DENSITY-DEPENDENT SEXUAL SELECTION IN THE FUNGUS BEETLE, *BOLITOTHERUS CORNUTUS*

JEFFREY CONNER[1]
Section of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853

Abstract.—The hypothesis that population density can affect sexual selection on male horn size was tested in a three-year study of a fungus beetle, *Bolitotherus cornutus*. Males of this species have horns that vary greatly in length. These horns are used in fights over females; longer-horned males win the majority of fights, regardless of population density. However, density does affect the relationship between horn length and access to females. In six populations of naturally and experimentally varying densities, longer-horned males gained a greater advantage in access to females in low-density populations than at high density. This increase in access to females causes an increase in the number of females inseminated by longer-horned males; thus, sexual selection for longer horns is stronger at lower densities.

Population density can affect the intensity of competition among organisms for limited resources. For male animals in particular, density can influence competition for mates. The effect of density on male competition has been most widely studied in anuran amphibians; several of these studies have shown that an increase in the density of males at a pond causes some males to stop calling to attract females and switch to actively searching for mates (see Arak [1983] for a review). Some of the anuran studies have also suggested that larger males have a mating advantage only in high-density populations. Thus, density-dependent sexual selection, defined broadly as variation with density in the strength or direction of selection on male traits, can occur.

A common problem in field studies that examine the effect of population density on sexual selection is that other factors, such as the operational sex ratio (Emlen, 1976), covary with density. Since the operational sex ratio can alter various aspects of animal mating systems (e.g., Lawrence, 1986, 1987*a*, 1987*b*), it, rather than population density, may be the cause of differences in sexual selection. Some ways to deal with this covariance are: 1) to include the operational sex ratio in the analysis as a covariate (this usually requires large sample sizes); 2) to select a species in which the opera-

tional sex ratio does not covary with density; and 3) to manipulate density experimentally while holding the operational sex ratio constant. The last two methods were employed in the present study, which deals with the effect of population density on sexual selection in a fungus beetle.

Bolitotherus cornutus is a tenebrionid fungus beetle that is found throughout eastern North America on polypore shelf fungi (principally *Ganoderma applanatum*) that grow on dead trees (Liles, 1956; Pace, 1967). Adult *B. cornutus* are active at night on the surface of the fungi, with most mating and aggressive behavior occurring between midnight and 7:00 A.M. Male *B. cornutus* possess pronotal horns that are used in aggressive encounters between males. Females lack horns and show no aggressive behavior. Horn length and elytral length (a measure of body size) are positively correlated (Brown and Siegfried, 1983; Conner, 1988). Previous laboratory (Brown and Bartalon, 1986) and field (Conner, 1988) studies suggest that horn length is more important than body size in determining mating success in *B. cornutus*; therefore, this study focuses on horn length and not on body size. These beetles undergo complete metamorphosis, so horn and elytral lengths remain fixed throughout adult life.

Courtship in *B. cornutus* begins when a male climbs onto the back of a female facing the opposite direction. The male rubs the tip of his abdomen over the female's head and thorax with a rhythmic side-to-side

[1] Present address: Department of Entomology, Cornell University, Ithaca, NY 14853.

TABLE 1. Summary of data taken at three trees over the three years of the study. Sex ratio is the proportion of males active on the fungi averaged over all censuses. Encounter rate is an estimate of the effective density of the three populations studied in 1986. The contrast coefficients are the coefficients used to compare the three high-density slopes to the three low-density slopes. The population density of tree 3 was experimentally increased in 1986, and the resulting high-density population is referred to as occurring on tree 3 EX.

Density	Year	Tree	Number of males	Males per fungus	Dates observed	Encounter rate (mean ± SE)	Sex ratio	Contrast coefficient
Low	1985	2	9	0.9	7/28–8/15	—	0.48	−0.33
	1986	1	29	1.9	7/19–7/29	2.2 ± 0.53	0.56	−0.33
	1986	3	12	1.0	7/19–7/29	1.4 ± 0.49	0.55	−0.33
High	1984	1	51	3.4	7/19–7/29[a]	—	0.49	+0.33
	1985	1	48	3.2	7/28–8/15[a]	—	0.53	+0.33
	1986	3 EX	32	2.7	8/3–8/18	3.9 ± 1.01	0.55	+0.33

[a] These dates were selected from observations conducted throughout 1984 and 1985 at tree 1 (see text for details).

movement (Brown et al., 1985). This courtship behavior lasts from 10 minutes to several hours, after which the male rapidly rotates 180 degrees and attempts to copulate. Females have control over whether a copulation attempt results in spermatophore transfer, and males guard females only after a successful insemination (Conner, 1989).

The purpose of this study was to determine whether population density affects the relationship between male horn length and access to females (copulation attempts) and the relationship between horn length and number of females inseminated. This information can provide insight into whether variation in density between and within populations leads to variation in sexual selection on male horn size in B. cornutus.

MATERIALS AND METHODS

Study Populations

Three populations, on three different dead trees in the same five-hectare patch of woods near Ithaca, NY, were studied during 1984–1986. One of the study sites was a large dead tree with 15 fungi (tree 1). This tree supported a dense population of beetles in 1984 and 1985 (3.4 and 3.2 males per fungus, respectively; Table 1). The density of this population was reduced to 1.9 males per fungus in 1986 by unknown natural causes (Table 1). A low-density population studied in 1985 (on tree 2) had 0.9 males per fungus (Table 1), while another low-density population studied in 1986 (on tree 3) had 1.0 males per fungus (Table 1). After nine days

of observation in 1986, the population on tree 3 was experimentally increased to 2.7 males per fungus by collecting 26 males and 25 females from tree 1 and moving them immediately to tree 3 (four of the 26 new males and two of the original 12 males died before the end of the experimental observation period and were eliminated from the analysis). Hereafter, "tree 3 EX" is used to indicate the site of the experimentally increased population.

The mating season lasts from late May until the end of August in the Ithaca area (Conner, 1988); each population was observed for 9–15 nights during the peak of this season (Table 1). Since adult B. cornutus can live for several years (Pace, 1967), these represented cross-sectional samples of portions of the beetles' lives. Tree 1 was observed throughout the mating seasons of 1984 and 1985 for a related study of selection on male morphology in B. cornutus (Conner, 1988). The observation periods from the high-density population at tree 1 in 1984 and 1985 used in this paper were chosen to correspond to the observation periods at the low-density sites. This was done to ensure that both high- and low-density populations were observed at the same time during the mating season. Populations that were studied on the same dates in the same years (trees 1 and 2 in 1985 and trees 1 and 3 in 1986) were observed at the same times on the same nights by the author and several field assistants.

The males used in the analyses (Table 1) were those present throughout the observation period at each tree; males that ap-

peared or disappeared during the observation period were not included in the analyses of access to females (75–82% of all males were included). This was done so that differences in lifespan did not affect the estimates of access to females.

Observational Methods

All adults in these populations were collected when they were first seen and taken to the laboratory for measuring and marking. Male horn lengths were measured to the nearest 0.2 mm with an ocular grid on a stereo microscope, and each individual was given a unique paint mark. This treatment did not seem to disturb the beetles, and 90% of marked beetles were observed at least once after release.

A headlamp, equipped with an infrared filter (Kodak Wratten #89B), which transmits some far-red visible light, was used for field illumination. The beetles remained active all night under illumination from this light, in contrast to the complete disruption of beetle behavior that was caused by a less-filtered red light.

At the beginning of each nightly observation period, all beetles active on the fungi were censused, and courtships in progress were noted. The population was then continuously monitored for copulation attempts, guarding, and male fights. Since copulation attempts last at least several minutes, it is likely that very few attempts were missed; the number of attempts that a male made is used in this report as a measure of a male's access to females. Guarding behavior lasts several hours and is a reliable indicator that the male has actually transferred sperm (Conner, 1989). Male fights, on the other hand, are short in duration (usually lasting only a few seconds), so many fights were not observed. Therefore, this observation scheme provided accurate data on the number of attempts and successful inseminations but not on the total number or frequency of fights.

To estimate how often males encountered conspecifics, focal samples (Altmann, 1974) of individual males were conducted in 1986. A focal sample consisted of observing a single male continuously for 30 minutes. A total of 12 males were sampled in each population; 11 of these were sampled twice, for

a total of 23 focal samples per population. The encounter rates (Table 1) show that the number of males per fungus is a good measure of relative density among sites. Note that the encounter rate increased almost threefold at tree 3 after the experimental manipulation (1.4 vs. 3.9 beetles encountered per 30 min).

The populations were censused a total of 1–3 times per night. The mean nightly sex ratio over the entire observation period at each population was calculated by averaging the number of males and females recorded in each census period over all censuses at each population. The proportion of males in each of these population averages is the sex ratio of beetles active in the mating area for that population. The sex ratios of all these populations were between 48% and 56% during the observation periods (Table 1); none of these is significantly different from 50% (G tests [Sokal and Rohlf, 1981 pp. 692–731]).

Data Analysis

Fighting success was estimated as the total number of fights a male won over the entire observation period minus the total number that the male lost; this estimate will be referred to as the net fights won. The relationship between horn length and fighting success was estimated using Pearson product-moment correlations.

The relationships between horn length and both access to females and insemination success were estimated as the slopes of separate univariate regressions of the number of copulatory attempts and the number of females inseminated on horn length. Both dependent variables were first standardized by dividing by the number of hours that each population was observed; thus, the dependent variables in these regressions are actually the number of copulatory attempts and the number of inseminations per hour. To test for differences among these slopes at different densities, linear models were fitted using the GLM procedure in the SAS statistical package (SAS Institute, 1985). The models used were:

attempts per hour
    = horn length + population
        + (horn length × population)

TABLE 2. Summary of male fight data. The numbers of each type of fight (male chases and courtships attacked) and the total numbers of fights are given. These numbers cannot be used to compare fight rates between populations (see text). Net fights won is the total number of fights won minus the total number of fights lost; values given are Pearson product-moment correlations. Sample sizes for these correlations were the number of males in each population given in Table 1.

Density	Year	Tree	Male chases	Courtships attacked	Total fights	Net fights won versus horn length (r)
Low	1985	2	10	34	44	0.28
	1986	1	44	77	121	0.39*
	1986	3	31	39	70	0.62*
High	1984	1	16	47	63	0.39**
	1985	1	64	103	167	0.48**
	1986	3 EX	80	148	228	0.64**
	Totals		245	448	693	

* $P < 0.05$; ** $P < 0.01$.

inseminations per hour

$$= \text{horn length} + \text{population} + (\text{horn length} \times \text{population})$$

where "population" is a categorical variable indicating the six different populations and the interaction term (horn length × population) represents the slopes of horn length versus the dependent variables in the six populations. The "estimate" statement in SAS was used to contrast the three higher-density slopes with the three lower-density slopes. The coefficients used for this contrast are given in Table 1.

Since *B. cornutus* adults can survive for more than one season, some of the males at tree 1 are represented in more than one of the three populations from this tree. In addition, the population at tree 3 EX (Table 1) is made up of males that were present before the density increase at tree 3 and males that were moved from tree 1; some of the latter group were also present during the observations at tree 1 in 1986. Therefore, not all of the data in the model discussed above are independent, since 31% of the 181 observations in the data were repeats of males represented elsewhere. To determine the seriousness of this lack of independence, the model was run again with a code for each male added as an additional independent variable.

Since tree 1 was observed throughout 1984 and 1985, lifetime access to females and insemination success for a group of 67 males

could be estimated (Conner, 1988). Male lifetime access to females was estimated as the total number of copulatory attempts a male made in his lifetime divided by the number of hours that the population was observed during his lifetime; lifetime insemination success was estimated in the same way. The relationship between horn length and access to females and that between horn length and insemination success were once again estimated as the slopes of separate univariate regressions of horn length on these two dependent variables. The lifetime slopes were contrasted with the three cross-sectional slopes from the low-density sites referred to above. The contrast coefficients for the lower-density sites were the same as those given in Table 1; the coefficients for the lifetime data were $+1$.

RESULTS

Male Competition

Two types of male fights were observed in this study; each type of fight interfered with male access to females. First, males chased other males off fungi containing females, thus preventing the losing male from courting. Second, males attacked courting couples and attempted to disrupt the courtship by prying the courting male off the female's back before a copulation attempt could occur. The numbers of each type of fight observed in each population are given in Table 2. Due to the observational methods used (see Materials and Methods) and
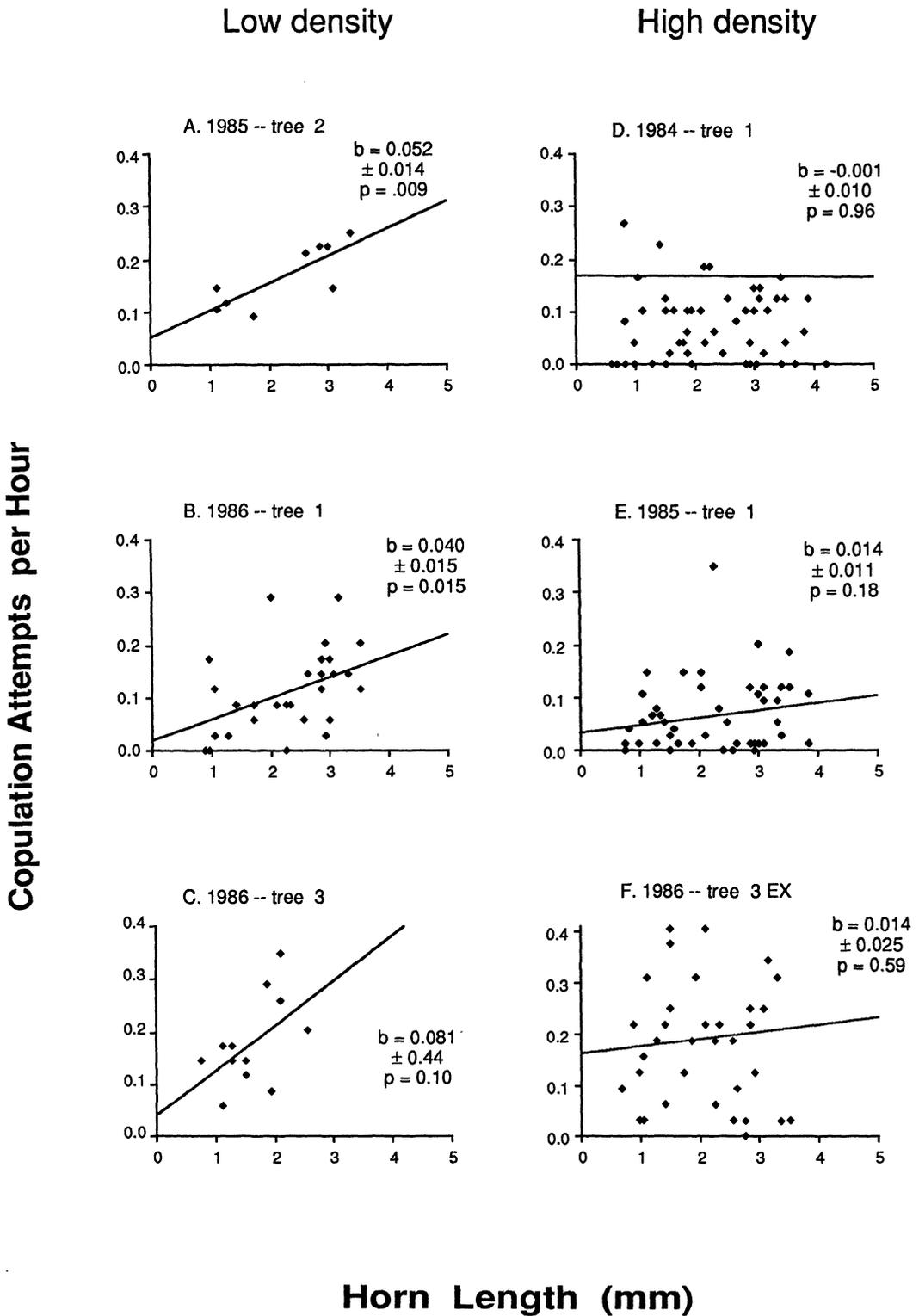
Low density   **High density**

Copulation Attempts per Hour

A. 1985 -- tree 2

$b = 0.052$
± 0.014
$p = .009$

D. 1984 -- tree 1

$b = -0.001$
± 0.010
$p = 0.96$

B. 1986 -- tree 1

$b = 0.040$
± 0.015
$p = 0.015$

E. 1985 -- tree 1

$b = 0.014$
± 0.011
$p = 0.18$

C. 1986 -- tree 3

$b = 0.081$
± 0.44
$p = 0.10$

F. 1986 -- tree 3 EX

$b = 0.014$
± 0.025
$p = 0.59$

Horn Length (mm)

FIG. 1. Scatter plots showing the relationship between male horn length and access to females in the three populations studied, with low-density populations on the left and high-density populations on the right. Each

the different numbers of males and different amount of observation time at each site, these data cannot be used to compare relative rates of fighting between sites. Males did not defend any particular territories or females; both males and females roamed widely among fungi on a single tree.

The longer-horned, larger males had a definite advantage in fights over females, regardless of population density. In five of the six populations there was a significant positive correlation between horn length and the net number of fights won (i.e., the number of fights won minus the number of fights lost) (Table 2). The mean horn lengths of the males did not differ significantly among the six populations (one-way ANOVA, $F_{[5, 175]} = 1.74$, $P > 0.1$).

Male Access to Females

One might expect that, if longer-horned males have greater success in fights over females, then they should have greater access to those females. In low-density populations, this is true. The slope of the regression of horn length on the number of copulatory attempts was strongly positive for the low-density populations at trees 2 and 3 and for the naturally lowered density population at tree 1 in 1986 (Fig. 1A–C). Two of these slopes are statistically significant (A and B), but the slope at tree 3 (C), the steepest of all, is not ($P = 0.10$).

In the naturally high-density population at tree 1 in 1984 and 1985 and in the population at tree 3 EX, the relationship between horn length and access to females was not statistically significant (Fig. 1D–F). Thus, longer-horned males did not have significantly greater access to females at high density.

The best test of the density effect is to compare the slopes of horn length versus access to females for the three high-density populations (tree 1 in 1984 and 1985 and tree 3 EX) to the slopes in the three low-density populations (trees 2 and 3 and tree 1 in 1986). The mean of the three low-den-

sity slopes was found to be significantly greater than the mean of the three high-density slopes (estimated difference between slope means = 0.048 ± 0.020, $t = 2.37$, $d.f. = 169$, $P = 0.019$). The code for each male, when added to the model as an additional independent variable, did not explain a significant portion of the variance in attempts per hour after the effects of the other independent variables were removed (type-IV mean square for male code = 0.0068, $F_{[120, 49]} = 1.43$, $P = 0.08$). Thus, the lack of independence in the data did not have a major effect on the relationship between population density and male access to females.

This effect of population density on male access to females caused differences in male insemination success at different densities. The slopes of the regressions of male horn size on the total number of females inseminated at the three low-density populations were significantly greater than the slopes at the three high-density populations (Table 3).

The lack of significance of the high-density slopes might suggest that long-horned males have no advantage in access to females or insemination success at high density. Alternatively, this lack of significance could be due to inflated sampling errors from estimating access to females over only a portion of the males' adult lifespans. Using the data for lifetime access to females at high density (tree 1 in 1984 and 1985), the weak relationship between horn length and access to females was found to be statistically significant (Fig. 2). The lifetime slope of horn size versus total insemination success was also significant ($b = 0.005 \pm 0.001$, $P = 0.0002$). Note that the magnitude of the lifetime high-density slope of horn size versus access to females ($b = 0.015$) is nearly identical to the cross-sectional high-density slopes in populations E and F in Figure 1 ($b = 0.014$). Thus, the cross-sectional data give a good approximation to the lifetime relationship in this case. While the lifetime

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point represents one male. The y-axis is the total number of times each male attempted to copulate with a female divided by the total number of hours of observation at that population; the x-axis is horn length in millimeters. The slopes of the least-squares regressions are given with their standard errors.

TABLE 3. Slopes (±SE) of the regressions of horn length on total number of females inseminated per hour of observation at the six populations, with results of the test for a difference between the means of the three high-density slopes and the three low-density slopes. The estimated difference between the low- and high-density slopes is 0.017 ± 0.005, $t = 3.59$, $d.f. = 169$, $P = 0.0004$.

Density	Year	Tree	Slope ± SE	P	Number of males
Low	1985	2	0.012 ± 0.011	0.28	9
	1986	1	0.010 ± 0.003	0.01	29
	1986	3	0.038 ± 0.017	0.05	12
High	1984	1	0.003 ± 0.003	0.20	51
	1985	1	0.003 ± 0.002	0.20	48
	1986	3EX	0.002 ± 0.003	0.54	32

slope is statistically significant, the cross-sectional slopes are not, due to the low standard error of the lifetime slope relative to those of the cross-sectional slopes. This difference in standard error is probably due to the increased sampling of males over their lifetimes and the fact that more males were sampled for the lifetime slope than for the cross-sectional slopes ($N = 67$ vs. $N = 48$ and 32).

The lifetime high-density slope of horn size versus access to females was significantly less than the mean of the three low-density slopes (estimated difference in slopes $= 0.042 \pm 0.016$, $t = 2.7$, $d.f. = 109$, $P = 0.008$), as was the lifetime slope of horn size versus insemination success (estimated difference in slopes $= 0.014 \pm 0.004$, $t = 3.3$, $d.f. = 109$, $P = 0.001$). Therefore, longer-horned males have some lifetime advantage in access to females and, thus, in insemination success at high density, but this advantage is significantly less than their advantage at low density.

DISCUSSION

The results presented here show that longer-horned male *B. cornutus* have a greater advantage in both access to females and overall insemination success in low-density populations. This indicates that density-dependent sexual selection on horn size probably occurs in this species. There are two potential problems with this conclusion. The first is that the density difference was based on cross-sectional rather than lifetime data. However, the cross-sectional estimates made at tree 1 in 1984 and 1985 are good approximations to the lifetime estimates; if the same is true at the low-density

sites, then the slopes reported here accurately reflect the relative strength of selection acting in the different populations.

The second potential problem is that insemination success was used here as an estimate of fitness rather than the number of eggs fathered. Other data (Conner, 1987) suggest, however, that the number of eggs fathered per inseminated female does not vary greatly with horn size in *B. cornutus*; thus, the estimates of the relationship between horn size and access to females should also reflect the relationship between horn length and overall fitness.

Despite the caveats mentioned above, it seems likely that the strength of sexual selection on horn size varies with density in *B. cornutus*. The question of how population density alters the advantage of long-horned males remains unanswered. One possibility is that the courtships of long-horned males are disrupted relatively more often at higher densities. At high density, long-horned males often have to contend with other long-horned males, while at low density there is usually only one long-horned male per fungus (pers. observ.). Population density is less likely to affect the rate of disruption of short-horned males' courtships, because long-horned males capable of disrupting the short-horned males' courtships are always present.

The data from tree 3 indicate that the average number of long-horned males' courtships that were disrupted increased 56% after the density was experimentally increased, while the disruptions of short-horned males increased by only 8%. These data are only suggestive, since the observational methods used in this study do not

permit accurate estimation of frequencies of disruption (see Materials and Methods). Only three courtship disruptions were observed during focal samples at tree 3 in a total of 23 hours of focal sampling. Clearly, the mechanism underlying the relationship between density and the advantage of long-horned males in terms of numbers of courtships requires further study.

Density-Dependent Sexual Selection in Other Species

In other studies of the effect of density on sexual selection, three outcomes have been reported: no change in the advantage of larger males at different densities (Warner and Hoffman, 1980; Howard and Kluge, 1985); a greater advantage to larger males at high density (Zeh, 1987; Kagarise Sherman, 1980); and a greater advantage to larger males at low density (McLain, 1982; this study). ("Larger" here refers to the male character studied in each case and not necessarily to overall body size.) There are at least two reasons for this diversity of results; these reasons are not mutually exclusive.

The first reason is that behavioral responses may differ with changes in density. In natural populations of a coral reef fish, the bluehead wrasse, Warner and Hoffman (1980) found no decrease in the mating success of territorial males with increasing density, probably because males at high density move their territories to decrease interference from nonterritorial males. Thus, territorial males altered their choice of territory location based on the density of nonterritorial males, thereby maintaining their mating advantage at all densities. However, long-horned male *B. cornutus* were apparently unable to alter their mating strategy to prevent their loss of advantage at high density, since they had no territories to move and did not migrate between trees to avoid encountering other long-horned males (Conner, 1988; see Lawrence [1987a] for an example of beetles migrating between patches to lessen the effects of male competition).

The other reason, and perhaps the more important one, is variability in the definition of density levels among studies of different species. What is defined as high density in one species may be low density in

Lifetime High Density

b = 0.015
± 0.006
p = 0.016

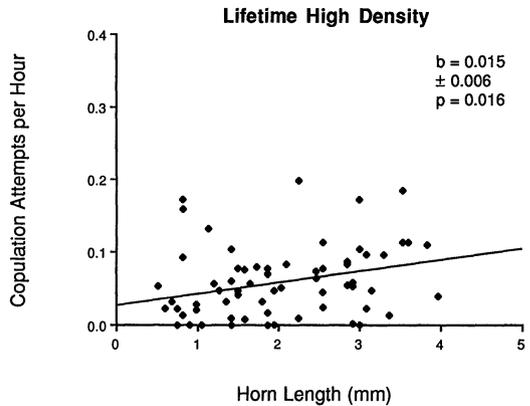(y-axis: Copulation Attempts per Hour; x-axis: Horn Length (mm))

FIG. 2. Scatter plot showing the relationship between horn length and lifetime access to females in a cohort of 67 males at the high-density site (tree 1) in 1984 and 1985. The figure is the same type of plot as in Figure 1, except that the y-axis is the total number of copulatory attempts a male made in his lifetime divided by the number of hours that the population was observed during his lifetime.

another. At very low densities, males rarely encounter one another at all, and male competition is not important (Ghiselin, 1974; Arak, 1983). In the low-density populations in this study, males did encounter one another fairly frequently (Table 1), and male competition did occur (Table 2). The studies showing that large male advantage occurs only at high densities may be those that have relatively low population densities overall. To make meaningful comparisons of the effect of population density across species, studies must include accurate measures of male encounter rates.

ACKNOWLEDGMENTS

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behaviour: Sampling methods. Behaviour 49:227–267.

ARAK, A. 1983. Male-male competition and mate choice in anuran amphibians, pp. 181–210. In P. Bateson (ed.), Mate Choice. Cambridge Univ. Press, Cambridge, U.K.

BROWN, L., AND J. BARTALON. 1986. Behavioral correlates of male morphology in a horned beetle. Amer. Natur. 127:565–570.

BROWN, L., J. MACDONELL, AND V. J. FITZGERALD. 1985. Courtship and female choice in the horned beetle Bolitotherus cornutus (Coleoptera: Tenebrionidae). Ann. Entomol. Soc. Amer. 78:423–427.

BROWN, L., AND B. D. SIEGFRIED. 1983. Effects of male horn size on courtship activity in the forked fungus beetle, Bolitotherus cornutus (Coleoptera: Tenebrionidae). Ann. Entomol. Soc. Amer. 76:253–255.

CONNER, J. 1987. Natural and sexual selection in a fungus beetle. Ph.D. Diss. Cornell Univ., Ithaca, NY.

———. 1988. Field measurements of natural and sexual selection in the fungus beetle, Bolitotherus cornutus. Evolution 42:736–749.

———. 1989. Older males have higher insemination success in a beetle. Anim. Behav. In press.

EMLEN, S. T. 1976. Lek organization and mating strategies in the bullfrog. Behav. Ecol. Sociobiol. 1: 283–313.

GHISELIN, M. T. 1974. The Economy of Nature and the Evolution of Sex. Univ. California Press, Berkeley.

HOWARD, R. D., AND A. G. KLÜGE. 1985. Proximate mechanisms of sexual selection in wood frogs. Evolution 39:260–277.

KAGARISE SHERMAN, C. 1980. A comparison of the natural history and mating systems of two anurans: Yosemite toads (Bufo canorus) and black toads (Bufo exsul). Ph.D. Diss. Univ. Michigan, Ann Arbor.

LAWRENCE, W. S. 1986. Male choice and competition in Tetraopes tetraophthalmus: Effects of local sex ratio variation. Behav. Ecol. Sociobiol. 18:289–296.

———. 1987a. Dispersal: An alternative mating tactic conditional on sex ratio and body size. Behav. Ecol. Sociobiol. 21:367–373.

———. 1987b. Effects of sex ratio on milkweed beetle emigration from host plant patches. Ecology 68: 539–546.

LILES, M. P. 1956. A study of the life history of the forked fungus beetle, Bolitotherus cornutus (Panzer) (Coleoptera: Tenebrionidae). Ohio J. Sci. 56:329–337.

McLAIN, D. K. 1982. Density dependent sexual selection and positive phenotypic assortative mating in natural populations of the soldier beetle, Chauliognathus pennsylvanicus. Evolution 36:1227–1235.

PACE, A. 1967. Life history and behavior of a fungus beetle, Bolitotherus cornutus (Tenebrionidae). Occas. Pap. Mus. Zool. Univ. Mich. 653:1–15.

SAS INSTITUTE. 1985. Users Guide: Statistics, Version 5 Ed. SAS Inst., Inc., Cary, NC.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd Ed. Freeman, San Francisco, CA.

WARNER, R. R., AND S. G. HOFFMAN. 1980. Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (Thalassoma spp.). Evolution 34:508–518.

ZEH, D. W. 1987. Aggression, density, and sexual dimorphism in chernetid pseudoscorpions (Arachnida: Pseudoscorpionida). Evolution 41:1072–1087.

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