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ECOLOGICAL CORRELATES OF MALE OUTCROSSING ABILITY IN A SIMULTANEOUS HERMAPHRODITE SNAIL

STEPHANIE J. SCHRAG,*† ARNE Ø. MOOERS,* G. TATA NDIFON,‡
and ANDREW F. READ*†§

*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.;
‡Department of Biological Sciences, Bayero University, P.M.B. 3011, Kano, Nigeria;
§A.F.R.C. Unit of Behaviour and Ecology, University of Oxford,
South Parks Road, Oxford OX1 3PS, U.K.

Abstract.—Phally, a genital dimorphism found in some species of self-compatible simultaneous hermaphrodites, presents an opportunity to examine factors maintaining outcrossing within an animal species that can self-fertilize. Both aphallics and euphallics can self-fertilize, but aphallics cannot donate sperm because they do not develop a functional prostate and penis. In this field study of Nigerian populations of the freshwater gastropod, *Bulinus truncatus* (Mollusca: Pulmonata), we evaluate ecological correlates of euphally to test hypotheses predicting a selective advantage of outcrossing due to the production of genetically variable offspring. The prevalence of euphally across 49 populations ranged from 0% to 81%. We found no association between prevalence of euphally and any of the following: population density, snail density, mollusk species abundance, water pH, oxidation-reduction potential, dissolved oxygen content, habitat instability (as estimated by habitat type), human activity, vegetation density, desiccation rate, and water chemistry variation. There was a significant but weak correlation between conductivity and proportion of euphallics ($r^2 = 10\%$), with lower ion concentrations favoring higher levels of euphally. The prevalence of the most abundant trematode taxon (Xiphidiocercariae) correlated positively with proportion of euphallics, explaining 10% of the variation in proportion of euphallics after we controlled for mean snail age and time of year. Trematode richness (number of taxa per population) was not associated with proportion of euphallics across sites when we controlled for time of year. However, indexes of trematode diversity that incorporated both prevalence and richness did correlate significantly with proportion of euphallics. These results are consistent with hypotheses predicting an advantage of outcrossing due to temporal fluctuations in the biotic environment.

Species that reproduce both by self-fertilization and cross-fertilization can serve as model systems for direct investigation of short-term factors maintaining outcrossing within populations. In the case of self-fertilization, as in asexual reproduction, all of an offspring's genes come from only one parent. This translates into a three-to-two advantage for a mutation for pure self-fertilization in a self-incompatible, randomly mating population, assuming no inbreeding depression and no loss of ability to contribute male gametes via outcrossing (Charlesworth

1980). Consequently, alleles increasing the rate of self-fertilization will quickly spread to fixation in populations with mixed mating systems, all things being equal (Fisher 1941; Nagylaki 1976; Lloyd 1979). The factors maintaining outcrossing in such populations have been subject to numerous theoretical and empirical studies, largely in plants (Jain 1976; Clay 1983; Waller 1984; Clay and Antonovics 1985; Mitchell-Olds and Waller 1985; Holtsford and Ellstrand 1990; Schmitt and Gamble 1990). In pulmonate snails (Mollusca: Gastropoda), the vast majority of which are simultaneous hermaphrodites (Heller 1993), a genital polymorphism involving the loss of male outcrossing ability has arisen at least 13 times (S. J. Schrag and A. F. Read, unpublished manuscript). This condition presents an opportunity to examine factors maintaining outcrossing within an animal species in the presence of recombination.

Some species of pulmonates have two sexual morphs, euphallic and aphallic. Euphallic individuals develop fully functional male and female tracts. In aphallics, the distal portions of the male tract never fully develop, although functional sperm are still produced by the hermaphrodite gland (Geraerts and Joosse 1984). Thus, both morphs can self-fertilize, but aphallics are not capable of sperm donation. Evidence of a cost of growing and maintaining a fully developed male tract has been detected in the laboratory (Jarne et al. 1992; Schrag and Rollinson 1994). Nonetheless, in natural populations, the proportion of euphallics varies from zero to one (de Larambergue 1939; Brown and Wright 1972; this study). If euphallics never successfully reproduced by donating sperm, selection would be expected to remove euphally because of the cost of growing and maintaining a full male tract. Consequently, euphally must be maintained because of a selective advantage of outcrossing.

Previous studies suggest that phally may have a strong heritable component in some (de Larambergue 1939) but not all (Schrag et al. 1992) populations. Parental phally morph does not influence the proportion of euphallic offspring produced (de Larambergue 1939; Jarne et al. 1992; Schrag et al. 1992). Temperature during egg and hatchling stages strongly influenced phally determination in two laboratory populations of *Bulinus truncatus* (Schrag and Read 1992), and we recently found that environmental phally determination occurs in the field (Schrag et al. 1994).

The fact that male outcrossing ability is proximately maintained by temperature reinforces the question of why selection maintains euphally within populations of aphallics, given the fitness cost associated with full development of the male reproductive tract. Here we evaluate the relationship between proportion of euphallics and snail density, parasite pressure, and water chemistry, both within and between populations, in order to investigate why outcrossing is maintained in natural populations of *B. truncatus*.

HYPOTHESES AND PREDICTIONS

Selection for outcrossing has been predicted to vary with the ease of finding a mate, the strength of inbreeding depression, and the benefits of producing genetically variable offspring (Schmitt and Ehrhardt 1987; Jarne et al. 1993). Hypothe-

ses based on reproductive assurance (Boycott 1917; Gerritsen 1980; Lively 1992) argue that morphs capable of outcrossing will be more common in populations with a high encounter rate between individuals, which leads to increased opportunities for mating. Such hypotheses have limited explanatory power since they do not address why mating under high density is advantageous. If mating is advantageous, however, reproductive assurance may help explain the distribution of euphally. In particular, the reproductive assurance hypothesis predicts that euphallics will be more common in high-density populations (Boycott 1917; Riedel 1953).

Experimental and theoretical investigations have demonstrated that outcrossing may be favored when reduced fitness of selfed offspring due to inbreeding depression outweighs the benefits of selfing (Jain 1976; Mitchell-Olds and Waller 1985; Charlesworth and Charlesworth 1987; Holtsford and Ellstrand 1990; Schmitt and Gamble 1990; Jarne et al. 1992). In fact, inbreeding depression is regularly viewed as the only general factor in outcrossing hermaphrodite populations that can be strong enough to prevent the evolution of self-fertilization (see, e.g., Lande and Schemske 1985; Charlesworth and Charlesworth 1987). Inbreeding depression may play such a role in *Bulinus truncatus,* although for reasons presented in the Discussion, we think this is less likely and do not investigate this hypothesis further.

The production of progeny that differ genetically from their parents and/or from their sibs may also generate selection for outcrossing, analogous to a number of hypotheses for the maintenance of sex (Williams 1975; Bell 1982; Stearns 1987; Michod and Levin 1988; Jarne et al. 1993). Relatively few empirical studies have investigated the three major hypotheses in this class (Schmitt and Ehrhardt 1987).

The spatial variation hypothesis predicts a selective advantage of outcrossing in heterogeneous environments with high intraspecific competition for resources (Bell 1982). When parents and offspring experience similar environments and resources are limited, offspring that are able to invade new niches will face less competition. Under these circumstances, the cost of outcrossing is said to be offset by the benefit of producing genetically variable offspring who will be more able to invade different niches than offspring identical to each other. The spatial variation hypothesis predicts that euphally will be more common in stable environments that have high competition for resources.

Implicit in these predictions is the assumption that outcrossing leads to higher levels of genetic variability among offspring than selfing (Mitchell-Olds and Waller 1985). This assumption does not always hold, and a lack of support for the spatial variation hypothesis in *Impatiens capensis,* an annual plant that produces obligately selfing flowers as well as flowers capable of outcrossing, has been attributed to a higher genetic variability in offspring that are the product of selfing (Schmitt and Ehrhardt 1987; McCall et al. 1989). Conditions generating more genetic variability in selfed progeny than in outcrossed progeny are model specific, and the relevant parameters for *B. truncatus* populations are not currently known. If selfed sibships were more genetically diverse than outcrossed sibships, then patterns opposite to our predictions might be found.

The temporal variation hypothesis predicts a selective advantage of outcrossing

in spatially uniform environments that vary unpredictably over time (Fisher 1930; Williams 1975). When offspring experience environments different from their parents', the cost of outcrossing is again said to be offset by the benefit of producing genetically variable offspring, which thereby increases the likelihood that some survive the new conditions (lottery model of Williams [1975]). Outcrossing in this case is assumed to generate genetic variability between parents and their offspring, and it does not pose the same problems as the among-sibling variation required by the spatial variation hypothesis. Unlike the spatial variation hypothesis, this view predicts that euphally will be more common in unstable environments in which conditions are likely to vary unpredictably between generations.

Fluctuations in the biotic environment, in particular some forms of antagonistic coevolution, can also favor outcrossing (Jaenike 1978; Hamilton 1980; Bell 1982). The most common version of this hypothesis, which we call the red queen hypothesis after Bell (1982), focuses on the interaction between parasites and their hosts. When parasites substantially decrease host fitness, coevolution between parasites and host can result in frequency-dependent selection favoring rare host genotypes (Hamilton 1980). A central prediction of the red queen hypothesis is that selection for rare genotypes should be stronger in populations in which parasites exert a greater selective pressure on their hosts. Simultaneous hermaphrodites that outcross will be more successful at generating novel genotypes than those that reproduce by selfing (Hamilton et al. 1990; see also Lively and Apanius, in press; C. M. Lively, unpublished manuscript). *Bulinus truncatus* in northern Nigeria is an intermediate host for at least 12 species of larval trematodes (Ndifon and Umar-Yahaya 1988–1990). Trematodes in a range of taxa (*Schistosoma:* Hairston 1965; Xiphidiocercariae: Betterton 1984) have been shown to reduce survival and fecundity of *B. truncatus* with patent infections. In the case of *B. truncatus,* the red queen hypothesis predicts that euphally will be more common in populations in which parasites exert a high selective pressure on their hosts. The prediction that the association between outcrossing and parasite pressure should be positive implicitly assumes that population differences in parasite pressure are greater than population differences in levels of resistance (including any reductions in infection levels due to outcrossing). This assumption is central to many other comparative tests of putative antiparasite adaptations (Bell 1982; Hamilton 1982; Hamilton and Zuk 1982; Burt and Bell 1987; Lively 1987; Read and Harvey 1989; Read 1991).

METHODS

Snails were collected from 49 freshwater sites in Kano State, Nigeria (12°N, 9°E), between November 24, 1991, and January 23, 1992. Sites were within a 200-km radius of Kano City (Schrag 1993; Schrag et al. 1994), a region of flat plains approximately 450 m above sea level (Olofin 1987). Sites included dams, night storage reservoirs, fish ponds, irrigation canals, slow-flowing rivers, borrow pits, temporary ponds, and one natural lake. Over the course of the study, different areas of the region were visited in an arbitrary order. Snails were collected by searching vegetation, sticks, and stones and by a long-handled net with 1-mm

mesh. Searching and collections were limited to an area within 3 m of shore since *Bulinus truncatus* typically lives in shallow water (Appleton 1978). At extremely low-density sites, searching was terminated after 2 h; otherwise, search times represented the time necessary for two people to find a total of at least 50 snails. All *B. truncatus* greater than 2 mm and all other mollusks (Ancylidae, *Bulinus globosus, Bulinus forskali, Biomphalaria pfeifferi, Lymnaea natalensis, Cleopatra* sp.) encountered while searching were collected and brought to the laboratory the same day in plastic pots containing vegetation but no water.

Proportion of Euphallics

Within populations, we scored snails for phally once ($N = 27$), twice ($N = 13$), or three times ($N = 9$) over the course of the study. We waited a minimum interval of 28 d (mean interval = 32 d) between repeated collections in order to track the change in proportion of euphallics across generations. Phally is determined during the first weeks after oviposition, prior to sexual maturity, and does not change once it develops (de Larambergue 1939). In the laboratory, newly hatched snails take approximately 4 wk to reach sexual maturity (approximately 3 mm in shell length).

During each collection for phally scoring, an effort was made to find 50 *B. truncatus* greater than 2 mm in shell length. Snails were scored nondestructively for phally the day of collection by inspection under a binocular microscope as described in an earlier article (Schrag et al. 1992). There was negligible mortality between collection and scoring. Any dead snails or snails in which phally was uncertain were dissected to determine the state of development of the male reproductive tract.

Density

Density of *Bulinus truncatus* was calculated at each site at the time of collection as total number of *B. truncatus* encountered divided by person-minutes of searching (minutes of collection multiplied by number of people collecting). Density of other mollusk species was calculated similarly. Shell length of all *B. truncatus* collected was measured from the apex to the base of the spire by a vernier caliper to the nearest 0.25 mm.

Water Chemistry

Water characteristics (pH, oxidation-reduction potential, and conductivity) were measured at each site with a Hanna Instruments water test meter. At nine sites these variables were measured at approximately 7-d intervals; at the remaining sites they were measured at the time of snail collection. Estimates of each variable were calculated as the average of readings from six within-site locations. In addition, dissolved oxygen was measured in milligrams per liter with a Jenway portable oxygen meter (model 9070) that automatically compensated for temperature. Dissolved oxygen readings at each site were the average of multiple readings of the oxygen meter.

Prevalence of Patent Trematode Infection

After phally scoring, all snails from each collection were placed individually in clear plastic containers filled with 5 mL of tap water and left under natural lighting and ambient temperature in the laboratory. After 24 h containers were scored for presence of cercariae by inspection with a hand lens or low-magnification binocular microscope. Cercariae are known to have both diurnal and nocturnal emergence patterns and to survive for an average of 48 h after shedding (Frandsen and Christensen 1984). At one site all snails died before we scored for infection; this site is excluded from our estimates of parasite pressure.

Prevalence is not a direct measure of the degree to which a species is exposed to infection. In particular, differences in prevalence between sites may reflect differences in exposure, resistance, or both. We assume that prevalence of patent infections reflects levels of exposure to parasites, a common assumption in both comparative (see, e.g., Read 1991) and field (see, e.g., Lively 1987) studies. Because most patent trematode infections take 4–5 wk to develop within their intermediate hosts (Anderson and May 1979), prevalence of patent infection is an estimate of parasite pressure some weeks prior to the scoring of infection.

When parasite prevalences are significantly higher or lower than 50%, small sample sizes bias estimates of parasite prevalence. Because trematode prevalence in this study was well below 50% (mean overall prevalence = 23%), we considered only prevalences based on scoring results of more than 10 individuals as suggested previously (Read and Harvey 1989).

Trematode Diversity

At each site, cercariae from individually shedding snails were identified to major group level according to morphological taxonomies provided in the literature (Frandsen and Christensen 1984; Ndifon and Umar-Yahaya 1988–1990). Cercariae to be identified were narcotized with methyl red, extended under a coverslip, and inspected under a compound microscope.

We estimated diversity of trematodes within populations by calculating the number of different trematode taxa at each site (trematode richness). At each site we also calculated three standard ecological measures of diversity that take into account both richness and prevalence (Magurran 1988). First is Simpson's index, D, defined as

$$D = \sum_{i=1}^{n} p_i^2,$$

where p_i is the prevalence of trematode taxa i, and n is the total number of trematode taxa. This index is weighted toward the abundance of the most common trematode taxa. Second is the Shannon index, H:

$$H' = \sum_{i=1}^{n} p_i \ln p_i,$$

which gives more weight to rare taxa. Finally, we calculated the Berger-Parker index, d, given as

$$d = \frac{N_{max}}{N},$$

where N is the number of snails scored for infection, and N_{max} is the number of snails infected with the most abundant trematode taxon.

Statistical Analysis

Preliminary analysis showed that a significant effect of season on a number of variables was obscured by an averaging of repeated measures. Consequently, only measurements from first visits to sites were included in cross-population analyses.

Variables with significant diurnal variation were standardized by calculating residuals of population means against time of day. When we controlled variables for time of year, we calculated residuals of population against day of data collection, with November 18, 1991, as day 1. All proportions were arcsine transformed, density and conductivity were log transformed, and trematode richness was square root transformed before applying parametric statistics. Spearman rank-correlation coefficients (r_s) were calculated when variables did not meet the assumptions of parametric statistics; otherwise, Pearson correlation coefficients (r) are reported. Because minor modifications in assumptions of both the parasite and spatial variation hypotheses may produce predictions in the direction opposite to those presented earlier in this article (see, e.g., Mitchell-Olds and Waller 1985; Read 1991), all probabilities are two-tailed.

RESULTS

A total of 3,830 *Bulinus truncatus* from 49 sites were scored for phally. Estimates of the proportion of euphallics in each population, based on the scoring results (mean $\pm$ 1 SE) of 48.5 $\pm$ 1.6 individuals per site, ranged from 0 to 0.81 (fig. 1). There was no evidence of a geographical relationship between site locality and proportion of euphallics. Indeed, sites less than 1 km apart differed in proportion of euphallics by as much as 50%; within 10 km along the same road, the range in proportion of euphallics spanned the range encountered over the course of the study.

Temperature-sensitive phally determination has been demonstrated in the laboratory (Schrag and Read 1992) and in these field populations (Schrag et al. 1994) and is at least partly responsible for significant variation in proportion of euphallics owing to season over the course of the study ($r^2 = 45\%$; Schrag et al. 1994). Consequently, we control for the effects of time of year in the following analysis.

Reproductive Assurance Hypothesis

Although density of *B. truncatus* varied within and between sites (mean density = 1.2 snails per person-minute; range across sites = 0.1–8.4), the relationship between density of *B. truncatus* and proportion of euphallics was not significant
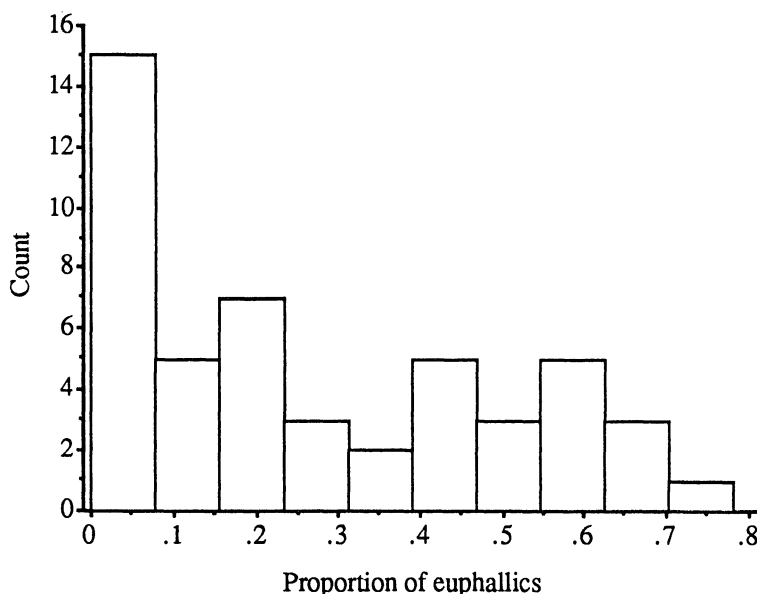
Fig. 1.—Frequency distribution of proportion of euphallics across 49 populations in the Kano City region, Nigeria. Only proportions from first visits are shown for sites visited more than once.

across sites ($r = -0.16$, $N = 49$, $P = .28$). Note that the direction of the correlation is negative, with some of the most dense sites having no or extremely low numbers of euphallics, contrary to the prediction that euphally will be common in dense populations in which snails have a high encounter rate.

Over the course of the study, the relationship between density and time of year was close to significant ($r = -0.26$, $N = 49$, $P = .08$). When we partialed out the effects of time of year, the relationship between density and proportion of euphallics was still not significant (partial $r = 0.02$, $P = .89$).

Spatial Variation Hypothesis

Theoretical, experimental, and field observations suggest that intraspecific competition at high population densities decreases growth and fecundity of African freshwater snails (reviewed in Brown 1980). Thus, the weak negative relationship between density and proportion of euphallics is also contrary to the spatial variation hypothesis. However, if density fluctuated predictably within populations, the hypothesis may still hold. In this case, the spatial variation hypothesis predicts that euphally will increase prior to increases in density because outcrossed offspring will have an advantage at high densities when intraspecific competition is strong.

At the 22 sites we visited more than once, density increased significantly between first and final collections (increase in 18 sites, decrease in four; binomial $p = 0.004$). In addition, the proportion of euphallics within sites increased sig-

TABLE 1

WATER CHARACTERISTICS AND THEIR RELATIONSHIP WITH PROPORTION OF EUPHALLICS, CONTROLLING
FOR THE EFFECTS OF TIME OF YEAR, AND WITH TIME OF YEAR

		CORRELATION WITH PROPORTION OF EUPHALLICS			CORRELATION WITH DATE		
	MEAN ± 1 SE	r	N	P	r	N	P
pH	8.2 ± .08	.06	49	.7	−.40	49	<.001
ORP (mV)	81.6 ± 4.0	−.20	49	.18	−.14	49	.340
DO$_2$ (mg/L)	7.2 ± .34	−.003	36	.98	−.28	36	.100
Conductivity (μS)	268.8 ± 50.3	−.32	49	.025	−.12	49	.410

NOTE.—Proportion of euphallics was arcsine transformed, and estimates of water characteristics were corrected for time of day as described in the text before calculating Pearson's correlation coefficients (r). ORP, oxidation-reduction potential; DO$_2$, dissolved oxygen.

nificantly over the course of the study (Schrag et al. 1994). Since density was increasing within sites, the spatial variation hypothesis predicts that the proportion of euphallics early in the season will correlate positively with the magnitude of within-site changes in density. However, the correlation between initial proportions of euphallics and the change in density between first and final visits (measured as final density minus first density) was negative and not significant ($r_s = −0.26$, $N = 22$, $P = .24$).

Density of other mollusk species may also reduce resources and lead to an increase in intraspecific competition. The mean density of other mollusks was 0.5 and ranged from zero to 4.9 snails per person-minute of searching. There was no significant relationship between density of other mollusk species and proportion of euphallics ($r = 0.21$, $N = 49$, $P = .15$) or between the number of mollusk species within a site and the proportion of euphallics ($r_s = 0.24$, $N = 49$, $P = .10$). When we controlled for time of year, the relationship between density of other mollusks and proportion of euphallics was still not significant (partial $r = −0.07$, $N = 49$, $P = .63$). Over the course of the study, there was no trend toward an increase or decrease in density of other mollusks at the sites we visited repeatedly (decrease in eight sites, no change in eight sites, increase in six sites) or in the number of mollusk species (decrease in three sites, no change in 14 sites, increase in four sites).

Water chemistry also indicates resource availability and thus may reflect levels of intraspecific competition. Presence/absence of snails in water bodies has been linked to pH, conductivity, and dissolved oxygen content (Brown 1980). Sites differed in pH, oxidation-reduction potential, dissolved oxygen, and conductivity (pH range = 7.1–9.9; oxidation-reduction potential = 36–140 mV; dissolved oxygen = 1.7–10.9 mg/L; conductivity = 59–1,812 μS). There was no evidence of a significant relationship between pH, oxidation-reduction potential, or dissolved oxygen and proportion of euphallics (table 1). Conductivity, however, correlated significantly with proportion of euphallics, with lower conductivities favoring higher proportions of euphallics. When we controlled for season, the

correlation between conductivity and proportion of euphallics remained significant (partial $r = -0.32$, $N = 49$, $P = .025$).

Temporal Variation Hypothesis

We found *B. truncatus* in three broad classes of habitat: dams, ponds, and irrigation systems (described in detail in Schrag 1993). With respect to water level and vegetation, dams were the most stable environments, and irrigation channels were the least stable. Few dams dry up completely and most support vegetation throughout the year, while water levels in irrigation channels depend on both season and farming activities. Proportion of euphallics, however, did not differ significantly with habitat type (95% confidence limits on proportion of euphallics in dams: 0.10–0.31; ponds: 0.15–0.41; irrigation systems: 0.14–0.69; ANOVA on arcsine-transformed data: $F = 1.26$, df = 2,45, $P = .29$). Proportion of euphallics in a population was still not related to habitat when the effects of season were controlled for ($F = 0.81$, df = 2,44, $P > .45$). Habitats also differed in water depth, substrate, vegetation density and diversity, and human activity. None of these characteristics showed a consistent relationship with proportion of euphallics (Schrag 1993).

Seasonal changes in water chemistry may also contribute to environmental instability. There was no evidence of a seasonal change in oxidation-reduction potential, conductivity, or dissolved oxygen over the course of the study (table 1). We noted that pH decreased over the course of the study, possibly because of decreasing temperatures in the dry-cool season. However, there was no significant within-site change in pH (decrease in 12 sites, no change in one site, increase in nine sites) and no overall relationship between pH and proportion of euphallics.

Red Queen Hypothesis

The selective pressure exerted by parasites on their hosts could be related to intensity of infection (number of parasites per host), parasite prevalence (proportion of sampled individuals that are infected), and parasite diversity (Clayton et al. 1992). Intensity of infection is not a meaningful measure of pressure in the case of larval trematodes, in which a single miracidium produces large numbers of cercariae within its host; the number of cercariae at any one time is thus largely dependent on time since infection. Mean parasite prevalences broken down by phally and cercarial morphological group are shown in table 2. The overall prevalence of patent trematode infection at each site correlated positively and almost significantly with the proportion of euphallics ($r = 0.26$, $N = 48$, $P = .07$; table 2). Snail age (size), however, introduces error into our measure of parasite prevalence. Most larval trematodes have a prepatent period of 4–5 wk within their snail hosts prior to cercarial shedding (Anderson and May 1979), and so there is a minimum age (size) below which infection will not be patent. Furthermore, prevalence of infection is likely to drop in older snails because of parasite-induced mortality. Indeed, across our sites there was a weak relationship between mean snail size and prevalence of patent infection, best described by a second-order polynomial regression ($r = 0.32$, $P = .09$). Consequently, we controlled

TABLE 2

MEAN WITHIN-SITE PREVALENCE OF PATENT TREMATODE INFECTION AND
ITS RELATIONSHIP WITH PROPORTION OF EUPHALLICS

	MEAN WITHIN-SITE PREVALENCE	PREVALENCE IN APHALLICS	PREVALENCE IN EUPHALLICS	PARTIAL CORRELATION WITH PROPORTION OF EUPHALLICS	
				r	P
Overall	.23 ± .03	.26 ± .04	.21 ± .04	.27	.072
Excluding Xiphidiocercariae	.12 ± .02	.12 ± .02	.10 ± .03	.17	.26
Xiphidiocercariae	.12 ± .02	.14 ± .03	.11 ± .03	.32	.032
Longifurcate	.06 ± .02	.05 ± .01	.06 ± .03	.11	.49
Amphistome	.02 ± .01	.03 ± .01	.01 ± .01	.05	.75
Brevifurcate	.01 ± .00	.01 ± .00	.00 ± .001	− .03	.86
Echinostome	.01 ± .01	.01 ± .01	.02 ± .08	.09	.54
Other	.04 ± .01	.03 ± .01	.02 ± .01	.05	.74

NOTE.—Mean prevalences are shown separately for aphallics and euphallics; correlations are based on prevalences in aphallics and euphallics combined. Prevalences of trematode infection and proportion of euphallics were arcsine transformed, and both variables were controlled for mean snail size (age) and time of year as described in the text. $N = 48$ in all cases.

prevalence measures for size by taking the residuals of a polynomial regression between mean snail size and prevalence of infection. There was also a relationship between mean snail size and proportion of euphallics (Schrag et al. 1994). When we partialed out the effects of mean snail size from both variables, the resulting relationship between overall parasite prevalence and proportion of euphallics became significant ($r = 0.33$, $N = 48$, $P = .024$).

Time of year, however, might generate this correlation. At the sites we visited repeatedly there was no correlation between parasite prevalences (corrected for size) at our first and second visits ($r_s = 0.21$, $N = 19$, $P = .36$), but across sites parasite prevalence varied significantly with time of year ($r = 0.4$, $N = 48$, $P = .02$). When we partialed out the effects of time of year, the resulting correlation between parasite prevalence and proportion of euphallics was marginally significant ($r = 0.27$, $N = 48$, $P = .072$; table 2).

Overall trematode prevalence may obscure associations between individual trematode taxa and proportion of euphallics. The prevalence of sexual *Potamopyrgus antipodarum*, a gastropod with sexual and parthenogenetic morphs, was found to correlate significantly with particular trematode taxa although not with overall prevalence of trematode infection when the effects of density were controlled for (Lively 1992). Indeed, the correlation between proportion of euphallics and prevalence of Xiphidiocercariae, the most abundant trematode taxon, was positive and significant when we controlled for both mean snail size and time of year ($r = 0.32$, $N = 48$, $P = .032$; fig. 2), while the relationships between other trematode classes and proportion of euphallics were not significant (table 2).

Across sites, the relationship between trematode richness and proportion of euphallics was positive and significant ($r = 0.30$, $N = 48$, $P = .04$) but not when
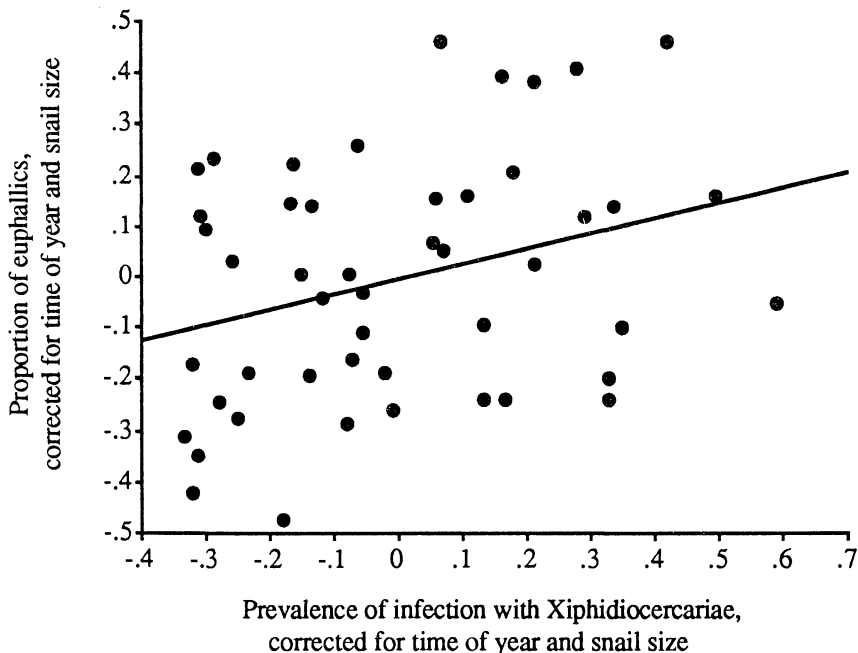
FIG. 2.—Relationship between proportion of euphallics and prevalence of patent infection with Xiphidiocercariae. Both variables were arcsine transformed and corrected for time of year and mean snail size as described in the text.

we partialed out the effects of time of year (table 3). However, the relationship between proportion of euphallics and all three indexes of trematode diversity was significant when we controlled for mean snail size and time of year (table 3). Because the mean prevalence of each class of trematode was low (table 2), these indexes correlated strongly with each other. They also all correlated strongly with prevalence of Xiphidiocercariae (mean $r = 0.70$). Consequently, these data do not allow us to separate statistically the influence of trematode diversity from the influence of prevalence of Xiphidiocercariae infection on proportion of euphallics.

Do aphallics and euphallics differ in their susceptibility to trematode infection? When we compared overall trematode prevalence to aphallics and euphallics either by pooling data across sites or by combining 2 × 2 tables according to the Cochran method (Armitage and Berry 1987), prevalence of infection was significantly higher in aphallics (pooled data, $\chi^2_{[1]} = 6.7$, $P = .01$; Cochran test, $\chi^2_{[1]} = 6.29$, $P < .05$; table 2). While this difference in parasite prevalence may reflect a true difference in exposure or susceptibility between aphallics and euphallics, it may also be generated by size and age differences between the two types. Over the course of this study, smaller (and therefore younger) snails were likely to be euphallic (Schrag et al. 1994). Within-site differences in parasite prevalence between aphallics and euphallics correlated strongly with within-site differences in mean size of aphallics and euphallics ($r_s = 0.48$, $P = .0029$), which

TABLE 3

PARTIAL CORRELATIONS BETWEEN MEASURES OF
TREMATODE DIVERSITY AND PROPORTION OF
EUPHALLICS, CONTROLLING FOR THE EFFECTS
OF TIME OF YEAR AND MEAN SNAIL SIZE

DIVERSITY MEASURE	CORRELATION WITH PROPORTION OF EUPHALLICS	
	r	P
Richness	.16	.30
Simpson	.37	.011
Shannon	.31	.039
Berger-Parker	.36	.013

NOTE.—Diversity measures are described in the
text under *Trematode Diversity*. N = 48 in all
cases.

suggests that infection prevalences in aphallics were higher in part because of the
relationship between size/age and prevalence.

There was no association between conductivity and size-corrected prevalence
of Xiphidiocercariae infection ($r = -0.10$, $N = 48$, $P = .69$).

DISCUSSION

Over a small geographical scale, the proportion of snails capable of sperm
donation varied significantly among natural populations of *Bulinus truncatus*
(mean proportion of euphallics = 27%; range = 0%–81%). We found no associa-
tion between population density and euphally across sites, inconsistent with stan-
dard interpretations of the reproductive assurance hypothesis for the maintenance
of euphally. Similarly, Lively (1992) was able to exclude this hypothesis for *Pota-
mopyrgus antipodarum*, a gastropod with sexual and parthenogenetic forms. Out-
crossing, however, may be maintained by reproductive assurance in some plant
species with mixed mating systems (see, e.g., Clay 1982; Barrett et al. 1987).

The maintenance of outcrossing in selfing populations is traditionally explained
either by selection against selfing due to deleterious effects of inbreeding depres-
sion or by selection for outcrossing due to the benefits of producing genetically
variable offspring. Reductions in fitness due to inbreeding depression must be
severe (outcrossed progeny must be at least two times as fit as selfed progeny)
to prevent the spread of selfing within populations (Charlesworth 1980; Maynard
Smith 1989). Although there are no direct measures of the magnitude of inbreed-
ing depression in populations of *B. truncatus,* several lines of evidence suggest
it is unlikely to be this severe. First, *B. truncatus* is a tetraploid of hybrid origin
(allotetraploid), and so selfing may not lead to increased homozygosity as rapidly
as in diploid organisms. Indeed, electrophoretic analyses of *B. truncatus* report
a high frequency of loci with fixed (nonsegregating) heterozygote patterns (Wright

and Rollinson 1981; Jelnes 1986; Njiokou et al. 1993*b*). Furthermore, tetraploidy can select for self-fertilization by reducing the inbreeding depression due to recessive lethal and sublethal mutations (Lande and Schemske 1985). Second, electrophoretic studies of natural populations of *B. truncatus,* the existence of 100% aphallic populations, and theoretical models of conditions required for the maintenance of aphally suggest that selfing rates are high in *B. truncatus* (Jarne et al. 1992; Njiokou et al. 1993*a*). Habitually self-fertilizing populations will have eliminated many lethal recessives and thus tend to have lower levels of inbreeding depression than outcrossing populations (Maynard Smith 1978; Lande and Schemske 1985). Third, laboratory experiments measuring the hatching success and survival of *B. truncatus* hatchlings produced by self-fertilization predict that the cost of selfing due to inbreeding depression is small in *B. truncatus* (Jarne et al. 1992).

Finally, if a population passes through the initial negative effects of inbreeding, it can evolve into a viable selfing population and is unlikely to revert back to outcrossing (Maynard Smith 1989). Observations of populations that are 100% aphallic in the field and that do not show intrapopulation variation in proportion of euphallics due to temperature (Schrag et al. 1994) suggest that inbreeding depression is not an insurmountable obstacle to the establishment of 100% selfing populations in *B. truncatus.* Consequently, our analyses have focused on the possible benefits of producing variable offspring by outcrossing.

In that context, we found no evidence of a link between euphally and resource availability (estimated by snail density, mollusk species abundance, water pH, oxidation-reduction potential, and dissolved oxygen content), contrary to predictions of the spatial variation hypothesis. We also found no association between levels of euphally and habitat instability (estimated by habitat type, human activity, vegetation density, rate of desiccation, and changes in water chemistry), contrary to predictions of the temporal variation hypothesis. This lack of association is also contrary to predictions of the spatial variation hypothesis that more stable habitats will have higher proportions of euphallics. We note, however, that, without comprehensive knowledge or perhaps better measures of all variables related to resource availability and habitat instability, we cannot dismiss the spatial or temporal hypotheses on the basis of these null results.

Conductivity, in contrast, explained a significant percentage of variation in proportion of euphallics ($r^2 = 10\%$, controlling for time of year), with lower ion concentrations correlated with higher levels of euphally. Conductivity in freshwater reflects the total concentration of seven major ions: Na^+, K^+, Ca^{++}, Mg^{++}, HCO_3^-, Cl^-, and SO_4^{--} (Beadle 1974). A similar association between conductivity (in particular, concentrations of Mg^{++}, Ca^{++}, Na^+, and Cl^-) and prevalence of males was found across bisexual and parthenogenetic populations of the freshwater snail, *Melanoides tuberculata,* in Israel (Heller and Farstey 1990). However, the relationships between water chemistry, snail biology, and habitat ecology are not well understood (Brown 1980; Jordan and Webbe 1982), though calcium is one of the essential elements for snail growth (Brown 1980). Middle ranges of conductivity (300–400 μS for *Biomphalaria pfeifferi*) are often optimal for African

freshwater snails; conductivities outside this range result in increased hatching time, delayed egg production, and decreased fertility (Brown 1980).

Overall prevalence of trematode infection correlated positively with proportion of euphallics but not when we controlled for the effects of mean snail size (age) and time of year. However, prevalence of Xiphidiocercariae, the most abundant trematode taxon, correlated positively and significantly with proportion of euphallics ($r^2 = 10\%$ when we partialed out the effects of snail size and time of year), in support of the red queen hypothesis. Overall trematode prevalence may not have reflected this trend as strongly because different trematode taxa can exert opposing selective pressure on hosts. For example, selection for sexual reproduction decreases as antagonism between parasites and hosts decreases, with mutualistic interactions favoring asexuality (Law and Lewis 1983). Furthermore, larval trematodes are known to interact with each other within molluscan hosts, in some cases predisposing and in others preventing hosts from further trematode infection (Loker et al. 1981; Sousa 1990).

Trematode richness did not correlate with prevalence of euphally when we controlled for time of year. Indexes of diversity that incorporated both prevalence and richness, in contrast, correlated significantly with prevalence of euphally when we controlled for snail size and time of year. It may be that diversity per se is an important source of parasite-mediated selection for outcrossing; however, because the diversity indexes we calculated correlated strongly with prevalence of Xiphidiocercariae infection, this data set does not allow us to distinguish these measures.

A similar relationship between prevalence of infection with the most abundant trematode taxon and prevalence of individuals capable of reproducing sexually was found across New Zealand populations of *P. antipodarum;* this relationship is not because of habitat type and is most consistent with the red queen hypothesis (Lively 1987, 1992). We note that, in *P. antipodarum,* the relationship between prevalence of Xiphidiocercariae and prevalence of males was not significant (Lively 1987); while Xiphidiocercariae was the most common infection in *B. truncatus* in the populations we sampled, the prevalence of Xiphidiocercariae infection in *P. antipodarum* was extremely low (mean prevalence = 1%).

Although the mean overall prevalence of trematode infection in our study (23%) was higher than in Lively's (1987) study (11%), prevalence of infection with the most abundant trematode taxon in both *P. antipodarum* (Lively 1992) and *B. truncatus* explained less than 15% of the total variation in prevalence of euphallics or males, when known third variables were controlled for. These correlations may be weak for a number of reasons (Lively 1992). In particular, we note that the red queen hypothesis predicts these correlations will be weak. First, both studies consider only parasite pressure due to trematodes; both *P. antipodarum* and *B. truncatus* act as hosts to parasites other than trematodes, and these may also contribute to overall parasite pressure host snails experience. Second, time lags in host-parasite coevolution are expected to result in weak correlations (Bell 1982; Frank 1991).

Furthermore, additional sources of noise might obscure a relationship between

parasite pressure and proportion of euphallics. As we pointed out in Methods, it is unclear how well parasite prevalence correlates with the strength of parasite-imposed selection. Furthermore, in *B. truncatus* the average life span in the field is approximately 3 mo (maximum of 6 mo; McCullough 1962), so within-population prevalence of trematode infection can fluctuate because of season over the course of an individual's lifetime (Betterton 1984; Schrag 1993). Consequently, point estimates of trematode prevalence may not accurately reflect parasite pressure in particular populations (see, e.g., Woolhouse and Chandiwana 1989). Also, proportions of euphallics fluctuate within populations (Schrag et al. 1994). Because a snail's phally does not change once it develops, point estimates of proportions of euphallics within populations may reflect past or future levels of trematode pressure and need not correlate with present trematode pressure to be consistent with the red queen hypothesis.

For these theoretical and empirical reasons, then, weak cross-population correlations between variation in breeding system and parasite prevalence are expected even when parasite-imposed selection is the main driving force. That we found such a correlation might be considered striking evidence in support of the red queen hypothesis. Equally, the weak correlation may show that parasite-imposed selection is actually relatively unimportant. We suspect that it is impossible to distinguish between these views by considering a single correlation in isolation. In this context, it is perhaps notable that of all the site-specific variables we considered, the two that correlated significantly with proportion of euphallics have been found to correlate similarly in other freshwater snails (trematode prevalence in *P. antipodarum* [Lively 1987, 1992] and conductivity in *M. tuberculata* [Heller and Farstey 1990]), despite the fact that these snails belong to different subclasses (*B. truncatus* is a pulmonate, while the other two are prosobranchs) and have different breeding systems (*B. truncatus* reproduces by selfing or outcrossing, while the other two reproduce parthenogenetically or sexually). Additional correlational support for the red queen hypothesis comes from a number of studies (comparative evidence: Bell 1982; Burt and Bell 1987; field evidence: Antonovics and Ellstrand 1984; Schmitt and Antonovics 1986; Lively et al. 1990; Burt and Bell 1991; Moritz et al. 1991). In contrast to the results reported here and by Lively (1987, 1992), however, no relationship was found between prevalence of males and either overall trematode prevalence or prevalence of infection of individual trematode taxa across *M. tuberculata* populations in Israel (Heller and Farstey 1990).

The correlation between trematode prevalence and proportion of euphallics we report here has the potential to explain the maintenance of temperature-sensitive phally determination: seasonal variation in parasite pressure due to Xiphidiocercariae and/or trematode diversity correlates with seasonal variation in proportion of euphallics (Schrag et al. 1994). In view of this conclusion and the above results, we suggest that parasite-mediated selection for outcrossing, as envisaged by the red queen hypothesis, provides the most parsimonious explanation for the maintenance of euphally in *B. truncatus* in northern Nigeria. The relative viability of outcrossed and selfed broods when exposed to parasites would allow direct tests of this view. Now that the parentage of offspring can be genetically determined

(Jarne et al. 1993), such an experiment may be feasible, as well as direct measurement of the genetic variability of selfed and outcrossed broods.

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