

SPERM PARASITISM IN ANTS: SELECTION FOR INTERSPECIFIC MATING AND HYBRIDIZATION

GARY J. UMPHREY¹

Department of Mathematics and Statistics, University of Guelph, Guelph, Ontario N1G 2W1 Canada

Abstract. Interspecific mating in eusocial Hymenoptera can be favored under certain conditions even if all hybrid offspring are completely infertile. This exploits two key features of the eusocial Hymenoptera: a haplodiploid genetic system and reproductive division of labor in females. Interspecifically mated queens can still produce viable sons that will mate intraspecifically. Apparent reduced fitness resulting from producing infertile daughter gynes can be also offset by advantages conferred by hybrid workers. An important advantage is likely to be superior ability at using marginal habitats. Interspecifically mated queens can nest in sites where intraspecific competition will be low. By mating interspecifically, a queen trades expected reproductive success through female offspring for a higher probability of achieving some reproductive success. Females that mate interspecifically can be considered “sperm parasites” on the males of the other species. I provide evidence that sperm parasitism is responsible for widespread hybridization in North America among two species of the ant subgenus *Acanthomyops* (genus *Lasius*), and review evidence for sperm parasitism in other hybridization phenomena in ants. Sperm parasitism in ants represents a novel form of social parasitism in ants and a dispersal polymorphism. It may also act as a precursor to the evolution of some other recently discovered phenomena, such as genetic caste determination.

Key words: *Acanthomyops*; ants; cleptogamy; dispersal polymorphism; hybridization; hybridogenesis; *Lasius*; mating strategies; mixed ESS; sperm parasitism.

INTRODUCTION

The usual interpretation of the occurrence of infertile interspecific hybrids in ants (as in most other organisms) is that they represent unfortunate “accidents” in which premating and postmating isolating mechanisms between species have been at least partially circumvented. For example, Holldobler and Wilson (1990:145), in discussing the perilous journey faced by new queen ants leaving their parent nest to establish a colony, noted that “the few individuals that navigate all the dangers must also avoid breeding with males of other species, thereby producing nonviable or sterile offspring.” While it has been argued that hybridization has played an underappreciated role in both plant and animal evolution (e.g., see Arnold 1997, 2004, Arnold et al. 1999, Dowling and Secor 1997, Mallet 2005, Seehausen 2004), the fitness consequences for the hybridizing parents are still typically considered maladaptive if hybrid offspring are infertile or nearly so.

The incidence of ant colonies producing apparently infertile hybrids is nonetheless surprisingly high among some pairs of species. One such case occurs in the subgenus *Acanthomyops* (genus *Lasius*; see Ward [2005] regarding the current taxonomic treatment). Wing

(1968), primarily on the basis of morphological and distributional evidence, was the first to hypothesize that *L. (A.) claviger* males occasionally mate interspecifically with *L. (A.) latipes* gynes wherever the species are sympatric, in northeastern North America west to Minnesota (see maps 1 and 3 of Wing [1968]). Colonies with interspecifically mated *L. (A.) latipes* queens successfully produce F₁ hybrid workers (morphologically intermediate between *L. (A.) claviger* and *L. (A.) latipes* workers, but difficult to distinguish from the latter), F₁ hybrid gynes, and typical *L. (A.) latipes* males. Wing (1968) found no evidence that the hybrid gynes ever successfully founded a colony. Umphrey and Danzmann (1998) used enzyme electrophoresis to corroborate essentially all of Wing’s conclusions; no evidence of backcrossing by F₁ was found, though the possibility of low level introgression could not be ruled out. Wing (1968) hypothesized that since *Acanthomyops* species found their colonies through temporary social parasitism on other *Lasius* species (e.g., *Lasius neoniger*), F₁ hybrid queens with intermediate behavioral patterns may not have the appropriate set of complex behavioral patterns necessary to be adopted into a *Lasius* nest.

Analyzing the same phenomenon over a century ago, Wheeler and McClendon (1903) incorrectly concluded that the F₁ hybrid gyne was a second form of *L. (A.) latipes* gyne, which they designated as the α -female; the true *L. (A.) latipes* gyne was designated as the β -female. Although the hybrid gynes were so clearly intermediate between the smaller *L. (A.) claviger* gynes and the much

Manuscript received 31 May 2005; revised 23 January 2006; accepted 30 January 2006; final version received 13 March 2006. Corresponding Editor: P. Nonacs. For reprints of this Special Feature, see footnote 1, p. 2141.

¹ E-mail: umphrey@uoguelph.ca

larger and morphologically bizarre *L. (A.) latipes* gynes (see Plate 1), Wheeler and McClendon (1903) rejected the hybridization hypothesis in favor of their dimorphic queens hypothesis, stating that "It is improbable that hybridization could occur so frequently in a state of nature as appears to be indicated by the high percentage of nests containing α -females and their occurrence in such widely separated localities. If we are really confronted a case of hybridism we are almost compelled to believe that the α -female must be sterile, notwithstanding her well-developed ovaries, or the two species would long since have merged into one." The actual proportion of nests containing hybrid gynes that were seen by Wheeler and McClendon (1903) is not known, but two estimates can be obtained for regional populations. Talbot (1973) reported finding 56 *L. (A.) "latipes"* colonies among the 110 *Acanthomyops* colonies she found in over 20 years of study at the Edwin S. George Reserve in Michigan. Six of the 25 gyne-producing colonies were producing "alpha-form" (= *L. (A.) latipes* \times *claviger*) gynes. Among gyne-producing colonies with *L. (A.) latipes* queens, the proportion with an interspecifically mated queen is thus estimated to be 0.24 ± 0.17 (point estimate \pm 95% confidence bound using the normal approximation for binomial proportions). Umphrey and Danzmann (1998) used colonies collected from two main sites separated by about 50 km in southern Ontario; of these, 22 colonies produced *L. (A.) latipes* gynes, 25 produced *L. (A.) latipes* \times *claviger* hybrid gynes, and four colonies produced both *L. (A.) latipes* and hybrid gynes. Pooling the samples across sites, the proportion of gyne-producing colonies with *L. (A.) latipes* queens producing only hybrid gynes was 0.49 ± 0.14 , while the proportion of gyne-producing colonies producing at least some hybrid gynes was an astonishing 0.57 ± 0.14 .

Pearson (1982, 1983a, b, 1987) studied a similar hybridization phenomenon in Dorset, England. Electrophoretic evidence demonstrated that colonies containing workers morphologically intermediate between *Lasius alienus* and *L. niger* were F₁ hybrids resulting from the mating of *L. alienus* gynes with *L. niger* males. Males produced in such colonies were sons of the *L. alienus* queens. No evidence of successful colony founding by F₁ hybrid gynes was found. Under a grid of 496 slate slabs over an eight hectare heathland study area, Pearson (1987) obtained 49 nest centers occupied by colonies with *L. alienus* workers and nine nest centers occupied by colonies with hybrid workers. Among colonies with *L. alienus* queens, the proportion that were interspecifically mated is estimated (with a 95% confidence bound) to be 0.16 ± 0.05 .

Seifert (1999) used high-precision stereomicroscopy and chorological data to estimate the extent of hybridization in the ant fauna of Central Europe. He concluded that 17 of the 164 ant species definitely hybridized and another two species were strongly suspected to hybridize. Many pairs of species hybridized

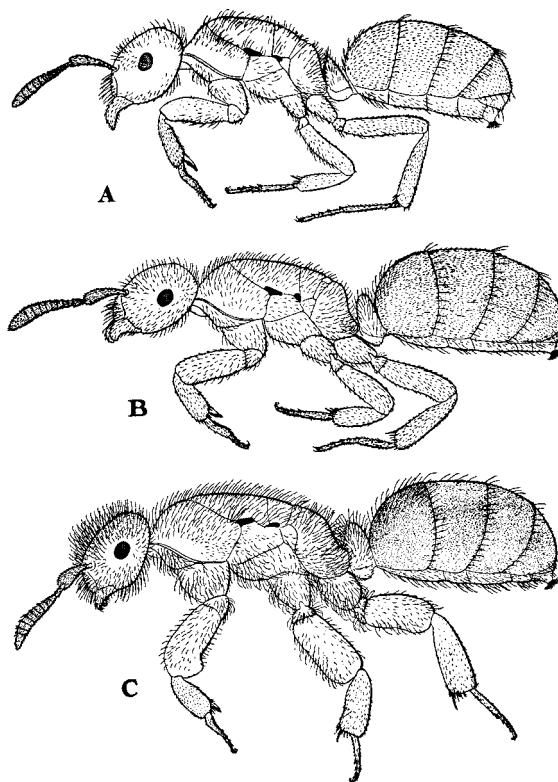


FIG. 1. A, *Lasius claviger* Roger α -Q; B, *Lasius latipes* Walsh α -Q; C, *L. latipes* β -Q. The wings are omitted.

PLATE 1. Fig. 1 of Wheeler and McClendon (1903), reprinted from the *Biological Bulletin*. The original caption is included. The drawing in (B) is actually a *Lasius latipes* \times *claviger* F₁ hybrid gyne, and (C) is the true *L. latipes* gyne.

at relatively low levels, but in local areas, 19% of *Lasius jensi* queens and 44% of *Leptothorax albipennis* queens in established nests had mated interspecifically (with *Lasius umbratus* males for *L. jensi*, and with *Leptothorax tuberum*, *L. nigriceps*, and *L. unifasciatus* males for *L. albipennis*). While Seifert's results remain to be confirmed genetically, they are entirely consistent with the hybridization phenomena involving *Lasius (Acanthomyops) latipes* \times *claviger* and *Lasius alienus* \times *niger*.

Wing (1968), Pearson (1983b, 1987) and Seifert (1999), as well as Wheeler and McClendon (1903), were all fully aware that interspecifically mated queens still produce sons of their own species and thus could achieve at least some reproductive success if they could successfully found nests with hybrid workers. Wing (1968), Pearson (1983b, 1987) and Seifert (1999) all recognized the advantage of colonies with interspecifically mated queens shifting their production of reproductives to males. But the key question of how the cost of producing infertile hybrid gynes can be offset has remained.

In this paper, I argue that the high levels of ant colonies containing interspecific hybrids in these cases,

and likely in other cases, may be occurring not simply as a result of “accidents” but rather through selection for interspecific mating. Fundamental to the argument is that the subsequent production of hybrid workers will allow a colony with an interspecifically mated queen either to avoid intense intraspecific competition for suitable nest sites among colonies with intraspecifically mated queens, or to outcompete colonies with intraspecifically mated queens under some set of environmental conditions. Heinze and Tsuji (1995) concluded that spatial and temporal distribution of habitats and the availability of nest sites were key factors in the evolution of diverse ant reproductive strategies. Tschinkel (1996) provided an elegant empirical cost-benefit analysis of how intense intraspecific competition for nest sites could have driven the evolution of a newly discovered, socially parasitic mode of nest founding in the monogyne form of the fire ant *Solenopsis invicta*. Using *Drosophila*, Bolnick (2001) obtained experimental evidence that intraspecific competition can drive niche width expansion. Essentially I argue here that interspecific mating in ants (and possibly in other eusocial Hymenoptera) could be considered an alternative form of dispersal mechanism that may allow a species to expand its ecological niche in the face of intense intraspecific competition for nest sites.

Since the reproductive benefits of mating interspecifically accrue only to the queen and at considerable cost to the heterospecific male she mates with, interspecific mating in ants can be considered a form of interspecific sexual parasitism. Seifert (1999) has used “cleptogamy” for the same phenomenon. I prefer sperm parasitism because of its simplicity and the fact that it is clear which gametes are being parasitized. Sperm parasitism as proposed here has an interesting parallel with hybridogenesis, also considered another form of “sexual parasitism” (see Moore 1984): the male genome in the hybrids is essentially “borrowed” for one generation before being discarded, but unlike hybridogenesis no unusual cytological mechanism is required. The term “sperm parasitism” is sometimes used in association with gynogenetic fish (e.g., Bohlen and Ritterbusch 2000, Schlupp et al. 2002, Schlupp 2005), but the term applies equally well for hybridogenetic organisms and its usage is unique within ants.

Recently the terms “social hybridogenesis” and “genetic caste determination” have been applied both to a hybridization phenomenon between *Solenopsis xyloni* gynes and *S. geminata* males (Helms Cahan and Vinson 2003), and the “dependent lineages” found within the genus *Pogonomyrmex* that are morphologically similar to *P. barbatus* and *P. rugosus*; the latter has been the subject of intense interest and investigation (see Ashe and Oldroyd 2002, Julian et al. 2002, Helms Cahan et al. 2002, 2004, Volny and Gordon 2002, Helms Cahan and Keller 2003, Parker 2004, Schwander et al. 2006, and all other papers in this feature). In both situations genetic evidence has demonstrated that the highly

heterozygous workers differ in genetic composition from the reproductive gynes produced in the colonies, hence “genetic caste determination.” Since the fathers of the workers come from populations genetically isolated from the populations that the mothers belong to but do not contribute genetically to the next generation of reproductives, fathers of the heterozygous workers are essentially sperm donors to hybridogenetic females.

The primary motivation of this paper is to develop a model of selection for facultative sperm parasitism in ants and demonstrate its application to *Lasius (Acanthomyops) latipes* × *claviger* hybridization. The model likely accounts for some other known hybridization phenomenon in ants, including *Solenopsis xyloni* × *geminata* hybrids. The application of the model to *Pogonomyrmex* awaits further data, as it is not clear how the “dependent lineages” originated (see Helms Cahan and Keller 2003, Anderson et al. 2006) or whether they are in fact reproductively isolated lineages (Linksvayer et al. 2006). Unifying all cases, however, is the fact that a worker caste genetically distinct from female reproductive offspring offers opportunities for colonies to establish and persist under some ecological conditions.

THE GENERAL MODEL

Members of the eusocial Hymenoptera (all ants and some bees and aculeate wasps) live in colonies, are haplodiploid, and usually have a reproductive division of labor in the female sex (Wilson 1971, Hölldobler and Wilson 1990). With rare exceptions (Bourke 1988), eggs produce males if unfertilized and females if fertilized. A female can be reared either as a gyne (reproductive female) or as a member of one or more worker castes. A monogynous colony has a single queen (inseminated gyne) and all female offspring are her daughters. Males may be the offspring of either the queen or one or more workers; the proportion of males produced by workers varies from 0 to 1, depending on the species and sometimes on the local environment (Bourke 1988, van der Have et al. 1988, Crozier and Pamilo 1996). The inclusive fitness of each colony member depends on maximizing the genetic output of the colony through the production of gynes and males, subject to the optimality constraints imposed by queen-worker conflict (Hölldobler and Wilson 1990, Crozier and Pamilo 1996).

The life span of an adult queen and the colony she founds can be divided into prereproductive and reproductive stages. During the prereproductive stage (the founding stage plus ergonomic stage of Hölldobler and Wilson 1990) in ants, the virgin gyne typically leaves the parent nest, mates, and locates a nest site. This stage continues through the early founding and growth of the new colony, and will range from a single warm season to five or more years (Oster and Wilson 1978).

Now consider a species (species A) of ant that forms monogynous colonies, and for which the gynes can mate with the males of another ant species (species B). Initially assume that an individual gyne mates either

entirely intraspecifically or entirely interspecifically. This is certain if the gyne mates with only one male, but it is also likely if she mates several times in a “swarm” composed mainly of males of a single species. The consequence of interspecific mating for a queen is that any daughter offspring she produces will be hybrids. If workers of species A are essentially infertile anyhow, the production of infertile hybrid workers will not necessarily result in a loss of fitness, but any reduced fertility in the hybrid gynes will result in reduced fitness. If the hybrid gynes are infertile or at least never successfully produce offspring, then the investment in female reproductives is completely lost. But since any sons the queen produces are pure species A males, interspecific mating need not result in a complete loss in fitness, if these males can mate with gynes produced by colonies with intraspecifically mated queens. Interspecific mating can always be considered adaptive as a “best of a bad situation” (BBS) strategy if, for example, if a gyne could not find a mate of her own species (Gross 1984, Parker 1984). Under certain conditions, however, hybrid workers can confer a benefit that will offset the cost of producing infertile hybrid gynes and favor a gyne to mate interspecifically even if both conspecific males and high quality nesting sites are potentially available.

For a defined population, let R be the event that a gyne reaches the reproductive stage, and let F be a random variable representing the lifetime inclusive fitness of the gyne. Where necessary, denote mating strategy with a subscript $i = 1$ for intraspecific mating and $i = 2$ for interspecific mating. The probability of reaching the reproductive stage for a gyne that is about to leave the colony and mate under strategy i is $P_i(R)$, and her expected lifetime inclusive fitness is $E[F_i]$ (her “unconditional expected fitness” under strategy i). However, the expected lifetime inclusive fitness of a queen that has reached the reproductive stage is $E[F_i|R]$ (the “conditional expected fitness” under strategy i); note that

$$E[F_i] = P_i(R)E[F_i|R]. \quad (1)$$

In general $P_i(R)$ will be very small due to the high mortality rate of new queens, thus $E[F_i]$ will be much less than $E[F_i|R]$. Also define a parameter c such that

$$E[F_2|R] = cE[F_1|R]. \quad (2)$$

It is possible to obtain $c \geq 1$ if colonies with interspecifically mated queens shift to all-male production and/or there is a heterotic advantage to a colony with hybrid workers in producing reproductives under the local conditions. But, in general, we would expect $c < 1$; that is, a colony that has reached the reproductive stage with an interspecifically mated queen will achieve, on average, only a fraction of the reproductive output it could have if it had an intraspecifically mated queen. Producing infertile gynes is the obvious reason for this, but other factors that may reduce c include possible reduced viability or reduced ergonomic efficiency of

hybrid workers, reduced production of reproductives, shorter expected colony life span, and lower mating success for male offspring. Selection will operate on the $E[F_i]$ values rather than the $E[F_i|R]$ values, however. To compensate for a lower $E[F_i|R]$ value for colonies with interspecifically mated queens, they must have a sufficiently higher probability of getting to the reproductive stage, that is $P_2(R) > P_1(R)/c$, for selection to favor interspecific mating ($P_2(R) \leq 1$; if $P_1(R)/c > 1$, selection cannot favor interspecific mating except as a BBS strategy). Note that no value of $c > 0$ is too small for selection to favor interspecific mating as long as $P_2(R)$ is sufficiently high in comparison to $P_1(R)$.

A simple situation favoring hybrid colonies is if there are “marginal” nest sites available that can be used successfully by colonies with hybrid workers, thus allowing an interspecifically mated queen to avoid high intraspecific competition for nest sites in habitat more optimal for colonies with intraspecifically mated queens. Ecological preferences of workers of the parent species will likely differ, and those of the hybrid workers are likely to be intermediate. The use of intermediate habitats by hybrids has been established in both plants and animals (e.g., Stebbins 1950, Wright and Lowe 1968, Grant 1981, Moore 1984, Arnold 1997). Colonies with hybrid workers may be able to occupy sites unusable to either parent species, thus expanding the ecological niche for species A (the “weed hypothesis”; see Wright and Lowe 1968; Moore 1984), or they may be able to outcompete colonies of both parent species in intermediate habitats (the “ecological intermediacy hypothesis”; see Moore 1984). Since an interspecifically mated queen of species A is not a hybrid herself, the “marginal” nest sites used would likely be in habitat more similar to that preferred by species A. Pearson (1982, 1983b) demonstrated such a situation in his study on *Lasius alienus* \times *niger* hybrids. The preferred nesting habitat is dry for *L. alienus* and wet for *L. niger* (Pearson 1982). Colonies with hybrid workers were found mainly at the edge of the area dominated by *L. alienus*, bordering the damper area (Fig. 1 of Pearson 1983b).

For a species in which each colony has one singly mated queen and the queen produces the males, it has been argued that the equilibrium sex ratio of reproductives (assuming complete outbreeding in the population) in terms of energetic investment in males is $s = 0.25$ if the workers control the sex ratio or $s = 0.50$ if the queen is in control of the sex ratio (Trivers and Hare 1976). The relative control of the sex ratio between the queen vs. the workers is a subject of much analysis (e.g., Nonacs 1986a, b, Crozier and Pamilo 1996, Passera et al. 2001). Boomsma (1989) concluded female bias has been systematically overestimated and the proportion of energetic investment in males is, on average, greater than 0.25. But under a “worse case” scenario, if a hybrid colony produced reproductives at the equilibrium sex ratio of $s = 0.25$, then 75% of its energetic investment in reproductives will have been wasted on the production

of infertile gynes. If all other factors are equal, this gives a value of $c = 0.25$, which is clearly a major decrease in $E[F|R]$ for mating interspecifically. However, if the probability of an interspecifically mated queen reaching the reproductive stage is greater than four times that for an intraspecifically mated queen, then selection would favor interspecific mating.

Clearly, interspecific mating cannot be a pure strategy, as males produced by interspecifically mated queens must mate with gynes produced by intraspecifically mated queens. I propose that it can, however, exist as part of a mixed evolutionarily stable strategy (ESS), in the sense of Maynard Smith (1982). A population with all queens interspecifically mated cannot exist, since males from such colonies must have fertile gynes with which to mate, but a strategy of interspecific mating can invade and spread in a population of intraspecifically mated queens, if there is a fitness advantage in doing so. Two probable factors make the model frequency dependent in the right way. First, the relative fitness value of males is directly proportional to the relative abundance of fertile gynes with which to mate. The second probable factor arises under the hypothesis that the primary advantage to interspecific mating is to allow use of "marginal" nest sites. In a steady state population, as the proportion of queens that mate interspecifically increases, the competition for "marginal" nest sites among such queens will increase, and the competition among the intraspecifically mated queens for "good" nest sites will decrease; on this basis, the function f such that $P_1(R) = f\{P_2(R)\}$ is strictly monotone decreasing. We would expect the value of interspecific mating relative to intraspecific mating to decline as p , the proportion of the population of queens that mate intraspecifically, decreases and $q (= 1 - p)$, the proportion of the population of queens that mate interspecifically, increases. If all gynes have the same access to each species of male and each type of nest site, the value of p such that $E[F_1] = E[F_2]$ will be the equilibrium (or evolutionarily stable) proportion, p_E , that should mate intraspecifically.

Each gyne in the population will "play the mating game" only once. It does not matter what the probability of any given individual gyne mating interspecifically is, it matters only that the proportion in the population that actually does is $q_E = 1 - p_E$. In practice, we would expect that species A gynes that fly near the "marginal" habitat are also more likely to encounter and mate with males of species B than are gynes flying near the center of the "good" habitat. Thus the probability that a gyne mates interspecifically is likely to be positively correlated with the proximity of its parent colony to marginal nest sites; this also increases the probability that an interspecifically mated queen is going to find the type of habitat in which she can successfully compete. The system can still be stable even if $E[F_1] > E[F_2]$, so that p_E is not the value of p that equalizes the unconditional expected fitness values. We would also expect interspecific mating to be a facultative

strategy, as a gyne should certainly mate intraspecifically if species B males are not present, but interspecifically as a BBS strategy if a conspecific male is not available.

A specific testable hypothesis generated by the model, robust to a wide range of conditions, is that the proportion of gynes mating interspecifically should be less than the proportion of colonies with interspecifically mated queens if natural selection is favoring interspecific mating; furthermore, how much less should reflect the costs of mating interspecifically. If interspecific mating is simply an "accident" where a few interspecifically mated queens happen to be lucky enough to establish nests, the proportion of gynes mating interspecifically will likely be greater than the proportion of colonies with interspecifically mated queens.

Interspecific matings are "purposeful" in the sense that selection could operate against the strengthening, and for the weakening, of premating reproductive isolating barriers for gynes of species A (it should operate to strengthen them for males of species B, although possibly not as strongly). Timing of the mating flights is one simple mechanism likely to have a genetic basis for selection to operate on. The proportion of species A gynes that are released at the same time as the males of species B could be adjusted by natural selection to try to obtain the correct p_E value for the local conditions. It also seems possible that if species B mating flights try to shift away from those of species A, mating flights for a proportion of species A gynes might "track" those of species B in evolutionary time.

Factors affecting costs and benefits of hybridization

Sufficient genetic compatibility to produce viable workers and male production by the interspecifically mated queens are necessary conditions, while a higher value of c makes it easier for selection to favor interspecific mating as part of a mixed ESS. Reduced viability for hybrid worker offspring (e.g., a higher proportion dying prior to adulthood) will reduce c , but reduced viability of hybrid gynes could increase c if it causes a shift towards producing more males; note that F_1 hybrid gynes do not appear to be produced as a result of *Lasius jensi* × *umbratus* matings (Seifert 1999). Workers must have a competitive advantage over species A workers (and possibly also over species B workers) under some set of conditions. They may be physiologically intermediate in, for example, their moisture and/or temperature preferences; these confounded variables may be the most important for niche separation of many pairs of closely related ant species (Talbot 1934). The F_1 hybrids can be expected to have very high levels of heterozygosity (Schlupp 2005), so hybrid vigor through heterosis may be possible (see Hubbs 1955, Bulger and Schultz 1979, Milborrow 1998, Burke and Arnold 2001). Hybrid workers may be less susceptible to disease or parasites, particularly if only F_1 hybrids are produced (see Boecklen and Spellenberg 1990, Floate and Whitham 1993, Penn et al. 2002; but

for cases of greater susceptibility, see Sage et al. 1986, Dupont and Crivelli 1988; also see Mouliia 1999).

Selection for sperm parasitism is easier if the queens normally produce all of the males, unless the queen would produce more males if hybrid workers were unable to do so. In many species, male production by workers is suppressed in the presence of the queen, but can occur after her death; this fitness loss will be nil or rather small for some species but could be considerable for species with short colony life spans (e.g., see Evans 1996).

Fitness decreases as s decreases if colonies with interspecifically mated queens invest in males at the same proportion. Factors that appear to influence the value of s include the degree of control over s exerted by the queen (Trivers and Hare 1976) and the number of times the queen mates, with multiple mating reducing worker control of the sex ratio (Woyciechowski and Łomnicki 1987). Theoretical advantages have been argued for each colony investing in each sex at the equilibrium sex ratio (Taylor and Sauer 1980) as well as for splitting the sex ratio (Roisin and Aron 2003). Most species show considerable variation in the actual sex ratio among colonies, including single-sex specialization (Nonacs 1986a, b, Boomsma and Grafen 1990, Crozier and Pamilo 1996, Reuter and Keller 2001). It clearly benefits a colony with an interspecifically mated queen to rear only male reproductives. The ability of a colony to shift its alate production should be influenced by how well it “knows” the mating strategy used by its queen. This might be probabilistically cued, for example, by the location of the colony’s nest site. Certain phenomena already noted in ants may be useful preadaptations. Nonacs (1986b) has reviewed the evidence that gyne production is favored when resources are abundant and male production when resources are scarce (but see Crozier and Pamilo 1993 for an alternative hypothesis). Colonies in “marginal” habitats may tend to produce a higher proportion of males if they perceive resources as being scarce. The tendency for young colonies to specialize in males would be beneficial if colonies with interspecifically mated queens have a shorter expected life span.

On a broad geographical basis, the quality of the habitat for providing nest sites will vary considerably. The relative abundance and spatial distribution of marginal habitat should affect the ability of the interspecifically mated queens to find suitable nest sites. Rarity may depress the value of $P_2(R)$ such that the “ c gap” cannot be overcome, but in some localities “marginal” nest sites may be more abundant than “good” nest sites. Habitat variation throughout the range of a species should affect both the absolute $E[F_i|R]$ values and their relative value c . Temporal variability of a habitat may open up nest sites for which both species A and species B are poorly adapted, but which hybrids can use. Human alteration of habitat has often been implicated in hybridization phenomena

(Wasserman 1957, White 1973, Pearson 1982, Moore 1984, Seifert 1999) but similar natural disturbances can occur from a variety of abiotic and biotic agents (Moore 1984).

Intraspecific competition can be expected on theoretical grounds to be particularly intense in many ant species by virtue of their trophic level in the food web and the large size and long life of their colonies (Hölldobler and Wilson 1990). Species with large colonies tend to be highly territorial toward conspecifics (Janzen 1967, Hölldobler and Lumsden 1980, Hölldobler and Wilson 1990). A founding queen typically has an extremely small chance of establishing a colony within the territory of a mature conspecific colony. Nest sites become available with the death of existing colonies; in some species the turnover rate can be low due to the great longevity of mature colonies. Janzen (1967), Tschinkel (1992, 1996), and Gordon and Kulig (1996, 1998) provide excellent examples documenting the intensity of intraspecific competition for establishing nests. Intraspecific competition can also reduce the fitness of reproductive colonies (e.g., see Pontin 1961), increasing the pressure to find alternative nesting sites. However, interspecific competition may make the use of marginal habitat in stable ecosystems with a high degree of species packing (such as in tropical rainforests) too difficult for selection to favor sperm parasitism.

Species B males should be both abundant and not too discriminating. In species B, strong sexual dimorphism that results in a numerical surplus of males may predispose the small males to being less discriminating, particularly if gynes typically mate singly. The cost to a species B male of interspecific mating is very high (likely a complete loss of reproductive fitness) and thus it might be expected that selection would not favor interspecific mating. But the cost is likely more than offset by greater selective pressure to find a suitable mate, since a nuptial flight is of short duration and often subject to intense predation. Incorrect mate recognition is not uncommon among insect males. Pollination of over 150 species of orchids depends on employing sexually deceptive chemical and physical mimicry to exploit the sexual aggressiveness of male insects (Ayasse et al. 2001, Schiestl et al. 2004). Gwynne and Rentz (1983) reported the classic case of male *Julidomorpha bakewelli* buprestid beetles attempting to copulate with discarded beer bottles that had a coloration and reflection pattern similar to that of the female elytra. A similar question arises as to why males would mate with females of unisexual hybridogenetic and gynogenetic species when they receive no reproductive benefits (Kawecki 1988, Schlupp 2005), but whatever the proximate factors are, the key thing is that they do.

Consequences of mixed matings

If a species A queen has mated with both species A and species B males, at least some daughter gynes are likely to be members of her own species, reducing her

loss in conditional expected fitness as long as the hybrid workers can confer a benefit as part of a mixed worker force. Further benefits accrue if any mechanism acts to select among female immatures so that a disproportionately higher share of gynes (relative to the proportion of species A sperm stored in the queen's spermatheca) are pure species A (e.g., if hybrid gynes are smaller and grow slower, they might be weeded out as larvae from becoming gynes). Under some conditions, a disproportionately higher share of workers being hybrids could be beneficial. Such a system has arisen in the *Pogonomyrmex* dependent lineages, where in each pair of dependent lineages a multiply-mated queen must mate with at least one male of the other lineage to produce workers, and at least one male of her own lineage if she is going to produce daughter gynes (Helms Cahan et al. 2006, Schwander et al. 2006). In the dependent lineages related to *P. barbatus*, homozygous (same-lineage) eggs in young colonies are culled by workers (Clark et al. 2006) or the proportion of homozygous offspring declines from eggs to larvae to pupae (Volny et al. 2006). Very few heterozygous (interlineage) gynes are produced in either pair of dependent lineages (Helms Cahan et al. 2002, 2004).

Another consequence of a mixed worker force is that an automatic genetic caste system is generated among the workers that may trigger an associated division of labor based on physical or behavioral differences. For example, suppose hybrid workers were on average larger than species A workers. If smaller workers are more likely to conduct a greater share of the brood rearing and larger workers are more likely to forage, excavate, and defend the nest, then species A workers would be better positioned to control which female larvae are reared as gynes, while the hybrid workers have tasks for which they are ergonomically superior.

Consequences of polygyny

Polygynous (multiple queen) colonies could contain both intraspecifically and interspecifically mated queens. This offers the potential advantage of at least part of the worker force being hybrids to intraspecifically mated queens as well as to interspecifically mated queens. Such a system appears to have evolved in at least some sites in Texas where the fire ants *Solenopsis xyloni* and *Solenopsis geminata* are sympatric. Hung and Vinson (1977) using enzyme markers, and Helms Cahan and Vinson (2003) using both enzyme and microsatellite markers, demonstrated that colonies producing *Solenopsis xyloni* × *geminata* F₁ workers largely produced not only *S. xyloni* males but mainly *S. xyloni* gynes; only a few F₁ hybrid gynes were found. Since *Solenopsis* queens were believed to mate singly but form polygynous colonies, Helms Cahan and Vinson (2003) concluded the colonies contained both intraspecifically mated and interspecifically mated (with *S. geminata*) queens. Almost all workers were F₁ hybrids, suggesting shunting of developing female hybrid larvae to workers

and *S. xyloni* female larvae to gynes (Helms Cahan and Vinson 2003).

Polygynous colonies could potentially accept mated hybrid F₁ gynes into the colony. A route for introgression is provided if mated F₁ gynes are able to produce any backcross reproductive offspring even if they are unable to found their own colony. Indeed Helms Cahan and Vinson (2003) reported finding a few backcross hybrid workers and gynes, as well as a single backcross male.

Helms Cahan and Vinson (2003) found no pure *S. xyloni* colonies, suggesting that hybrid workers are essential for colony survival, at the sites studied. An interesting conflict thus arises. At least one interspecifically mated queen is required for colony survival, yet intraspecifically mated queens will potentially achieve higher reproductive success unless one or more of the following occur: (1) interspecifically mated queens specialize in producing males, (2) intraspecifically mated queens have a lower probability of ending up in a reproductively successful colony than an interspecifically mated queen, (3) relatedness among queens in a colony confers indirect fitness benefits to an interspecifically mated queen, (4) hybrid workers suppress reproduction of sexuals by intraspecifically mated queens in favor of reproduction of males by their own mother.

Unidirectional vs. reciprocal sperm parasitism

In *Lasius (Acanthomyops) latipes* × *claviger*, *Lasius alienus* × *niger*, and *Solenopsis xyloni* × *geminata*, hybridization is unidirectional. There appears to be no reason why facultative sperm parasitism cannot be a reciprocal phenomenon between two species, and indeed hybridization is reciprocal under the hypothesis of obligate dependent lineages within *Pogonomyrmex*. But in order for sperm parasitism to be selected for in both directions, it is necessary not only that reciprocal hybridization can occur but that hybridization is selected for in both directions. Wirtz (1999) found that hybridization appeared to be unidirectional in 50 out of 80 studies with sufficient mitochondrial DNA data. Wirtz (1999) reviewed eleven prezygotic and three postzygotic causes for unidirectional hybridization. We can usefully distinguish between proximate factors that prevent or restrict hybridization in one direction and ultimate factors that influence whether or not interspecific mating can pay as other than a BBS strategy.

Among proximate causes, a wide variety of physical or behavioral differences in reproductives may restrict interspecific matings to one-way crosses. Jessen and Klinkicht (1990) documented this phenomenon in their cross-breeding experiments involving five species of the socially parasitic ant genus *Epimyrma*. Crosses of *E. adlerzi* gynes with *E. corsica* males and *E. kraussei* gynes with *E. corsica* males failed completely, although the reciprocal crosses were very successful. They attributed the failures as likely due to the relatively small size of *E. corsica* males, noting that "they tried to mate with the

heterospecific [gynes] but possibly were too small to give tactile signals with their antennae on top of the female's head and simultaneously insert the genital apparatus into the female's genitalia." When the gynes of the two species differ in average size, the larger gynes may be a superstimulus to the other species' males, whereas the smaller gynes may be perceived as very poor quality mates (or not even perceived as potential mates) by heterospecific males. I consider this to be a strong candidate as a hypothesis for why hybridization is unidirectional in *Lasius (Acanthomyops) latipes* × *claviger*. There could well be asymmetries in how each species responds to the sex pheromones of the other species.

Even if copulation takes place reciprocally, barriers for preventing fertilization by interspecific sperm may be more effective in one direction (Wirtz 1999). If fertilization does occur, Wirtz (1999, citing Baird et al. 1992, Wu and Polopoli 1994) noted that several genetic mechanisms can provide an asymmetric postmating barrier to the development of viable hybrid offspring. Microorganisms such as *Wolbachia*, which is typically inherited maternally, can potentially cause unidirectional cytoplasmic incompatibilities (see Mandel et al. 2001).

Among possible ultimate factors, Pearson (1983b) suggested that hybrid workers may be more useful if they are larger, say, at least under some conditions. The parent species may differ in one or more important components of male production strategy: queen versus worker reproduction, the value of *s*, and the ability of individual colonies to shift the sex ratio. If species A usually mates earlier in a season than species B, it may be easier for some gynes to remain in the nest for later mating with males of species B than it would be for species B to accelerate gyne production to mate with males of species A. There needs to be a ready supply of males of the other species; interspecific mating may be favored by gynes of the less common or more patchily distributed species (Wirtz 1999, Randler 2002). Differences in mature colony sizes, colony life span and nest site turnover rate, and reproductive output will result in differing intensities of intraspecific competition. One species may be more resistant to the local community of pathogens and other parasites, so hybrid workers with some or all of this greater resistance will be of greater benefit to a queen of the less resistant species.

TESTING THE SPERM PARASITISM MODEL IN *ACANTHOMYOPS*

Nest queens in mature *Acanthomyops* colonies are rarely found (see Cover and Sanwald 1988); nonetheless, a strong case can be made that sperm parasitism as outlined in the general model is operating in *Lasius (Acanthomyops) latipes* × *claviger* hybridization. As previously noted, Talbot's (1973) data generates 95% confidence limits of 0.24 ± 0.17 for the proportion of interspecifically mated queens in the population of gyne-

producing colonies with *L. (A.) latipes* queens at the George Reserve. For Umphrey and Danzmann's (1998) data pooled across sites in southern Ontario, the estimated proportion of gyne-producing colonies with *L. (A.) latipes* queens that were producing at least some hybrid gynes was 0.57 ± 0.14 (if mixed gyne colonies are excluded, the proportion of gyne-producing colonies with *L. (A.) latipes* queens that were interspecifically mated was 0.53 ± 0.14). Even the lower limits of the confidence intervals represent a high proportion of colonies with interspecifically mated *L. (A.) latipes* queens that have successfully made it to the reproductive stage. But what proportion of *L. (A.) latipes* gynes mate interspecifically with *L. (A.) claviger* males during the mating flights?

It is very unlikely to be as high as the proportion of reproductive colonies with interspecifically mated queens, and indeed is very likely to be much less, since the great majority of *L. (A.) latipes* gynes take their mating flights substantially earlier in the year than do most *L. (A.) claviger* males. Talbot (1973) carefully documented brood development and flight times of *Acanthomyops* colonies in her 20+ years of study at the George reserve. She noted that *L. (A.) claviger* was the latest of all five *Acanthomyops* species in developing reproductives, and that "the distinctive feature of the *A. claviger* flights was that they occurred at lower temperatures than those of other *Acanthomyops* species at the Reserve. They did not start until the temperature fell below 70°F [21.1°C] and they continued until 64°F [17.8°C] was reached. Thus they began at about the temperature when flights of other species were ending." Although *L. (A.) claviger* flights typically occurred after her field season concluded, in the one year she stayed into October she recorded flights on 2 and 3 October. In contrast, Talbot (1973) observed 33 *L. (A.) latipes* flights, which took place between August 17 and September 27; of these, 16 took place in the last week of August and eight in the first week of September. She reported temperatures at flight time were 81°F down to 73°F (27.2°C to 22.8°C). Talbot's observations in Michigan are highly concordant with my own in southern Ontario. Typically, *L. (A.) latipes* flies in mid-August to mid-September, but the occasional colony will have later flights. Most *claviger* reproductives fly later in the year than most *L. (A.) latipes*, though I have observed both species flying at the same time (as did Wheeler and McClendon 1903). But while there are certainly opportunities for interspecific mating to occur for some *L. (A.) latipes* queens, this must represent a relatively small fraction of the *L. (A.) latipes* gynes taking mating flights. Given the proportion of reproductive colonies with interspecifically mated *L. (A.) latipes* queens, it can be concluded that, on average, an interspecifically mated *L. (A.) latipes* gyne must have had a higher probability of reaching the reproductive stage than an intraspecifically mated *L. (A.) latipes* gyne, and likely much higher, as predicted by the

general model, to offset the cost of producing hybrid gynes.

What advantage does a colony with hybrid workers have for reaching the reproductive stage? Mature *Acanthomyops* colonies are very large and capable of immense alate production. They can also be very long lived; Talbot (1973) had one colony under observation for 21 years that was still producing *L. (A.) latipes* males and hybrid gynes when she wrote her paper. These conditions are expected to generate intense intraspecific competition for nest sites. In southern Ontario, *L. (A.) latipes* typically nests only in well-drained sandy soils, whereas *L. (A.) claviger* nests in a wide range of soil types ranging from sand to clay. Talbot (1963) described the soil at the George Reserve as being "loose sandy soil," suitable for both species. But while *L. (A.) latipes* colonies were largely restricted to field margins with scattered oak trees, Talbot (1973) found *L. (A.) claviger* to be the most versatile of the *Acanthomyops* species in habitat usage, nesting not only in the preferred *L. (A.) latipes* habitat but also in the interiors of woods. It appears that *L. (A.) latipes* is more specialized in its preferred habitat than *L. (A.) claviger*, and I suspect that *L. (A.) claviger* is more moisture-tolerant than *L. (A.) latipes*. I postulate that hybrid workers are more moisture-tolerant than *L. (A.) latipes* workers, allowing colonies with interspecifically mated queens to be much more successful in nest sites somewhat damper on average than those usually preferred by *L. (A.) latipes*. This hypothesis is still subject to field testing in *Acanthomyops*, but the scenario is reflected in the nesting site pattern illustrated by Pearson (1983b) in his study of *Lasius alienus* × *niger* hybrids.

DISCUSSION

Sperm parasitism may be more likely to arise in ants than in other eusocial Hymenoptera; I know of no really good candidate cases in wasps or bees, although a hybridization case reported in *Melipona* by Nascimento et al. (2000) might merit further study. The eusocial wasps and bees are much less taxonomically diverse than ants (Wilson 1971), and, in many species, their workers are more likely to produce a large proportion of the males (Bourke 1988). Intraspecific competition in colony establishment may be less intense in bees and wasps, as they do not produce the immense number of reproductives characteristic of some ant species, and many species produce annual colonies. Hybridization may have more serious consequences to the ergonomic efficiency of a flying insect than a wingless insect (Schneider et al. 2003). Also, since flying results in a much larger foraging territory, hybrid bees or wasps may be unable to exploit marginal habitats like hybrid ant workers could, as ants have more microhabitat specialists.

Sperm parasitism may be a subtle phenomenon that presents taxonomic problems in recognizing cases in nature. It is likely that hybridizing species are closely related, morphologically very similar (at least in the

worker caste), and perhaps sibling species. Most ant taxonomy is based on workers since reproductives are collected much less often, so it may be difficult to recognize hybridizing species as being genetically isolated if morphologically intermediate hybrid workers are fairly common. The presence of hybrid gynes presents a similar problem if this caste is used. If the males of the two species are morphologically distinct (for example, in genitalia) but the female castes are poorly differentiated, workers and gynes from hybrid colonies with associated males may be allocated to the species of the nest queen, rather than recognized as hybrids. Clusters of sibling species are quite common in ants (Crozier 1981), so other cases will likely be discovered with modern molecular methods. It would also seem prudent to verify genetically that all known cases of dimorphic queens are being properly interpreted, and that one of the queen morphs is not an interspecific hybrid.

The mixed ESS model for sperm parasitism predicts that selection can favor interspecific mating even if "good" nest sites and conspecific males are available and even if hybrid colonies obtain, on average, only a small proportion of the reproductive output of colonies with intraspecifically mated queens. By mating interspecifically, queens can increase their expected reproductive output by trading potential reproductive output for a higher probability of reaching the reproductive stage. The role of differential probability in successfully founding a mature, reproductive colony is made clear by differentiating between the expected fitness for a gyne at the time of leaving the parent nest to mate (the "unconditional expected fitness") and the expected fitness for a queen (and her colony) that has successfully reached the reproductive stage. Similar arguments may have been overlooked in evaluating hybridization phenomena outside the eusocial Hymenoptera.

On a colony level, sperm parasitism clearly has tremendous costs when many nonreproducing F₁ gynes are produced, as occurs for many colonies with interspecifically mated *Lasius (Acanthomyops) latipes* queens. An interesting parallel can be made between sperm parasitism and the classic example of a balanced polymorphism presented in many introductory biology texts, the maintenance of sickle cell trait in areas in Africa with high rates of malaria. In each case a very heavy cost (sickle cell anemia in individuals homozygous for sickle cell trait, nonreproducing F₁ gynes) is offset by the benefits conferred (greater resistance to malaria by individuals with sickle cell trait, advantages provided by hybrid workers). Sickle cell trait is but one of several otherwise deleterious alleles which are selectively maintained in the human population in malaria-endemic areas (Fortin et al. 2002). It remains to be determined how important heterozygosity itself is in selection for producing hybrid workers in ants. The obligate nature of hybridogenesis in the *Pogonomyrmex* dependent lineages suggests that locking in heterozygosity at one

or more loci is likely to be the critical factor in maintaining these systems.

The model has been developed here without invoking any unusual cytological mechanisms, such as thelytoky. But when selection favors interspecific mating such that hybrid gynes are produced in great quantities as they are in the *Lasius (Acanthomyops) latipes* × *claviger* hybridization phenomenon, then repeated opportunities for unusual cytological mechanisms to arise are created. Arnold (1997) has stressed that rarely are all hybrids completely infertile, so hybridization provides opportunities for new genotypes to establish. Hybridization may also play a major role in the generation of unusual cytological mechanisms (Normark 2003). Clearly the mechanism discovered by Percy et al. (2004), in which *Cataglyphis cursor* queens conditionally use parthenogenesis to produce daughter gynes while producing workers sexually, would be a tremendous asset to an interspecifically mated queen if hybrid workers were useful. Even more peculiar possibilities are suggested by the recent discovery of clonal reproduction by males and females in *Wasmannia auropunctata* (Fournier et al. 2005). Gynes are produced as clones of their mother, and clonal production of males is likely achieved by eliminating the maternal genome in diploid eggs. If a mechanism arose in which a portion of fertilized eggs laid by an interspecifically mated queen produced males by eliminating the maternal genome, the father would no longer be parasitized. But if all reproductive-destined eggs encountered the same fate, the roles of which species is being parasitized would be reversed, and the phenomenon would properly be described as androgenesis, or egg parasitism.

Umphrey and Danzmann (1998) noted that the pattern of hybridization in *Lasius (Acanthomyops) latipes* × *claviger*, with hybrids occurring wherever the species were sympatric and any backcrossing of F₁ hybrid gynes rarely if ever occurring, differed sharply from the usual concept of hybrid zones of varying width (often narrow) in which parapatric populations meet and hybridize (e.g., Barton and Hewitt 1985, Moore and Price 1993). The hybrid zone definition of Arnold (1997) is sufficiently broad to capture any hybridization phenomena, but the pattern of hybridization is still unusual. This hybridization pattern, the fact that selection can favor interspecific mating in ants (and other eusocial Hymenoptera), even if all hybrids are sterile, recent discoveries on genetic caste determination (possibly) involving hybridization, and the theoretical possibilities of what might yet be discovered in nature will not only provide rich avenues for further research for myrmecologists but results of substantial general interest to all biologists.

ACKNOWLEDGMENTS

I am deeply indebted to Peter Nonacs for his generous advice and continual encouragement throughout the development of this paper. I also thank Ross Crozier, Laurent Keller, Ian MacNeill, Peter Taylor, and Phil Ward for their comments on

previous versions of the manuscript. The suggestions of two anonymous reviewers have been invaluable. I also thank Stefan Cover for kindly sharing his insights on *Acanthomyops* biology.

LITERATURE CITED

- Anderson, K. E., J. Gadau, B. M. Mott, R. A. Johnson, A. Altamirano, C. Strehl, and J. H. Fewell. 2006. Distribution and evolution of genetic caste determination in *Pogonomyrmex* seed-harvester ants. *Ecology* **87**:2171–2184.
- Arnold, M. L. 1997. Natural hybridization and evolution. Oxford University Press, Oxford, UK.
- Arnold, M. L. 2004. Transfer and origin of adaptations through natural hybridization: were Anderson and Stebbins right? *Plant Cell* **16**:562–570.
- Arnold, M. L., M. R. Bulger, J. M. Burke, A. L. Hempel, and J. H. Williams. 1999. Natural hybridization: how low can you go and still be important? *Ecology* **80**:371–381.
- Ashe, A., and B. Oldroyd. 2002. Genetic determination of caste in harvester ants. *Trends in Ecology and Evolution* **17**:448–449.
- Ayasse, M., R. J. Paxton, and J. Lengo. 2001. Mating behavior and chemical communication in the order Hymenoptera. *Annual Review of Entomology* **46**:31–78.
- Baird, S. E., M. E. Sutherlin, and S. W. Emmons. 1992. Reproductive mechanisms that isolate six species of three genera. *Evolution* **46**:585–594.
- Barton, N. H., and G. M. Hewitt. 1985. Analysis of hybrid zones. *Annual Review of Ecology and Systematics* **16**:113–148.
- Boecklen, W. J., and R. Spellenberg. 1990. Structure of herbivore communities in two oak (*Quercus* spp.) hybrid zones. *Oecologia* **85**:92–100.
- Bohlen, J., and D. Ritterbusch. 2000. Which factors affect sex ratio of spined loach (genus *Cobitis*) in Lake Müggelsee? *Environmental Biology of Fishes* **59**:347–352.
- Bolnick, D. L. 2001. Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature* **410**:463–466.
- Boomsma, J. J. 1989. Sex-investment ratios in ants: has female bias been systematically overestimated? *American Naturalist* **133**:517–532.
- Boomsma, J. J., and A. Grafen. 1990. Intraspecific variation in ant sex ratios and the Trivers-Hare hypothesis. *Evolution* **44**:1026–1034.
- Bourke, A. F. G. 1988. Worker reproduction in the higher eusocial Hymenoptera. *Quarterly Review of Biology* **63**:291–311.
- Bulger, A. J., and R. J. Schultz. 1979. Heterosis and interclonal variation in thermal tolerance in unisexual fishes. *Evolution* **33**:848–859.
- Burke, J. M., and M. L. Arnold. 2001. Genetics and the fitness of hybrids. *Annual Review of Genetics* **35**:31–52.
- Clark, R. M., K. E. Anderson, J. Gadau, and J. H. Fewell. 2006. Behavioral regulation of genetic caste determination in a *Pogonomyrmex* population with dependent lineages. *Ecology* **87**:2201–2206.
- Cover, S. P., and R. Sanwald. 1988. Colony founding in *Acanthomyops murphyi*, a temporary social parasite of *Lasius neoniger*. Pages 405–417 in J. C. Trager, editor. *Advances in myrmecology*, E. J. Brill, Leiden, The Netherlands.
- Crozier, R. H. 1981. Genetic aspects of ant evolution. Pages 356–370 in W. R. Atchley and D. Woodruff, editors. *Evolution and speciation, essays in honour of M. J. D. White*. Cambridge University Press, Cambridge, UK.
- Crozier, R. H., and P. Pamilo. 1993. Sex allocation in social insects: problems in prediction and estimation. Pages 369–383 in D. L. Wrensch and M. A. Ebbert, editors. *Evolution and diversity of sex ratio in insects and mites*. Chapman and Hall, New York, New York, USA.

- Crozier, R. H., and P. Pamilo. 1996. Evolution of social insect colonies: sex allocation and kin selection. Oxford University Press, Oxford, UK.
- Dowling, T. E., and C. L. Secor. 1997. The role of hybridization and introgression in the diversification of animals. *Annual Review of Ecology and Systematics* **28**:593–619.
- Dupont, F., and A. J. Crivelli. 1988. Do parasites confer a disadvantage to hybrids? *Oecologia* **75**:587–592.
- Evans, J. D. 1996. Queen longevity, queen adoption, and posthumous indirect fitness in the facultatively polygynous ant *Myrmica tahoensis*. *Behavioral Ecology and Sociobiology* **39**:275–284.
- Floate, K. D., and T. G. Whitham. 1993. The “hybrid bridge” hypothesis: host shifting via plant hybrid swarms. *American Naturalist* **141**:651–662.
- Fortin, A., M. M. Stevenson, and P. Gros. 2002. Susceptibility to malaria as a complex trait: big pressure from a tiny creature. *Human Molecular Genetics* **11**:2469–2478.
- Fournier, D., A. Estoup, J. Orivel, J. Foucaud, H. Jourdan, J. Le Breton, and L. Keller. 2005. Clonal reproduction by males and females in the little fire ant. *Nature* **435**:1230–1234.
- Gordon, D. M., and A. W. Kulig. 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecology* **77**:2393–2409.
- Gordon, D. M., and A. W. Kulig. 1998. The effect of neighbours on the mortality of harvester ant colonies. *Journal of Animal Ecology* **67**:141–148.
- Grant, V. 1981. Plant speciation. Second edition. Columbia University Press, New York, New York, USA.
- Gross, M. R. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. Pages 55–77 in G. W. Potts and R. J. Wootton, editors. *Fish reproduction: strategies and tactics*. Academic Press, London, UK.
- Gwynne, D. T., and D. C. F. Rentz. 1983. Beetles on the bottle: male buprestids mistake entomologists for females (Coleoptera). *Journal of the Australian Entomological Society* **22**:79–80.
- Heinze, J., and K. Tsuji. 1995. Ant reproductive strategies. *Researches on Population Ecology* **37**:135–149.
- Helms Cahan, S., G. E. Julian, S. W. Rissing, T. Schwander, J. D. Parker, and L. Keller. 2004. Loss of phenotypic plasticity generates genotype-caste association in harvester ants. *Current Biology* **14**:2277–2282.
- Helms Cahan, S., G. E. Julian, T. Schwander, and L. Keller. 2006. Reproductive isolation between *Pogonomyrmex rugosus* and two lineages with genetic caste determination. *Ecology* **87**:2160–2170.
- Helms Cahan, S., and L. Keller. 2003. Complex hybrid origin of genetic caste determination in harvester ants. *Nature* **424**:306–309.
- Helms Cahan, S., J. D. Parker, S. W. Rissing, R. A. Johnson, T. S. Polony, M. D. Weiser, and D. R. Smith. 2002. Extreme genetic differences between queens and workers in hybridizing *Pogonomyrmex* harvester ants. *Proceedings of the Royal Society of London B* **269**:1871–1877.
- Helms Cahan, S., and S. B. Vinson. 2003. Reproductive division of labor between hybrid and nonhybrid offspring in a fire ant hybrid zone. *Evolution* **57**:1562–1570.
- Hölldobler, B., and C. J. Lumsden. 1980. Territorial strategies in ants. *Science* **210**:732–739.
- Hölldobler, B., and E. O. Wilson. 1990. *The ants*. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.
- Hubbs, C. L. 1955. Hybridization between fish species in nature. *Systematic Zoology* **4**:1–20.
- Hung, A. C. F., and S. B. Vinson. 1977. Interspecific hybridization and caste specificity of protein in fire ant. *Science* **196**:1458–1460.
- Janzen, D. H. 1967. Interaction of the bull’s-horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. *University of Kansas Science Bulletin* **47**:315–558.
- Jessen, K., and M. Klinkicht. 1990. Hybridization in the social parasitic ant genus *Epimyrma* (Hymenoptera, Formicidae). *Insectes Sociaux* **37**:273–293.
- Julian, G. E., J. H. Fewell, J. Gadau, R. A. Johnson, and D. Larrabee. 2002. Genetic determination of the queen caste in an ant hybrid zone. *Proceedings of the National Academy of Sciences (USA)* **99**:8157–8160.
- Kawecki, T. J. 1988. Unisexual/bisexual breeding complexes in Poeciliidae: why do males copulate with unisexual females? *Evolution* **42**:1018–1023.
- Linksvayer, T. A., M. J. Wade, and D. M. Gordon. 2006. Genetic caste determination in harvester ants: possible origin and maintenance by cyto-nuclear epistasis. *Ecology* **87**:2185–2193.
- Mallet, J. 2005. Hybridization as an invasion of the genome. *Trends in Ecology and Evolution* **29**:229–237.
- Mandel, M. J., C. L. Ross, and R. G. Harrison. 2001. Do *Wolbachia* infections play a role in unidirectional incompatibilities in a field cricket hybrid zone? *Molecular Ecology* **10**:703–709.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge, UK.
- Milborrow, B. V. 1998. A biochemical mechanism for hybrid vigour. *Journal of Experimental Botany* **49**:1063–1071.
- Moore, W. S. 1984. Evolutionary ecology of unisexual fishes. Pages 329–398 in B. J. Turner, editor. *Evolutionary genetics of fishes*. Plenum, New York, New York, USA.
- Moore, W. S., and J. T. Price. 1993. Nature of selection in the northern flicker hybrid zone and its implications for speciation theory. Pages 196–225 in R. G. Harrison, editor. *Hybrid zones and the evolutionary process*. Oxford University Press, New York, USA.
- Mouliou, C. 1999. Parasitism of plant and animal hybrids: are facts and fates the same? *Ecology* **80**:392–406.
- Nascimento, V. A., S. H. Matusita, and W. E. Kerr. 2000. Evidence of hybridization between two species of *Melipona* bees. *Genetics and Molecular Biology* **23**:79–81.
- Nonacs, P. 1986a. Ant reproductive strategies and sex allocation theory. *Quarterly Review of Biology* **61**:1–21.
- Nonacs, P. 1986b. Sex-ratio determination within colonies of ants. *Evolution* **40**:199–204.
- Normark, B. B. 2003. The evolution of alternative genetic systems in insects. *Annual Review of Entomology* **48**:397–423.
- Oster, G. F., and E. O. Wilson. 1978. *Caste and ecology in the social insects*. Princeton University Press, Princeton, New Jersey, USA.
- Parker, G. A. 1984. Evolutionarily stable strategies. Pages 30–61 in J. R. Krebs and N. B. Davies, editors. *Behavioural ecology: an evolutionary approach*. Second edition. Blackwell Scientific, Oxford, UK.
- Parker, J. D. 2004. A major evolutionary transition to more than two sexes? *Trends in Ecology and Evolution* **19**:83–86.
- Passera, L., S. Aron, E. L. Vargo, and L. Keller. 2001. Queen control of sex ratio in fire ants. *Science* **293**:1308–1310.
- Pearcy, M., S. Aron, C. Doums, and L. Keller. 2004. Conditional use of sex and parthenogenesis for worker and queen production in ants. *Science* **306**:1780–1783.
- Pearson, B. 1982. The taxonomic status of morphologically-anomalous ants in the *Lasius niger/Lasius alienus* taxon. *Insectes Sociaux* **29**:95–101.
- Pearson, B. 1983a. The classification of morphologically intermediate ants in the *Lasius alienus/Lasius niger* taxon. *Insectes Sociaux* **30**:100–105.
- Pearson, B. 1983b. Hybridisation between the ant species *Lasius niger* and *Lasius alienus*: the genetic evidence. *Insectes Sociaux* **30**:402–411.

- Pearson, B. 1987. The sex ratio of heathland populations of the ants *Lasius alienus*, *Lasius niger* and their hybrids. *Insectes Sociaux* **34**:194–203.
- Penn, D. J., K. Damjanovich, and W. K. Potts. 2002. MHC heterozygosity confers a selective advantage against multiple-strain infections. *Proceedings of the National Academy of Sciences (USA)* **99**:11260–11264.
- Pontin, A. J. 1961. Population stabilization and competition between the ants *Lasius flavus* (F.) and *L. niger* (L.). *Journal of Animal Ecology* **30**:47–54.
- Randler, C. 2002. Avian hybridization, mixed pairing and female choice. *Animal Behaviour* **63**:103–119.
- Reuter, M., and L. Keller. 2001. Sex ratio conflict and worker production in eusocial Hymenoptera. *American Naturalist* **158**:166–177.
- Roisin, Y., and S. Aron. 2003. Split sex ratios in perennial social Hymenoptera: a mixed evolutionary stable strategy from the queen's perspective? *American Naturalist* **162**:624–637.
- Sage, R. D., D. Heyneman, K. Lim, and A. C. Wilson. 1986. Wormy mice in a hybrid zone. *Nature* **324**:60–63.
- Schiestl, F. R., R. Peakall, and J. Mant. 2004. Chemical communication in the sexually deceptive orchid genus *Cryptostylis*. *Botanical Journal of the Linnean Society* **144**:199–205.
- Schlupp, I. 2005. The evolutionary ecology of gynogenesis. *Annual Review of Ecology, Evolution and Systematics* **36**:399–417.
- Schlupp, I., J. Parzefall, and M. Schartl. 2002. Biogeography of the Amazon molly, *Poecilia formosa*. *Journal of Biogeography* **29**:1–6.
- Schneider, S. S., L. J. Leamy, L. A. Lewis, and G. DeGrandi-Hoffman. 2003. The influence of hybridization between African and European honeybees, *Apis mellifera*, on asymmetries in wing size and shape. *Evolution* **57**:2350–2364.
- Schwander, T., S. Helms Cahan, and L. Keller. 2006. Genetic caste determination in *Pogonomyrmex* harvester ants imposes costs during colony founding. *Journal of Evolutionary Biology* **19**:402–409.
- Seehausen, O. 2004. Hybridization and adaptive radiation. *Trends in Ecology and Evolution* **19**:198–207.
- Seifert, B. 1999. Interspecific hybridisations in natural populations of ants by example of a regional fauna (Hymenoptera, Formicidae). *Insectes Sociaux* **46**:45–52.
- Stebbins, G. L. 1950. Variation and evolution in plants. Columbia University Press, New York, New York, USA.
- Talbot, M. 1934. Distribution of ant species in the Chicago region with reference to ecological factors and physiological toleration. *Ecology* **15**:416–439.
- Talbot, M. 1963. Local distribution and flight activities of four species of ants of the genus *Acanthomyops* Mayr. *Ecology* **44**:549–557.
- Talbot, M. 1973. Five species of the ant genus *Acanthomyops* (Hymenoptera: Formicidae) at the Edwin S. George Reserve in southern Michigan. *Great Lakes Entomologist* **6**:19–22.
- Taylor, P. D., and A. Sauer. 1980. The selective advantage of sex-ratio homeostasis. *American Naturalist* **116**:305–310.
- Trivers, R. L., and H. Hare. 1976. Haplodiploidy and the evolution of the social insects. *Science* **191**:249–263.
- Tschinkel, W. R. 1992. Brood raiding and the population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta*. *Ecological Entomology* **17**:179–188.
- Tschinkel, W. R. 1996. A newly-discovered mode of colony founding among fire ants. *Insectes Sociaux* **43**:267–276.
- Umphrey, G. J., and R. G. Danzmann. 1998. Electrophoretic evidence for hybridization in the ant genus *Acanthomyops*. *Biochemical Systematics and Ecology* **26**:431–440.
- van der Have, T. M., J. J. Boomsma, and S. B. J. Menken. 1988. Sex-investment ratios and relatedness in the monogynous ant *Lasius niger* (L.). *Evolution* **42**:160–172.
- Volny, V. P., and D. M. Gordon. 2002. Genetic basis for queen-worker dimorphism in a social insect. *Proceedings of the National Academy of Sciences (USA)* **99**:6108–6111.
- Volny, V. P., M. J. Greene, and D. M. Gordon. 2006. Brood production and lineage discrimination in the red harvester ant (*Pogonomyrmex barbatus*). *Ecology* **87**:2194–2200.
- Ward, P. S. 2005. A synoptic review of the ants of California (Hymenoptera: Formicidae). *Zootaxa* **936**:3–68.
- Wasserman, A. O. 1957. Factors affecting interbreeding in sympatric species of spade-foots (genus *Scaphiopus*). *Evolution* **11**:320–338.
- Wheeler, W. M., and J. F. McClendon. 1903. Dimorphic queens in an American ant (*Lasius latipes* Walsh). *Biological Bulletin* **4**:149–163.
- White, M. J. D. 1973. Animal cytology and evolution. Third edition. Cambridge University Press, Cambridge, UK.
- Wilson, E. O. 1971. The insect societies. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.
- Wing, M. W. 1968. Taxonomic revision of the Nearctic genus *Acanthomyops* (Hymenoptera: Formicidae). *Memoir* 405. Cornell University Agricultural Experiment Station, Ithaca, New York, USA.
- Wirtz, P. 1999. Mother species–father species: unidirectional hybridization in animals with female choice. *Animal Behaviour* **58**:1–12.
- Woyciechowski, M., and A. Łomnicki. 1987. Multiple mating of queens and the sterility of workers among eusocial Hymenoptera. *Journal of Theoretical Biology* **128**:317–327.
- Wright, J. W., and C. H. Lowe. 1968. Weeds, polyploids, parthenogenesis, and the geographical and ecological distribution of all-female species of *Cnemidophorus*. *Copeia* **1968**:128–138.
- Wu, C.-I., and M. F. Polopoli. 1994. Genetics of postmating reproductive isolation in animals. *Annual Review of Genetics* **27**:283–309.