

- of other North American desert reptiles. *Bull. Amer. Mus. Nat. Hist.* 114:251–326.
- PUNZO, F. 1982. Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uma notata*. *J. Herpet.* 16:329–331.
- RIDLEY, M. 1983. The explanation of organic diversity: The comparative method and adaptations for mating. Clarendon, Oxford, U.K.
- RUSSELL, A. P. 1979. Parallelism and integrated design in the foot structure of gekkonine and diplo-dactyline geckos. *Copeia* 1979:1–21.
- SNYDER, R. C. 1954. The anatomy and function of the pelvic girdle and hind limb in lizard locomotion. *Amer. J. Anat.* 95:1–46.
- . 1962. Adaptations for bipedal locomotion of lizards. *Amer. Zool.* 2:191–203.
- STEBBINS, R. C. 1944. Some aspects of the ecology of the iguanid genus *Uma*. *Ecol. Monogr.* 14:313–332.
- TAYLOR, C. R. 1948. Soil mechanics. Wiley & Sons, London, U.K.
- WILLIAMS, E. E., AND J. A. PETERSON. 1982. Convergent and alternative design in the digital adhesive pads of scincid lizards. *Science* 215:1509.

Corresponding Editor: T. J. Case

*Evolution*, 40(4), 1986, pp. 874–876

### FEMALE DIMORPHISM IN A MALE-MONOMORPHIC SPECIES

SCOTT P. CARROLL

*Department of Biology, University of Utah, Salt Lake City, UT 84112*

AND

JENELLA E. LOYE

*Department of Entomology, University of California, Berkeley, CA 94720*

Received February 19, 1986. Accepted April 7, 1986

Examples of distinct morphological classes within the males of a species include numerous insects (scarabaeid beetles, figwasps, and others [Eberhard, 1979; Hamilton, 1979]), birds (ruffs [Hogan-Warburg, 1966]), fish (bluegill sunfish [Gross and Charnov, 1980] and Pacific salmon [Gross, 1985]); and mammals (red deer [Darling, 1937]). Such polymorphisms in the elaboration of horns, antlers, exaggerated mandibles, and fighting ability are related to mating competition and may evolve through disruptive selection acting on the trade-off between the mating advantage of sexually selected traits versus the survivorship cost of bearing them (Gadgil, 1972).

Polymorphisms also occur in females but usually only in populations in which males are also polymorphic, e.g., the light and dark morphs of the peppered moth (Kettlewell, 1958), the lesser snow goose (Cooke and Findley, 1982), and the arctic skua (O'Donald and Davis, 1959) and also wing-length polymorphisms in homopteran leafhoppers (Denno, 1979), and water striders (Vepsäläinen, 1978); and the mimetic complexes observed in *Heliconius* (Turner, 1965). Such shared polymorphisms are usually related to predator avoidance or to life-history organization.

Because the potential for increasing reproductive success through enhanced mating effort is much less for females than for males in most mating systems, dichotomization of female mating types into distinct morphs is comparatively less likely to arise. An exceptional example in which females alone are polymorphic involves the mimetic complexes in *Papilio* butterflies (Clarke and Sheppard, 1963). Other examples of female polymorphism are the two color morphs in damselflies of the genus *Ischnura* (Robertson, 1985)

and in the mayfly *Dolania americana* (Peters and Peters, 1977). The damselfly females show a cryptic morph and a brighter one that may function as a male mimic (Robertson, 1985). The mayfly females have either light or dark abdomens, but because they are active only in the pre-dawn (Peters and Peters, 1977), it is difficult to ascribe a mating or predator avoidance function to the color patterns.

Here we report a striking case of female dimorphism in a male monomorphic species. In the treehopper *Microcetrus perditus* (Insecta: Homoptera: Membracidae [Deitz, 1975]) females may possess either greatly enlarged, or very small, pronotal "horns," while males possess only small horns. We describe these morphologies and examine possible causes of both the dimorphism and its sex-limited expression.

Insects of this small genus are solitary, sedentary, and highly cryptic. They are widespread in eastern North America (Kopp and Yonke, 1973), feeding on the sap of oak (Van Duzee, 1917; Kopp and Yonke, 1973; pers. observ.) and possibly hickory (Quisenberry et al., 1978). Adults feed and mate on exposed twigs, and after ovipositing in such twigs, females may guard the eggs until they hatch (Loye, unpubl.). Observations reported here are from central Oklahoma in 1983 and 1985.

As in other membracids, the pronotum of this species is enlarged dorsally and covers portions of the head and abdomen as well as the thorax. Rising forward from the thorax, the pronotum expands into a pair of projections that are either laterally bent and sharp (males) or more upright and rounded (females). Females may be classified as either "long-horned" or "short-horned," whereas males fall into a single distinct class (Fig. 1). The lack of overlap between the

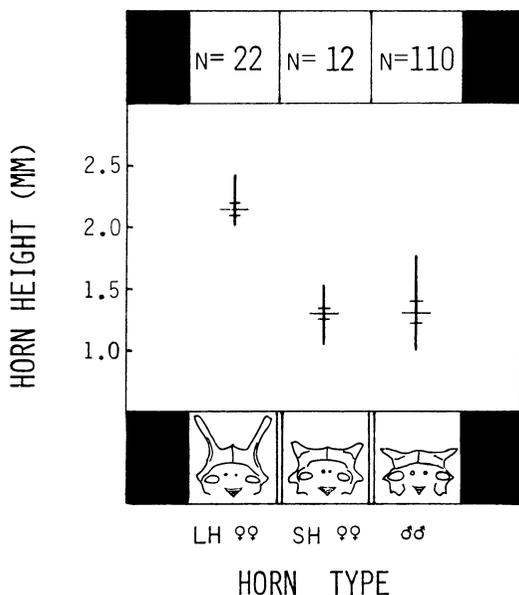


FIG. 1. Horn lengths for long-horned females (LH), short-horned females (SH), and males of treehopper *Microcentrus perditus*. Vertical lines indicate the range, large cross lines indicate the mean, and pairs of small cross lines show  $\pm 1$  SD. Mean  $\pm$  SD for LH:  $2.14 \pm 0.13$  mm, SH:  $1.30 \pm 0.13$  mm, males:  $1.31 \pm 0.16$  mm. There is no overlap in horn lengths between LH and the other classes; LH values are significantly greater than SH ( $Z = 4.75$ ,  $P < 0.0001$ , one-tailed Mann-Whitney  $U$ -test).

female horn types strongly implies that these are distinct morphs rather than extremes of a continuous distribution. Female body length is quite uniform (8–9 mm) and does not differ between the two types. We have observed males mating with or courting females of each morph.

The bizarre pronotal elaborations of treehoppers have traditionally been explained in terms of crypsis, but they may also serve a sensory function (Wood and Morris, 1974; Wood, 1975). Crypsis seems an obvious function in *M. perditus*, since the adult color and form resemble that of oak twigs so strongly as to make visual detection exceedingly difficult. But what factors have led to pronotal dimorphism in females and not in males?

In temperate North America, birds are undoubtedly the most important treehopper predators (pers. observ.), and the sharply pointed, laterally directed horns of male *M. perditus* should reduce their chances of being swallowed (as has been shown for lizard predation on a tropical treehopper [Wood, 1977]). Sticky-trap collections indicate that male *M. perditus* disperse aerially up to 10 times more frequently than do females (assuming an initial 1:1 adult sex ratio, Loye, unpubl.), and the sharp male horns may be particularly effective against aerial insectivores that cannot readily employ a solid substrate for dismantling the prey, as can glean-ing birds. Thus, there may be strong selection on males for conformation to a mechanically protective horn morphology.

Maternal egg-tending, in addition to the more sedentary female habit, may increase the intensity of selection favoring cryptic females, and ultimately explain the existence of female dimorphism in this insect. When guarding their progeny from parasitoid wasps or predatory mites, egg-tending females doggedly maintain their position on the twig even if molested (Loye, pers. observ.; Brown, 1976). In contrast, males deftly slip beneath the twig and may fly off if further disturbed. Maternal behavior thus exposes females to greater potential danger from glean-ing insectivores and crypsis may be their only defense. The female horn dimorphism is remarkable in that long-horned females strongly resemble the dead, woody spurs that are numerous along oak twigs during the treehopper's late summer and autumn reproductive period, while the short-horned females resemble the oak leaf buds present in the spring when overwintering adults resume feeding, and when glean-ing insectivores return. The cryptic advantage afforded by the short-horned morph in the spring may thus be reduced relative to the long-horned morph as the season progresses.

The exact selective regime responsible for the origin and maintenance of this polymorphism is not yet identified. The polymorphism may have resulted from disruptive selection if females of intermediate horn size were less cryptic, as suggested above (sensu Clarke and Sheppard, 1960), coupled with temporal variation in selection due to seasonal differences between the morphs in cryptic advantage. Any frequency-dependence in the search images of predators (Clarke, 1962) would further contribute to the stability of the female dimorphism.

The fact that the mean horn size of males is identical to that of short-horned females lends credence to the hypothesis of disruptive selection, in that the short-horned condition may be one of the peaks of cryptic advantage. At this point we do not know enough about the genetics of pronotal size in treehoppers to evaluate which models are most likely to apply. However, in the case of *M. perditus*, the contrast between a mechanical constraint on male pronotal morphology and variation in the background environment of females constrained to cryptic defense may account for this unusual case of female dimorphism in a male monomorphic species.

#### ACKNOWLEDGMENTS

We thank our friends and colleagues in Ecology and Evolution at the University of Utah for their suggestions, especially Orlando Cuellar, George Edmunds, Monica Geber, Mark McGinley, and Victor Rush.

#### LITERATURE CITED

- BROWN, R. L. 1976. Behavioral observations on *Aetalion reticulatum* (Hem., Aetalionidae) and associated ants. *Insectes Sociaux* 23:99–108.
- CLARKE, B. 1962. Balanced polymorphism and the diversity of sympatric species. *Syst. Assoc. Publ.* 4: 47–70.
- CLARKE, C. A., AND P. M. SHEPPARD. 1960. Super-genes and mimicry. *Heredity* 14:175–185.
- . 1963. Interactions between major genes and polygenes in the determination of the mimetic patterns of *Papilio dardanus*. *Evolution* 17: 404–413.

- COOKE, F., AND C. S. FINDLEY. 1982. Polygenic variation and stabilizing selection in a wild population of lesser snow geese (*Anser caerulescens*). *Amer. Natur.* 120:543-550.
- DARLING, F. F. 1937. A Herd of Red Deer. Doubleday, N.Y.
- DEITZ, L. L. 1975. Classification of the higher categories of the New World treehoppers (Homoptera: Membracidae). *N.C. Agr. Exp. Sta. (Raleigh, NC) Tech. Bull.* 225:1-177.
- DENNO, R. F. 1979. The relation between habitat stability and the migratory tactics of planthoppers (Hemiptera: Delphacidae). *Misc. Publ. Entomol. Soc. Amer.* 11:41-49.
- EBERHARD, W. G. 1979. The function of horns in *Podischnus agenor* and other beetles, pp. 231-258. *In* M. S. Blum and N. A. Blum (eds.), *Sexual Selection and Reproductive Competition in Insects*. Academic Press, N.Y.
- GADGIL, M. 1972. Male dimorphism as a consequence of sexual selection. *Amer. Natur.* 106:574-580.
- GROSS, M. R. 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313:47-48.
- GROSS, M. R., AND E. L. CHARNOV. 1980. Alternative male life histories in bluegill sunfish. *Proc. Nat. Acad. Sci. USA* 77:6937-6940.
- HAMILTON, W. D. 1979. Wingless and fighting males in fig wasps and other insects, pp. 167-220. *In* M.S. Blum and N. A. Blum (eds.), *Sexual Selection and Reproductive Competition in Insects*. Academic Press, N.Y.
- HOGAN-WARBURG, A. J. 1966. Social behaviour of the ruff, *Philomachus pugnax* (L.). *Ardea* 54:109-229.
- KETTLEWELL, H. B. D. 1958. A survey of the frequencies of *Biston betularia* L. (Lep.) and its melanistic forms in Britain. *Heredity* 12:51-72.
- KOPP, D. D., AND T. R. YONKE. 1973. Treehoppers of Missouri. I. Subfamilies Centrotinae, Hoplophorioninae, and Membracinae (Homoptera: Membracidae). *J. Kans. Entomol. Soc.* 46:42-64.
- O'DONALD, P., AND P. E. DAVIS. 1959. The genetics of color phases in the Arctic skua. *Heredity* 13:481-486.
- PETERS, W. L., AND J. G. PETERS. 1977. Adult life and emergence of *Dolania americana* in north-western Florida (Ephemeroptera: Behningiidae). *Int. Rev. ges. Hydrobiol.* 62:409-438.
- QUISENBERRY, S. S., T. R. YONKE, AND D. D. KOPP. 1978. Key to the genera of certain immature treehoppers of Missouri with notes on their host plants. *J. Kans. Entomol. Soc.* 51:109-122.
- ROBERTSON, H. M. 1985. Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: Females mimicking males. *Anim. Behav.* 33:805-809.
- TURNER, J. R. G. 1965. Evolution of complex polymorphism and mimicry in distasteful South American butterflies, p. 267. *In* P. Freeman (ed.), *Proceedings 12th International Congress of Entomology*. London.
- VAN DUZEE, E. P. 1917. Catalogue of the Hemiptera of America North of Mexico. *Tech. Bull. Calif. Agr. Expt. Sta. (Berkeley, CA) Entomol.* 2:1-902.
- VEPSÄLÄINEN, K. 1978. Wing dimorphism and diapause in *Gerris*: Determination and adaptive significance, pp. 218-253. *In* H. Dingle (ed.), *Evolution of Insect Migration and Diapause*. Springer-Verlag, N.Y.
- WOOD, T. K. 1975. Studies on the function of the membracid pronotum. II. Histology. *Proc. Entomol. Soc. Wash.* 77:78-82.
- . 1977. Defense in *Umbonia crassicornis*: Role of the pronotum and adult aggregations (Homoptera: Membracidae). *Ann. Entomol. Soc. Amer.* 70:524-528.
- WOOD, T. K., AND G. K. MORRIS. 1974. Studies on the function of the membracid pronotum. I. Occurrence and distribution of articulated hairs. *Can. Entomol.* 106:143-148.