

UCLA

UCLA Previously Published Works

Title

Sex-Ratio Determination Within Colonies of Ants

Permalink

<https://escholarship.org/uc/item/3d17f36q>

Journal

Evolution, 40(1)

ISSN

0014-3820

Author

Nonacs, Peter

Publication Date

1986

DOI

10.2307/2408617

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed



Sex-Ratio Determination Within Colonies of Ants

Peter Nonacs

Evolution, Vol. 40, No. 1 (Jan., 1986), 199-204.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28198601%2940%3A1%3C199%3ASDWCOA%3E2.0.CO%3B2-U>

Evolution is currently published by Society for the Study of Evolution.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ssevol.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact jstor-info@jstor.org.

SEX-RATIO DETERMINATION WITHIN COLONIES OF ANTS

PETER NONACS

Department of Biological Sciences, Simon Fraser University, Burnaby, B.C. V5A 1S6 Canada

Received February 13, 1985. Accepted July 24, 1985

Trivers and Hare (1976) propose that in social Hymenoptera a queen and her daughter workers can be in conflict over the relative amount invested in the two sexes. A worker is three times more related to a full sister than to a brother, while the queen is equally related to both sons and daughters. They present a wide array of evidence which suggests that wherever conflict occurs, the workers are likely to win and produce female-biased sexual investment ratios. Several subsequent studies, however, appear to indicate that, within some individual colonies, queens can exert enough influence to produce sex ratios favorable to their interests (Brian, 1979; Forsyth, 1981; Pamilo and Rosengren, 1983). Herbers's study (1984) is perhaps the most thorough investigation of worker-queen conflict within a single hymenopteran species. She presents two major lines of evidence suggesting that workers of the ant species *Leptothorax longispinosus* attempt to maximize inclusive fitness at the expense of their queen's and that an active conflict occurs within colonies. First, proportional investment in females by colonies follows the order predicted by kin selection where, queenless > monogynous > oligogynous (2–4 functional queens) > polygynous (≥ 5 queens). Queenless colonies are the most female-biased, because the workers could produce their optimal sex ratio without opposition from a queen. Oligogynous and polygynous colonies are the least female-biased, because increasing queen number reduces the asymmetry in relatedness between brothers and sisters, and queen and worker investment equilibria converge (Trivers and Hare, 1976). Also, the queen-to-worker ratio is increased, which should favor the queens doing better in conflict situations. The second line of evidence is that worker number is often correlated negatively with proportional investment in males for monogynous, oligogynous, and polygynous colonies. This supports the conflict hypothesis in that the larger the work force, the more difficult it may be for a queen to affect the sex ratio.

Overall, Herbers's results and the variance in investment ratios between colonies found by numerous studies (see Nonacs [1986] for a review), appear to suggest that a dynamic conflict occurs between workers and queens over sex ratio. Male production seems to be increased in direct proportion to the ability of queens to succeed in the conflicts. I propose, however, that the sex ratios produced by individual colonies primarily reflect the workers' interests. I will support this hypothesis in two ways.

First, I will show that Herbers's study (as the particular case in point) and the variance in investment ratios from many other ant species are equally well (or better) explained by a proximate mechanism of resource availability as by worker-queen conflict. Second, I will argue that because the fitness of any given colony's investment ratio depends on the sex ratio of the interbreeding population, colonies producing male-biased broods can still be harmonious with a hypothesis of total worker control although, superficially, they may appear queen-influenced.

The patterns of investment observed by Herbers, particularly in reference to worker number, may also be explained by a resource availability hypothesis. Larger colonies with more workers may generally be expected to collect more food (Oster and Wilson, 1978 pp. 26–74; Brian et al., 1981; Elmes and Wardlaw, 1982). It is reasonable to assume that with more food, sexual production increases. In many species, investment in males is negatively correlated with total sexual production (Nonacs, 1986). In other words, with increasing resources, colonies are more likely to favor female production. Therefore, worker number may be only spuriously correlated to investment ratios due to its relationship to ergonomic efficiency.

Available data sets from 18 monogynous, five polygynous, and one slave-making species measure sexual production and worker number. These can be tested as to whether one, both, or neither accurately predicts sex ratio. For each species, I have examined the partial correlations among the total amount of sexuals produced (measured as biomass), the number of adult workers, and the male proportion of the total sexual biomass (R), which was normalized by arcsine square root transformation.

The relationship between total sexual biomass and proportion invested in males is strong (Table 1). When worker number is controlled, seven correlations are significantly negative ($P < 0.025$). In total, 20 of 24 correlations are negative, a significant trend across species (sign test, $P < 0.002$).

With total sexual biomass controlled, however, there is almost no relationship between worker number and proportion invested in males (Table 1). In only two species are the correlations significant, with one being negative and the other positive. Moreover, there is no trend across species as the correlations are equally split between negative and positive (12 of 24 negative).

When R is controlled, there are positive corre-

TABLE 1. Partial correlation coefficients within species between *R* (proportion of investment in males), TOTAL (total biomass of sexuals), and worker number. In each pairwise comparison, the third variable is held constant. *N* is the number of colonies examined. *Leptothorax longispinosus* does not include data from Herbers (1984). * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Monogynous				
Species (reference)	<i>N</i>	Partial correlation coefficients		
		<i>R</i> and TOTAL	<i>R</i> and # workers	TOTAL and # workers
<i>Aphaenogaster rudis</i> (Headley, 1949; Talbot, 1951; Trivers and Hare, 1976)	14	−0.6701*	+0.3442	+0.5517
<i>A. treatea</i> (Talbot, 1954; Trivers and Hare, 1976)	12	−0.7252*	−0.0323	+0.3932
<i>Camponotus ferrugineus</i> (Pricer, 1908; Trivers and Hare, 1976)	6	+0.6974	−0.9355*	+0.8029
<i>C. pennsylvanicus</i> (Pricer, 1908; Trivers and Hare, 1976)	4	−0.8196	+0.6837	+0.9195
<i>Formica pallidefulva nitidiventris</i> (Talbot, 1948; Trivers and Hare, 1976)	19	−0.3231	+0.1228	+0.8488***
<i>Lasius flavus</i> (Pickles, 1940)	10	−0.3696	+0.0403	+0.7521*
<i>Leptothorax curvispinosus</i> (Headley, 1943; Trivers and Hare, 1976)	10	−0.2975	−0.3750	+0.0250
<i>L. longispinosus</i> (Headley, 1943; Trivers and Hare, 1976)	13	−0.6524*	+0.4311	+0.6382*
<i>Myrmica ruginodis</i> [macrogyne] (Brian and Brian, 1951; Mizutani, 1981; Elmes, pers. comm.)	32	−0.5389**	−0.2855	+0.0572
<i>M. schencki</i> (Talbot, 1945; Trivers and Hare, 1976)	10	−0.2168	−0.5815	−0.1379
<i>M. sulcinodis</i> (Elmes, 1974, pers. comm.)	104	−0.2552**	+0.0136	+0.3601***
<i>Pogonomyrmex montanus</i> (MacKay, 1981)	35	−0.0571	+0.2217	+0.4017*
<i>P. rugosus</i> (MacKay, 1981)	4	−0.8416	−0.4373	−0.6332
<i>P. subnitidus</i> (MacKay, 1981)	7	−0.7354	+0.3346	+0.6864
<i>Prenolepis imparis</i> (Talbot, 1943; Trivers and Hare, 1976)	12	−0.3851	+0.3706	+0.8892***
<i>Stenamma brevicorne</i> (Talbot, 1975; Trivers and Hare, 1976)	8	−0.2983	−0.0660	+0.4602
<i>S. diecki</i> (Talbot, 1975; Trivers and Hare, 1976)	10	+0.0547	+0.4100	−0.6537
<i>Tetramorium caespitum</i> (Brian et al., 1967; Brian, 1979)	80	−0.0020	−0.0075	+0.0851
Proportion of negative correlation coefficients		16/18	8/18	3/18
Number of significant ($P < 0.05$) correlations		5 (all negative)	1 (negative)	6 (all positive)

TABLE 1. Continued.

Polygynous and slave-making				
Species (reference)	N	Partial correlation coefficients		
		R and TOTAL	R and # workers	TOTAL and # workers
<i>Formica pallidefulva incerta</i> (Talbot, 1948; Trivers and Hare, 1976)	12	+0.3056	-0.3118	+0.5909
<i>Harpagoxenus americanus</i> (Wesson, 1939)	19	-0.0094	-0.2357	-0.2409
<i>Myrmica rubra</i> (Brian, 1972; Elmes, 1976)	11	-0.3873	+0.1969	+0.1445
<i>M. ruginodis</i> [microgyne] (Mizutani, 1981; Elmes, pers. comm.)	8	+0.6190	-0.6315	+0.9632***
<i>M. sabuleti</i> (Brian, 1972; Elmes, pers. comm.)	126	-0.2566**	+0.1760*	+0.3945***
<i>M. scabrinodis</i> (Elmes, pers. comm.)	12	-0.9229***	-0.3264	-0.0719
Proportion of negative correlation coefficients		4/6	4/6	2/6
Number of significant ($P < 0.05$) correlations		2	1	2
		(both negative)	(positive)	(both positive)

lations between total biomass of sexuals and worker number. Altogether, 19 of 24 are positive, a significant trend (sign test, $P < 0.006$) and eight of the 19 positive correlations are significant at $P < 0.03$ (Table 1). This strongly suggests that larger colonies produce more sexuals. When Herber's data are reanalyzed with controls for total sexual biomass, a similar pattern emerges. There is no significant correlation between worker number and the proportional investment in males ($r = -0.099$, $P = 0.164$; Herbers, pers. comm.). Herbers (pers. comm.) found a strong negative relationship between total sexual biomass and R when worker number is controlled ($r = -0.450$, $P < .001$), and she also determined that total sexual biomass positively correlates with worker number ($r = 0.204$, $P = 0.021$). All the results are for 1981 only.

In other studies, Ward (1983) found no significant relationship between colony size and sex ratio in three ant species of the genus *Rhytidoponera*. Boomsma et al. (1982) found significant positive correlations between colony size and female production and total sexual production and female production in some populations of *Lasius niger*. These correlations, however, did not control for the effects of the other variable.

Worker-queen conflict and resource level hypotheses differ in their predictions of the effect on sex ratios with increases in queen number. The monogyny/polygyny distinction is important for the worker-queen conflict hypothesis. Worker number should affect investment ratios much more in monogynous species. *Harpagoxenus americanus*, a slave-maker, can be included with the polygynous species because the *H. americanus* workers do not care for brood, and therefore the queen's optimum invest-

ment ratio is expressed (Trivers and Hare, 1976; Nonacs, 1986). If sex ratios are mediated by resource availability, however, correlations between R and total sexual biomass should be negative for all species.

The results do not appear to differ across the monogynous and polygynous species groups for any set of correlations (Table 1). The consistent negative correlations between R and total sexual biomass indicate its independence of queen number. However, contrary to predictions of worker-queen conflict, there is no consistent relationship between R and worker number in monogynous species.

If the effect of worker number on sex ratio disappears when total investment is considered, queen number might be similarly related to sex ratios through resource availability to sexual function. From alate numbers and weights (Herbers, 1984, table 7 and table 4, respectively), I calculated the dry weight investment in sexuals per nest and the proportion invested in males for queenless, monogynous, oligogynous, and polygynous colonies (Table 2). In 1981, the ordering of male investment is as predicted by kin selection (queenless < monogynous < oligogynous < polygynous). This, however, is also the order predicted by the resource availability hypothesis (as measured through total investment). For 1982, when oligogynous and polygynous colonies are combined, they are found to invest less in males than do monogynous ones. This is contrary to kin-selection predictions but consistent with a resource availability hypothesis, because monogynous colonies are investing less in sexuals than are polygynous ones. Notice, however, that queenless colonies are clearly more consonant with kin selection in 1982.

TABLE 2. The dry weight investment and proportion invested in males per nest for the colony types in Herbers (1984). O + P refers to oligogynous and polygynous colonies combined.

Colony type	1981		1982	
	Dry weight investment	R	Dry weight investment	R
Queenless	2.87	0.250	2.30	0.249
Monogynous	2.68	0.332	7.44	0.479
Oligogynous	1.62	0.576	14.32	0.381
Polygynous	1.59	0.614	5.53	0.377
O + P	1.61	0.589	8.82	0.379

In Herbers' reanalysis (pers. comm.) of the 1981 data, she found by analysis of variance that, when queen number and total biomass of sexuals are included as covariates, total sexual biomass has a highly significant effect on proportional investment in males ($P < 0.001$), while queen number is marginally nonsignificant ($P < 0.069$). However, by partial correlation with total sexual investment controlled, queen number does significantly correlate with R ($r = 0.183$, $P = 0.035$). Therefore, while sex ratios are clearly most sensitive to total investment in sexuals, increases in queen number may indeed have a weak effect in increasing the proportional investment in males.

There is considerable evidence that worker ants manipulate sex ratios to their advantage (Nonacs, 1986). For 33 monogynous species, including the 18 in Table 1, the average proportion of sexual investment in males was $R = 0.282$, which is quite close to the predicted 3:1 female bias. Moreover, this proportion was significantly different from that for a group of polygynous species ($R = 0.522$). The worker control hypothesis is further supported by the lack of a relationship between worker number and the proportional investment in males (Table 1), which may indicate that workers always control sex ratio independent of colony size. An alternative hypothesis for the observed sex ratios, local mate competition (Alexander and Sherman, 1977), was inconsistent with the sex ratios found in slave-making species because, 1) males seem very limited in the number of females they can inseminate, 2) numerous colonies produce unisexual male broods, which cannot be explained by a lack of a diploid-egg source, and 3) high variance in sex ratios between colonies, which is deleterious when mating is restricted to small groups (see Taylor and Sauer, 1980).

The variance in colony sex ratios is high because most colonies produce extremely sex-biased broods. Over 60% of all monogynous colonies favor one sex by a ratio 5:1 or greater (Nonacs, 1986). This is neither an argument against kin selection (sensu Alexander and Sherman, 1977) or for an active conflict between workers and queens. If a large interbreeding population is at equilibrium, then all

sex ratios are equally fit (Williams, 1979; Taylor and Sauer, 1980). Therefore, even colonies which produce nothing but queen-laid males cannot be assumed to be acting against the inclusive fitness interests of its workers.

Leptothorax longispinosus shows sexual specialization with over 72% of all colonies produced single sex broods (Herbers, 1984). This pattern is difficult to reconcile with a hypothesis of worker-queen conflicts in which both sides have a possibility of winning. For example, 17 *L. longispinosus* queenless colonies (45%) produced only males. This would imply that queens win conflicts even when they are absent. *L. longispinosus* produces worker-laid males, but it seems unlikely to wholly account for the males in queenless colonies (Herbers, 1984). Furthermore, worker laying in and of itself does not necessarily result in all-male broods (Oster et al., 1977; Charnov, 1978; Benford, 1978). Therefore, it appears that it may be advantageous for *L. longispinosus* workers to raise all-male broods under certain conditions.

The population equilibrium value for workers may be affected by worker laying (see also Taylor, 1981), use of more than one male's sperm by queens (Alexander and Sherman, 1977), and polygyny. These factors, however, may have little predictive power as to what sex ratio a given colony will produce. When resource availability is low, male production may always be favored. Females seem favored when resources are abundant. There are several field studies that support a resource availability hypothesis. Brian (1979) found more investment in females in optimal habitats than in marginal ones for *Lasius alienus* and *Tetramorium caespitum*. Boomsma et al. (1982) found that *L. niger* colonies in an area of intense competition with *L. flavus* (which the authors assumed was indicative of resource stress) produced less female-biased sex ratios than colonies in an area where *L. flavus* was absent. Moreover, reduced resources appeared to affect female production more than that of males. Similar results were found for *L. flavus* sexual production when it was in competition with *L. niger* (Pontin, 1961). Finally, Owen et al. (1980) found that small, weak bumblebee colonies tended to only produce males.

Can actual unresolved worker-queen conflict be found in monogynous colonies? This question appears unanswerable only if the effects of resource availability are considered. For example, polygynous species, in which worker-queen conflict may be considerably reduced or absent (Trivers and Hare, 1976), behave similarly to monogynous species in that they mainly produce highly sexually biased broods and have negative correlations between total investment and proportional male investment (Nonacs, 1986). This pattern of sexual production appears favored by all members of a colony, independent of whether the individuals therein have different sex-ratio investment equilibria. Only when resource level is moderate might there be a conflict. With increasing resource level, workers may favor

switching to female production earlier than do their monogynous queens. If every colony producing sexuals in a population is lumped together, this may obscure any effects of worker-queen conflict. Therefore, Herbers may have observed only a weak relationship between queen number and proportional investment in males because there may have been no conflict of interest in the majority of colonies she examined.

If resource availability can be demonstrated to have an effect, it will shed light on the proximate mechanism by which sex ratio is determined. However, this does not answer the question of why ants have evolved to favor sexual specialization or why female production may be favored under conditions of resource abundance. Adequately explaining reproductive strategies in an evolutionarily advantageous context is difficult, because many aspects of colony dynamics are too poorly known to evaluate hypotheses critically. More information about resource level effects on both the entire brood and individual development of sexuals, along with studies of community structure and mating behavior of both sexes could provide the basis for further testing of evolutionary hypotheses and scenarios.

ACKNOWLEDGMENTS

I thank the following for their helpful comments: M. V. Abrahams, R. V. Cartar, L. M. Dill (whose NSERC grant A6869 supported this study), M. R. Gross, P. C. Lee, R. C. Sargent, and R. C. Ydenberg. I especially thank G. W. Elmes for kindly allowing me the use of his population data and J. M. Herbers for graciously and knowledgeably answering my questions.

LITERATURE CITED

- ALEXANDER, R. D., AND P. W. SHERMAN. 1977. Local mate competition and parental investment in social insects. *Science* 196:494-500.
- BENFORD, F. A. 1978. Fisher's theory of sex ratios applied to the social Hymenoptera. *J. Theoret. Biol.* 72:701-727.
- BOOMSMA, J. J., G. A. VAN DER LEE, AND T. M. VAN DER HAVE. 1982. On production ecology of *Lasius niger* (Hymenoptera:Formicidae) in successive coastal dune valleys. *J. Anim. Ecol.* 51:975-991.
- BRIAN, M. V. 1972. Population turnover in wild colonies of the ant *Myrmica*. *Ekol. Polska* 20: 43-53.
- . 1979. Habitat differences in sexual production by two co-existent ants. *J. Anim. Ecol.* 48:943-953.
- BRIAN, M. V., AND A. D. BRIAN. 1951. Insolation and ant population in the West of Scotland. *Trans. R. Entomol. Soc. Lond.* 102:303-330.
- BRIAN, M. V., R. T. CLARKE, AND R. M. JONES. 1981. A numerical model of an ant society. *J. Anim. Ecol.* 50:387-405.
- BRIAN, M. V., G. ELMES, AND A. F. KELLY. 1967. Populations of the ant *Tetramorium caespitum* Latreille. *J. Anim. Ecol.* 36:337-342.
- CHARNOV, E. L. 1978. Sex-ratio selection in eusocial Hymenoptera. *Amer. Natur.* 112:317-326.
- ELMES, G. W. 1974. Colony populations of *Myrmica sulcinodis* Nyl. (Hym. Formicidae). *Oecologia* 15:337-343.
- . 1976. Some observations on the microgyne form of *Myrmica rubra* L. (Hymenoptera, Formicidae). *Insectes Soc.* 23:3-22.
- ELMES, G. W., AND J. C. WARDLAW. 1982. A population study of the ants *Myrmica sabuleti* and *Myrmica scabrinodis*, living at two sites in the south of England. I. A comparison of colony populations. *J. Anim. Ecol.* 51:651-664.
- FORSYTH, A. 1981. Sex ratio and parental investment in an ant population. *Evolution* 35: 1252-1253.
- HEADLEY, A. E. 1943. Population studies of two species of ants, *Leptothorax longispinosus* Roger and *Leptothorax curvispinosus* Mayr. *Ann. Entomol. Soc. Amer.* 36:743-753.
- . 1949. A population study of the ant *Aphaenogaster fulva* ssp. *aquia* Buckley. *Ann. Entomol. Soc. Amer.* 42:265-272.
- HERBERS, J. M. 1984. Queen-worker conflict and eusocial evolution in a polygynous ant species. *Evolution* 38:631-643.
- MACKEY, W. P. 1981. A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants (Hymenoptera:Formicidae). *Psyche* 88:25-74.
- MIZUTANI, A. 1981. On the two forms of the ant *Myrmica ruginodis* Nylander (Hymenoptera, Formicidae) from Sapporo and its vicinity, Japan. *Jap. J. Ecol.* 31:131-137.
- NONACS, P. 1986. Ant reproductive strategies and sex allocation theory. *Q. Rev. Biol.* In press.
- OSTER, G. F., I. ESHEL, AND D. COHEN. 1977. Worker-queen conflict and evolution of social insects. *Theoret. Popul. Biol.* 12:49-85.
- OSTER, G. F., AND E. O. WILSON. 1978. *Caste and Ecology in the Social Insects*. Princeton Univ. Press, Princeton, NJ. 352 pp.
- OWEN, R. E., F. H. RODD, AND R. C. PLOWRIGHT. 1980. Sex ratios in bumble bee colonies: Complications due to orphaning? *Behav. Ecol. Sociobiol.* 7:287-291.
- PAMILO, P., AND R. ROSENGREN. 1983. Sex ratio strategies in *Formica* ants. *Oikos* 40:24-35.
- PICKLES, W. 1940. Fluctuations in the populations, weights and biomasses of ants at Thornhill, Yorkshire, from 1935 to 1939. *Trans. R. Entomol. Soc. Lond.* 90:467-485.
- PONTIN, A. J. 1961. Population stabilization and competition between the ants *Lasius flavus* (F.) and *L. niger* (L.). *J. Anim. Ecol.* 30:47-54.
- PRICER, J. L. 1908. The life history of the carpenter ant. *Biol. Bull.* 14:177-217.
- TALBOT, M. 1943. Population studies of the ant, *Prenolepis imparis* Say. *Ecology* 24:31-44.
- . 1945. Population studies of the ant *Myr-*

- mica schencki* ssp. *emeryana* Forel. Ann. Entomol. Soc. Amer. 38:365-372.
- . 1948. A comparison of two ants of the genus *Formica*. Ecology 29:316-325.
- . 1951. Populations and hibernating conditions of the ant *Aphaenogaster (Attomyra) rudis* Emery. Ann. Entomol. Soc. Amer. 44:302-307.
- . 1954. Populations of the ant *Aphaenogaster (Attomyra) treatae* Forel on abandoned fields on the Edwin S. George Reserve. Cont. Lab. Vertebr. Biol. Univ. Mich. 69:1-9.
- . 1975. Habitats and populations of the ant *Stenamma diecki* Emery in southern Michigan. Great Lakes Entomol. 8:241-244.
- TAYLOR, P. D. 1981. Sex ratio compensation in ant populations. Evolution 35:1250-1251.
- TAYLOR, P. D., AND A. SAUER. 1980. The selective advantage of sex-ratio homeostasis. Amer. Natur. 116:305-310.
- TRIVERS, R. L., AND H. HARE. 1976. Haplodiploidy and the evolution of the social insects. Science 191:249-263.
- WARD, P. S. 1983. Genetic relatedness and colony organization in a species complex of ponerine ants. II. Patterns of sex ratio investment. Behav. Ecol. Sociobiol. 12:301-307.
- WESSON, L. G. 1939. Contribution to the natural history of *Harpagoxenus americanus* (Hymenoptera: Formicidae). Trans. Amer. Entomol. Soc. 65:97-122.
- WILLIAMS, G. C. 1979. The question of adaptive sex ratio in outcrossed vertebrates. Proc. R. Soc. Lond. B 205:567-580.

Corresponding Editor: R. H. Crozier

Evolution, 40(1), 1986, pp. 204-206

GEOGRAPHIC VARIATION IN HOUSE FLY SIZE: ADAPTATION OR LARVAL CROWDING?

W. C. BLACK IV AND E. S. KRAFSUR

Department of Entomology, Iowa State University, Ames, IA 50011

Received May 23, 1985. Accepted July 23, 1985

Morphometric analysis of geographic variation in species is often used to study and reveal modes of adaptation (e.g., *Drosophila robusta* [Stalker and Carson, 1947]; *Pemphigus populi-transversus* [Sokal et al., 1971]; *Culicoides* spp. [Atchley, 1971]). To study geographic adaptation in house flies (*Musca domestica* L.), Bryant (1977) and Bryant and Turner (1978) measured 14 morphometric characters in flies from "isolated" (widely separated) locations throughout the United States. Principal component analysis on correlations among characters showed that body size was the major source of variation among flies and that characters developed isogonically (character size ratios remained constant in small and large flies). Variance components of size among geographic locations accounted for 27% of the total variance. Bryant (1977) reported an equivalent amount of variation among flies sampled on different dates at a single location. He concluded that "... changes within and among years at one locality parallel in magnitude and direction the total observed geographic variation of this species in the United States!" (Bryant, 1977 p. 587). Bryant nevertheless interpreted size as an adaptation to latitude, altitude, and season and concluded that houseflies genetically "track" changes in the environment.

We studied seasonal and spatial sources of size variation in the house fly in Ames, Iowa, during investigations on the population ecology (Krafsur et al., 1985; Krafsur, 1985) and genetics (Black and Krafsur, 1985) of the species. Our results, described fully in Black and Krafsur (unpubl.) cast doubt on Bryant's conclusion that geographical variation among flies represents genotypic adaptation. We present evidence that the large geographical variation noted by Bryant resulted from his sampling flies in such a way that seasonal and geographical effects were confounded. We show that adult size, deemed geographically adaptive by Bryant, was greatly and decisively influenced by larval density.

MATERIALS AND METHODS

House flies were collected from five farms on six sampling dates from July 7 to October 10, 1982. In 1983, house flies were collected from six farms on eight sampling dates from May 23 to November 7. All farms were located within a 25-km radius. Ten females were randomly selected from each sample, and head widths measured as a convenient index of body size.

To study the effects of larval density on size, larvae were raised to adults at six different densities. Gravid females were collected at a pork farm, placed