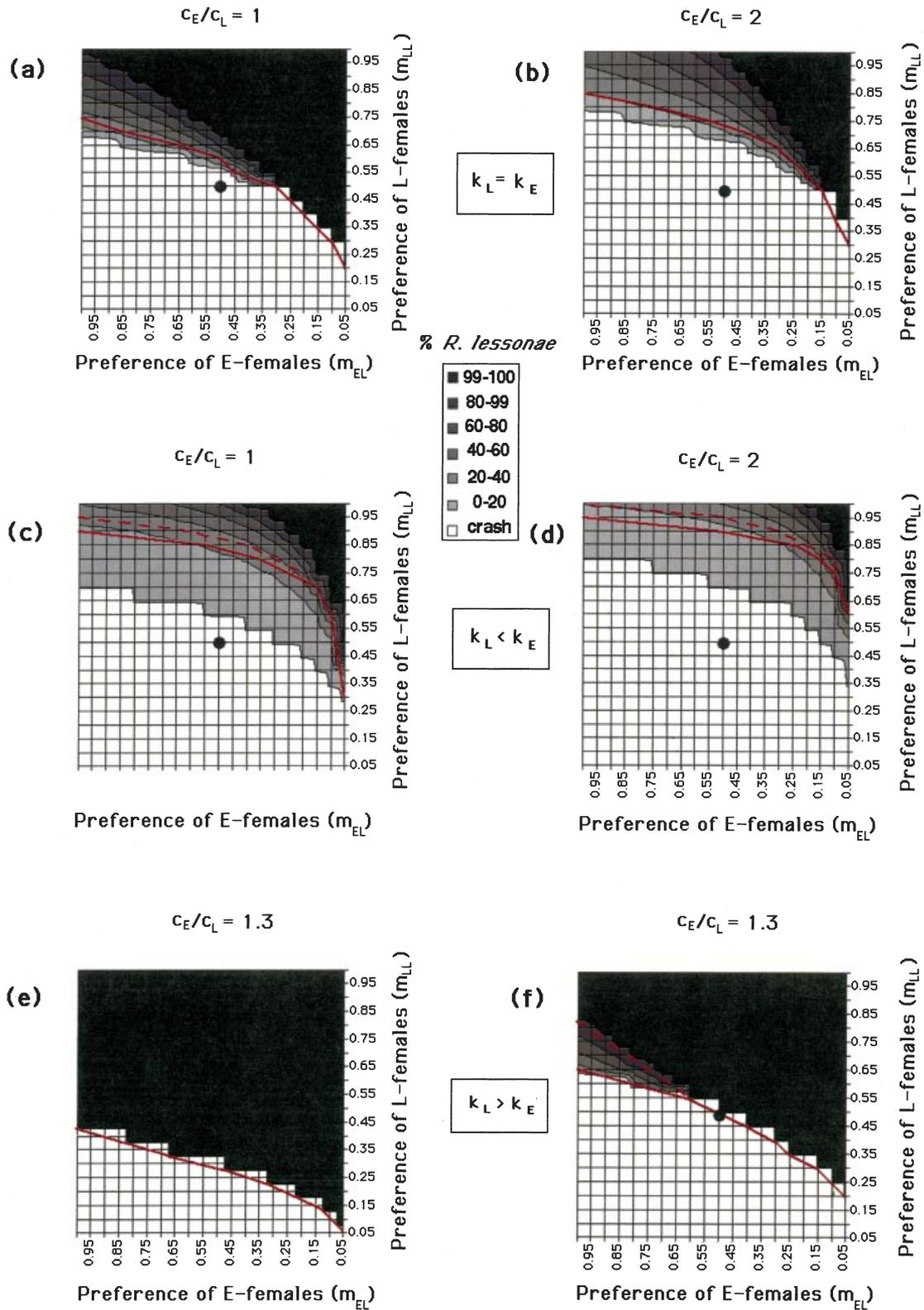
(grey), and about half of the possible combinations of female preferences result in transient populations (white). Transient populations crash after a variable time period because the successful hybrid drives its host extinct. Such population crashes occur even for moderate preferences of host females for host males ($0.5 < m_{LL} < 0.65$), when they are combined with moderate to high hybrid preferences for host males ($0.5 < m_{EL} < 1.0$).

Fecundity ratio and asymmetric larval competition

The fecundity ratio has a greater effect on whether the two species coexist at all (compare Fig. 3a,c with Fig. 3b,d), whereas the relative competitive abilities of larvae are more important in determining the actual species composition (compare Fig. 3a,b with Fig. 3c,d). The latter only holds as long as hybrid larvae are not inferior (cf. Fig. 3e,f).

The species ratio always reaches an equilibrium if the larvae of both species are competitively equal ($k_L = k_E$, Fig. 3a,b). Then the proportion of hosts solely depends on the fecundity ratio (r_c) and the female preferences:

$$\frac{L_A^*}{L_A^* + E_A^*}$$
$$= \frac{r_c\left[r_c m_{EL}(2 - 3m_{LL} + m_{LL}^2) - m_{LL}^2\right]}{m_{LL}(1 - r_c m_{LL}) + r_c m_{EL}[r_c(2 - 3m_{LL} + m_{LL}^2) + m_{LL} - 2]}.$$

However, subpopulation sizes oscillate in most cases as soon as the proportion of hosts exceeds 20% (above red lines, Fig. 3). Doubling hybrid fecundity relative to that of the host ($r_c = 2$, natural range 1.3–3.3) more than halves the proportion of host-dominated (two darkest greys) and pure host populations (Fig. 3a,b). Pure host populations only occur for unrealistically low hybrid preferences ($m_{EL} < 0.5$, Fig. 3b). This reduction is accompanied by an increased occurrence of mixed and of transient populations (Fig. 3a,b). The hybrid sex ratio only depends on the preferences of host females for the two male types

$$\frac{E_A^{m*}}{E_A^{f\,*}} = \frac{m_{LL}}{[1 + (1 - m_{LL})]} \tag{11}$$

and varies between 1 : 1 and 1 : 1.5 for realistic preferences for host males ($m_{LL} > 0.5$).

The equilibrium species ratio seems to depend on all model parameters when hybrid larvae are superior ($k_L < k_E$). The proportion of hosts at equilibrium can be calculated for the special case that $m_{LL} = 1$:

$$\frac{L_A^*}{L_A^* + E_A^*} = \frac{1}{r_c m_{EL}}\left[\frac{1 - s_A}{s_A R_L}\right]^{(k_E - k_L)/k_E}$$

where $R_L = (s_J s_T c_L)/2$. Here, the relative competitiveness appears as an exponent ($(k_L - k_E)/k_E$) and weighs the influence of survival rates and of host fecundity relative to that of the hybrid. Therefore, species differences in competitiveness have more influence on the actual

composition of mixed populations than differences in fecundity.

The species ratio in most cases oscillates like the subpopulation sizes if $k_E = 1.5\ k_L$ (Fig. 3c,d). Hybrid superiority reduces the proportion of pure host populations by a factor of five to seven (Fig. 3a,c and Fig. 3b,d). They only occur for unrealistically low hybrid preferences of $m_{EL} < 0.5$. This reduction is accompanied by a doubling of mixed populations (Fig. 3a,b) and by a three- to six-fold increase of hybrid-dominated populations (two lightest grey, Fig. 3b,d and Fig. 3a,c). In contrast to the effects of increasing hybrid fecundity, it is not paralleled by an increase in population crashes.

A reversal of the asymmetry in larval competition in favour of host larvae has dramatic effects for the hybrid. For an observed fecundity ratio of $r_c = 1.3$ (G. Abt, unpublished) a direct reversal results in pure host or in transient populations (compare Figs 3e and 4c; $k_L = 1.5\ k_E$ vs. $k_E = 1.5\ k_L$). Only if the asymmetry is less pronounced a very limited range of preference combinations allows for mixed populations ($k_E = 1.2\ k_L$, Fig. 3f).

Two habitats connected by species-specific dispersal (model B)

Adult dispersal is assumed to connect two different breeding sites. In habitat 1 all larvae do equally well ($k_L = k_E$), whereas in habitat 2 hybrid larvae are superior ($k_E = 1.5\ k_L$). The fecundity ratio has the observed value of 1.3 (G. Abt, unpublished). We examined two types of adult dispersal: (1) 'ecological dispersal' where both species leave the respective unfavourable larval site and (2) 'reproductive dispersal' where the hybrid follows its sexual host to habitat 1.

Ecological dispersal at observed species- and sex-specific rates

Ecological dispersal of species-specific fractions of males and females (estimates from Holenweg, 1999) affects the species composition mainly in habitat 1 where tadpoles perform equally. Compared to the same site in isolation, dispersal increases the range of female preferences leading to pure host populations by about 10% and decreases the possibilities for coexistence by a similar amount (Fig. 4a,b). It also produces a result impossible without dispersal – pure hybrid populations in habitat 2 (hatched area, Fig. 4d). They arise for a wide range of host female preferences for host males ($m_{LL} = 0.3$–0.8). With 6–23 frogs, however, population sizes are very small. Although in habitat 1 dispersal induces fluctuations up to 10% in an originally stable species ratio (Fig. 4a,b), it seems to have little effect in habitat 2 (cf. Fig 4c,d). The hybrid sex ratio ranges from 1 : 1.2 to 1 : 2.3 in habitat 1. In habitat 2 it spans from 1 : 1.3 for high preferences of host and hybrid females to 1 : 6.2 for low hybrid preferences.
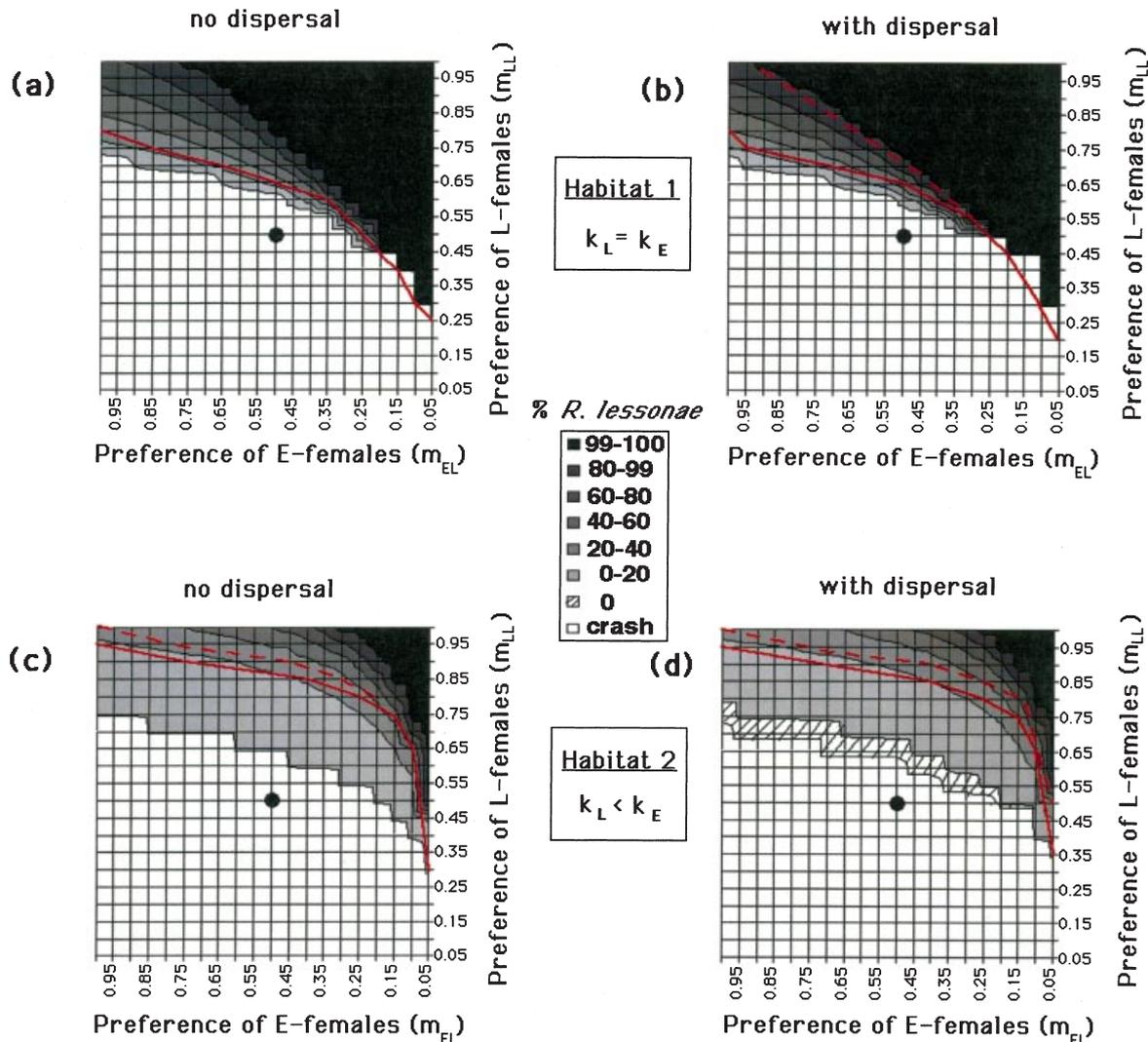
Fig. 4 Comparison of *R. lessonae* (L) percentages in mixed L/E populations with and without species- and sex-specific ecological dispersal, for different combinations of female preference for L-males (m_{LL}, m_{EL}). Fecundity ratio ($r_c = c_E/c_L = 1.3$) and fractions of dispersing adults stem from a field site near Zurich (Holenweg, 1999; G. Abt, unpublished). (a), (b) In habitat 1, larvae are competitively equal ($k_L = k_E = 5000$). (c), (d) In habitat 2, *R. esculenta* larvae are superior ($k_E = 1.5 \times k_L$). In *R. esculenta*, fractions of 0.12 females and 0.16 males leave habitat 1 and in *R. lessonae*, proportions of 0.24 females and 0.08 males leave habitat 2. Red lines: below solid line population sizes and species ratio are stable, below broken line, the ratio varies by up to 10% (percentages then are means over the last 10 of 1000 years); in (a) the species ratio is always stable. Black dot indicates the centre to facilitate comparisons between graphs.

Ecological vs. reproductive dispersal

For both types of dispersal the major changes in species composition occur where tadpoles perform equally (Fig. 5 left). However, ecological dispersal (mainly of the hybrid) enhances the differences in species composition between sites, whereas reproductive dispersal reduces them and clearly favours the spread of the hybrid by increasing its overall proportion (cf. arrows in Fig. 5a,c left).

Ecological dispersal

In habitat 1, the percentage of hosts increases with increasing emigration of hybrids, but the extent varies depending on female preferences (Fig. 5a,b left). The proportion of hosts starts from lower and increases more dramatically for lower female preferences. For nearly total female preference for host males ($m_{LL} = m_{EL} = 0.95$) host percentage increases from 69 to 100% with increasing hybrid emigration and host immigration (Fig. 5a left). For experimentally derived female preferences ($m_{LL} = m_{EL} = 0.7$, see Introduction) the host proportion

also increases from 20 to 96% with increasing hybrid emigration (Fig. 5b left), but is unaffected by host immigration. This indicates an interaction effect between dispersal and female preferences. In habitat 2, ecological dispersal increases the proportion of hybrids by <5% if $m_{LL} = m_{EL} = 0.95$ (Fig. 5a right), whereas populations either crash (white area) or stay at 98–100% hybrids if $m_{LL} = m_{EL} = 0.7$ (Fig. 5b right). In pure hybrid populations (dashed area) numbers fall from about 350 frogs in mixed populations to below 10. Ecological dispersal can induce fluctuations of up to 10% in an originally stable species ratio in habitat 1 (not shown). In habitat 2, patterns are similar with and without dispersal. The species ratio varies by about 10% for $m_{LL} = m_{EL} = 0.95$ and is stable for $m_{LL} = m_{EL} = 0.7$ (not shown). The hybrid sex ratio is higher and more affected by dispersal for lower female preferences. In habitat 1 it ranges from 1 : 1.5 to 1 : 1.9 for $m_{LL} = m_{EL} = 0.7$ (1 : 1.3 without dispersal, eqn (11)) and is not affected for $m_{LL} = m_{EL} = 0.95$ (1 : 1.1, eqn (11)). The respective sex ratios in habitat 2 are 1 : 2 and 1 : 1.3.

Reproductive dispersal
Dispersal has the opposite effect on species compositions in habitat 1 if hybrids follow their sexual hosts and immigrate from habitat 2 (Fig. 5c). Under nearly total female preference for host males, the percentage of hosts decreases from 69 to 40% with reproductive dispersal (Fig. 5c left), whereas it increases from 69 to 100% with ecological dispersal (Fig. 5a left). In habitat 2 the proportion of hosts increases by up to 9% as long as more hybrids than hosts leave, and otherwise it slightly decreases (Fig. 5c right). Reproductive dispersal can induce fluctuations of up to 11% in habitat 1 which originally had a stable species ratio (not shown). In habitat 2 the ratio varies by up to 13% with dispersal, compared to 10% without (not shown). The hybrid sex ratio is lower with ecological dispersal, and amounts to 1 : 1.1–1 : 1.2 in habitat 1 (1 : 1.1 without dispersal, eqn 11) and to about 1 : 1.3 in habitat 2.

Discussion

Our model for an isolated habitat shows that female choice and interspecific fecundity differences are important in limiting coexistence of sexual host and hemiclonal hybrid. The degree of hybrid superiority in larval competition mainly affects the actual composition of mixed populations and whether sexual parasitism has a stabilizing effect on host dynamics. The two-habitat model demonstrates how dispersal interacts with competition and mate choice, to determine the species composition and its stability at the two sites.

More than half of the possible combinations of female preferences usually result in transient populations where the hybrid outnumbers its host, drives it extinct and then dies out for lack of mating partners. For a limited range of female preferences, host and hybrid can coexist even when they are equally viable, fecund and competitive

and only differ in their reproductive modes. These results emphasize the importance of assortative mating for the persistence of hybridogenetic systems (cf. waterfrogs, Som *et al.*, 2000; *Poeciliopsis*, Moore & McKay, 1971). They contradict results from a population genetics model with nonoverlapping generations, suggesting that coexistence requires higher fecundity and offspring viability of backcrosses (Graf, 1986). Our finding also implies that interspecific differences in habitat preferences are not as crucial for coexistence as suggested by an ecological model for all three waterfrog species (Guex *et al.*, 1993). Similarly, coexistence in the *Poeciliopsis* complex does not require niche separation (Moore & McKay, 1971).

Generally, increasing hybrid fecundity and/or larval competitiveness clearly increases the range of female preferences leading to mixed populations at the expense of pure host populations. As *R. esculenta* produces larger clutches and seems superior in larval competition, this may explain why pure *R. lessonae* populations are rare (Graf & Polls Pelaz, 1989). Experiments have demonstrated asymmetric effects of density on *R. lessonae* and *R. esculenta* larvae under various ecological conditions (e.g. Semlitsch & Reyer, 1992; Semlitsch, 1993), but so far their population level consequences remain unclear. According to our results, these larval effects may strongly influence the dynamics and composition of mixed populations. Although increasing fecundity increases the occurrence of transient populations and evenly affects all classes of mixed populations relatively, increasing competitiveness mainly increases the proportion of populations with 80–99% hybrids and reduces that of pure host populations. This polarization and the drastic effects of hybrid inferiority (Fig. 3e,f) suggest that, where coexistence is possible, competitive differences could be more important for the hybrid's success than differences in fecundity.

Parasitism tends to stabilize host dynamics if density-dependent processes are involved (e.g. Reeve, 1988). In sexually parasitic waterfrogs, interspecific larval competition depends on density. The hybrid's minimum effect on host subpopulation size in a single habitat is to reduce fluctuation amplitude. Generally, sexual parasitism leads to simultaneous equilibria in subpopulation sizes and

Fig. 5 Influence of species-specific dispersal between two mixed L/E populations on the percentage of *R. lessonae*, for different fractions of dispersing adults (μ_{Li}, μ_{Ei}). The fecundity ratio has the observed value of $r_c = c_E/c_L = 1.3$. In habitat 1, larvae are competitively equal (left, $k_L = k_E = 5000$), whereas in habitat 2, *R. esculenta* larvae are superior (right, $k_E = 1.5 \times k_L$). Ecological dispersal: *R. esculenta* leaves habitat 1 (μ_{E1}) and *R. lessonae* leaves habitat 2 (μ_{L2}). Reproductive dispersal: both species leave habitat 2 (μ_{L2}, μ_{E2}). Female preferences are (a), (c) $m_{LL} = m_{EL} = 0.95$ and (b) $m_{LL} = m_{EL} = 0.7$ (e.g. Abt & Reyer, 1993). Comparing (a) and (b) shows the influence of female preferences in case of ecological dispersal. Comparing (a) and (c) reveals the difference between ecological and reproductive dispersal. Arrows point in the direction of an increasing *R. lessonae* proportion.

Ecological dispersal

Habitat H1

$m_{LL} = m_{EL} = 0.95$

Habitat H2

(a) Emigration of E from H1 (μ_{E1}) / Emigration of L from H2 (μ_{L2})

$m_{LL} = m_{EL} = 0.7$

(b) Emigration of E from H1 (μ_{E1}) / Emigration of L from H2 (μ_{L2})

% *R. lessonae*
- 99–100
- 80–99
- 60–80
- 40–60
- 20–40
- 0–20
- 0
- crash

Reproductive dispersal

Habitat H1

$m_{LL} = m_{EL} = 0.95$

Habitat H2

(c) Emigration of E from H2 (μ_{E2}) / Emigration of L from H2 (μ_{L2})
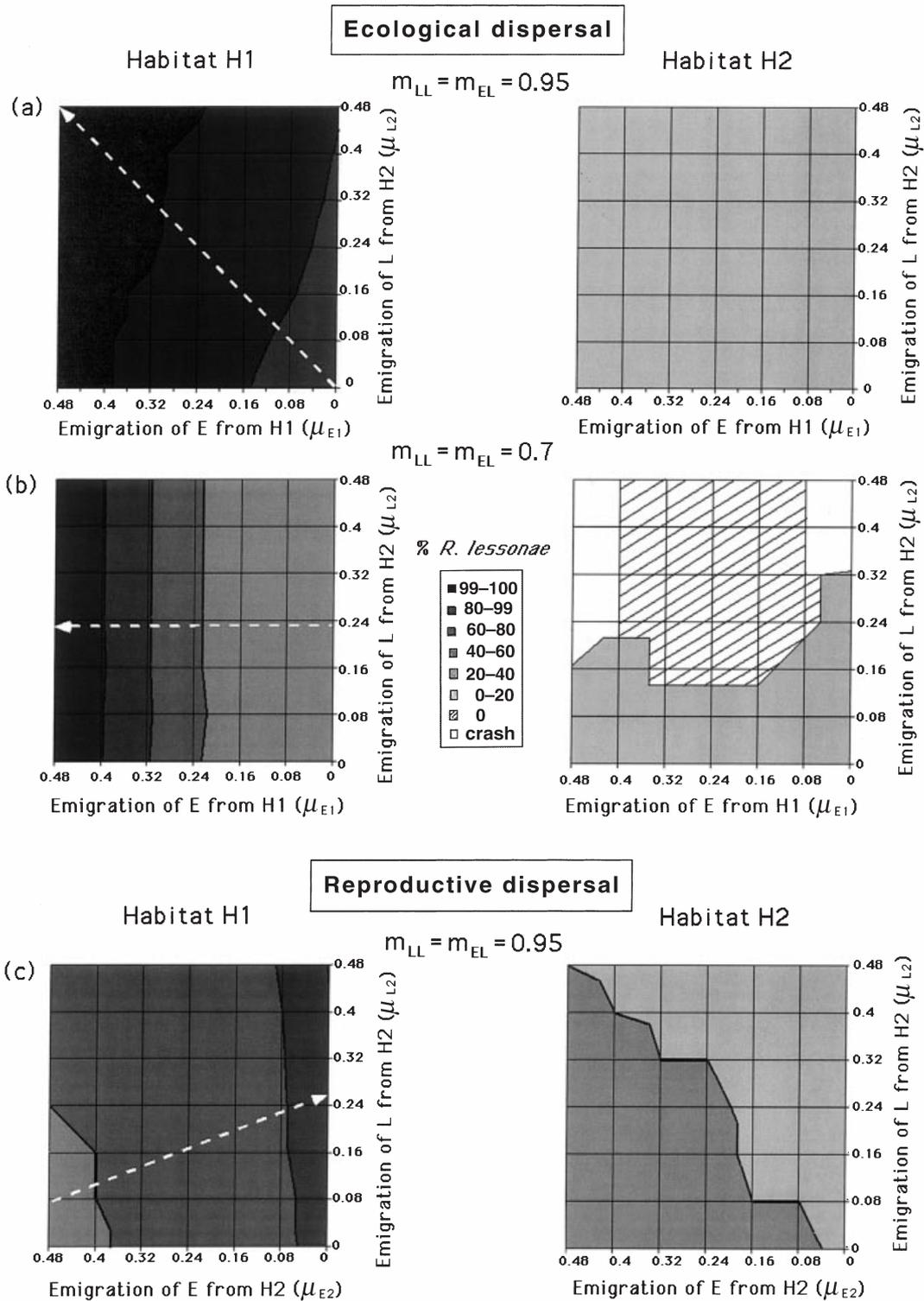
species ratios only when the hybrid proportion exceeds 80%. The occurrence of equilibrium subpopulation sizes increases if the hybrid's fecundity and competitiveness

increase. The species ratio usually varies by 10–20%, but occasionally less than that. The relation between 'usually' and 'occasionally' depends on the fecundity ratio. The

species composition always reaches an equilibrium when host and hybrid larvae perform equally (cf. Som *et al.*, 2000), despite oscillating subpopulation sizes. Competitive hybrid superiority restricts equilibrium species ratios to populations with 80–99% hybrids.

Dispersal between neighbouring resource patches strongly affects the dynamics and diversity of communities and is often thought to stabilize population dynamics (e.g. Reeve, 1988; Hastings, 1993). It has not been explicitly incorporated in earlier models of waterfrog coexistence (e.g. Graf, 1986; Som *et al.*, 2000), although dispersal seems likely to occur in juveniles (e.g. Berven, 1990) and regularly occurs in adults (Holenweg, 1999). Here, we consider density-independent adult dispersal between a breeding site where all larvae perform equally and a site where hybrid larvae are competitively superior. We distinguish ecological dispersal away from the respective unfavourable larval habitat from reproductive dispersal where hybrids follow their hosts to increase their reproductive chances. Three results are especially interesting. Firstly, both types of dispersal affect the species composition more where all larvae perform equally, although in opposite directions. Secondly, dispersal can destabilize a stable species ratio by inducing fluctuations up to 10% if larvae perform equally, or can leave the patterns effectively unchanged. Finally, for some female preference combinations, ecological dispersal can lead to pure hybrid populations, and host dispersal can lose its influence on species composition. These results indicate interaction effects between dispersal and both competition and mate choice. Recent results on possible consequences of multistage density-dependence suggest that the effects of dispersal may be different if it should also depend on density (cf. Hellriegel, 2000).

Conclusions

If we accept variation of less than 10% as stable, our models can explain the remarkable stability in species ratios over ecological time that seems to exist within hybridogenetic populations, even when population sizes fluctuate (*Poeciliopsis*: Moore, 1976; waterfrogs: Berger, 1977; Holenweg, 1999). Moreover, the range of hybrid sex ratios resulting from the model (1 : 1.1–1 : 6.2) covers the observed range of 1 : 1.3–1 : 4 (see Materials and methods). Our results also offer a potential explanation as to why species ratios vary so widely among populations, ranging from about 95 : 5–5 : 95 in waterfrogs (Berger, 1977; Semlitsch *et al.*, 1997). Either one or several of the four factors studied here, and/or their interactions, have to differ among populations.

Ecological stability is necessary but not sufficient for evolutionary stability. Clonal vertebrate taxa are thought to represent evolutionary dead ends (Maynard Smith, 1978; Milinski, 1993). With 60 000–150 000 years (about 200 000 generations), the oldest known clonal lineage (*Poeciliopsis*) is indeed relatively young compared

to most sexual species (Maynard Smith, 1992; Quattro *et al.*, 1992; Vrijenhoek, 1994). Nevertheless, it exceeds the 10 000–100 000 generations, which seem to suffice for a disappearance of clonal lineages (Lynch & Gabriel, 1990). Various mechanisms could contribute to such a possible evolutionary success of hybridogenetic taxa: (1) the expression of deleterious mutations on the clonal genome can be sheltered by the sexual genome (Spinella & Vrijenhoek, 1982), (2) occasionally, new nuclear material may be incorporated from the sexual host (Hedges *et al.*, 1992; Spolsky *et al.*, 1992) or from recombination between two different clonal genomes (Schmidt, 1993) and (3) multiple primary hybridization events between different parental strains can lead to clonal diversity, with each clone or hemiclone adapted to its narrow 'frozen niche' (Vrijenhoek, 1979, 1994; Semlitsch *et al.*, 1997).

Different localities do indeed vary in the number and composition of hybrid hemiclones (Poeciliopsis: Vrijenhoek, 1979; waterfrogs: Semlitsch *et al.*, 1997). Combined with the above mechanisms this is likely to result in interclonal selection and clone × environment interactions for assortative mating, fertility, competitiveness and/or dispersal patterns. According to our models, these in turn will differentially affect the relative fitnesses of (hemi) clones and sexual hosts and hence, the dynamics and composition of mixed populations. Waterfrogs being bisexual, our models and conclusions are also relevant for genotype × environment interactions involving two tightly coupled sexual organisms of different genotypes, ecotypes, or species. Interspecific hybrids, for instance, are thought either to be superior to both parents in certain habitats or to be confined to narrow 'tension zones', where dispersal from the parental areas balances selection against hybrids (reviewed by Arnold, 1997). Testing these hypotheses requires detailed empirical and theoretical analyses of the factors considered here, as they are likely to shape hybrid zones.

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Appendix

Rescaled form of model A: Isolated habitat without dispersal

The aim is to reduce the number of parameters for analytical investigations. Here the reduction is from seven to five parameters. Roughly speaking, survival up to the end of the first year and hatchling number per adult are combined into the parameter R, whereas subpopulation sizes and the parameter describing competition impact are scaled by $1/R$ or juvenile survival$/R$ (see below).

(1) Subpopulation of the sexual host (H)

$$H_T(t) = R_L \frac{m_{LL}H_A(t)}{m_{LL}H_A(t) + 2(1 - m_{LL})r_c P_A^m(t)} H_A(t)$$

$$H_J(t + 1) = \exp\left[-\frac{H_T(t) + r_c(P_T^f(t) + P_T^m(t))}{k'_L}\right] H_T(t)$$

$$H_A(t + 1) = s_A(H_A(t) + H_J(t))$$

with the new variables $H_T = (s_J L_T)/R_L$, $H_J = L_J/R_L$ and $H_A = L_A/R_L$, and the new parameters $R_L = (s_J s_T c_L)/2$, $r_c = c_E/c_L$ and $k'_L = (s_J k_L)/R_L$.

(2) Subpopulation of the sexual parasite (P)

$$P_T^f(t) = r_c R_L \left[\frac{m_{EL}H_A(t)}{H_A(t) + 2r_c P_A^m(t)} P_A^f(t) \right.$$
$$\left. + \frac{2(1 - m_{LL})r_c P_A^m(t)}{m_{LL}H_A(t) + 2(1 - m_{LL})r_c P_A^m(t)} H_A(t)\right]$$

$$P_T^m(t) = r_c R_L \frac{m_{EL}H_A(t)}{H_A(t) + 2r_c P_A^m(t)} P_A^f(t)$$

$$P_J^f(t + 1) = \exp\left[-\frac{H_T(t) + r_c(P_T^f(t) + P_T^m(t))}{k'_E}\right] P_T^f(t)$$

$$P_J^m(t + 1) = \exp\left[-\frac{H_T(t) + r_c(P_T^f(t) + P_T^m(t))}{k'_E}\right] P_T^m(t)$$

$$P_A^f(t + 1) = s_A(P_A^f(t) + P_J^f(t))$$

$$P_A^m(t + 1) = s_A(P_A^m(t) + P_J^m(t))$$

with the new variables $P_T = (s_J E_T)/(r_c R_L)$, $P_J = E_J/(r_c R_L)$ and $P_A = E_A/(r_c R_L)$, and the new parameter $k'_E = (s_J k_E)/R_L$.

Equilibrium and invasion analysis

The sexual host can reach an equilibrium size when it is on its own

$$H_A^* = \frac{k'_L}{R_L} \ln\left[\frac{s_A R_L}{1 - s_A}\right] \quad \left(= \frac{L_A^*}{R_L}\right). \tag{A1}$$

This nonzero equilibrium is asymptotically stable if

$$1 < s_A(1 + R_L). \tag{A2}$$

This necessary and sufficient condition was derived from the linear approximation $h(t + 1) = s_A h(t) + (1 - s_A)(1 - \ln[s_A R_L/(1 - s_A)])h(t - 1)$ (see Elaydi, 1996). Under the same condition (A2) the zero equilibrium is unstable (linear approximation $h(t + 1) = s_A h(t) + s_A R_L h(t - 1)$).

When the host is at equilibrium (A1) the sexual parasite can invade if male and female parasites both can increase in numbers. Female numbers increase if $\Delta P_A^f = P_A^f(t + 1) - P_A^f(t) > 0$. This is fulfilled if

$$\frac{1}{r_c m_{EL} + 2(1 - m_{LL})} \left[\frac{(1 - s_A)}{s_A R_L}\right]^{(k_E - k_L)/k_E} < 1. \tag{A3}$$

Male numbers increase if $\Delta P_A^m = E_A^m(t + 1) - P_A^m(t) > 0$. This is fulfilled if

$$\frac{1}{r_c m_{EL}} \left[\frac{(1 - s_A)}{s_A R_L}\right]^{(k_E - k_L)/k_E} < 1. \tag{A4}$$

As $r_c m_{EL} < [r_c m_{EL} + 2(1 - m_{LL})]$, the sexual parasite can invade when it is rare if inequality (A4) holds. For the parameter ranges used here, we always have $(1 - s_A)/s_A R_L < 1$.

Non-zero two-species equilibria can be determined only for special cases:

(a) '$k'_L = k'_E = k'$ (cf. Fig. 3a,b): When the two species are equally competitive the equilibrium subpopulation sizes are

$$H_A^* = \frac{m_{LL}k(1 + 2r_c D)}{m_{LL}R_L + 2r_c D[r_c R_L m_{EL}(2 - m_{LL}) + m_{LL}]}$$
$$\times \ln\left[\frac{s_A m_{LL}R_L}{(1 - s_A)[2r_c D(1 - m_{LL}) + m_{LL}]}\right]$$

$$P_A^{m*} = D H_A^*$$

$$P_A^{f*} = \frac{2 - m_{LL}}{m_{LL}} D H_A^*$$

with

$$D = \frac{m_{LL}[r_c R_L m_{EL}(2 - m_{LL}) - m_{LL}]}{2r_c D[m_{LL}^2 - r_c m_{EL}(2 - 3m_{LL} + m_{LL}^2)]}.$$

(b) '$m_{LL} = 1$': When host females choose their own males only, the sex ratio of the sexual parasite also is 1 : 1 ($P_A^m = P_A^f = 1/2\,P_A$, cf. Fig. 1) and the equilibrium subpopulation sizes are

$$H_A^* = \frac{k'_L(s_A R_L)^{(k'_E - k'_L)/k'_E} \ln\left[\frac{s_A R_L}{1 - s_A}\right]}{R_L\left[(1 + r_c m_{EL})(s_A R_L)^{(k'_E - k'_L)/k'_E} - (1 - s_A)^{(k'_E - k'_L)/k'_E}\right]}$$

$$P_A^* = \left[m_{EL}\left(\frac{s_A R_L}{1 - s_A}\right)^{(k'_E - k'_L)/k'_E} - \frac{1}{r_c}\right] H_A^*.$$