

ADVANCES IN REPRODUCTIVE PHYSIOLOGY

VOLUME TWO

Edited by
ANNE McLAREN

Advances in REPRODUCTIVE PHYSIOLOGY

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Anne McLaren

*Institute of Animal Genetics
Edinburgh*

1967

LOGOS PRESS
ACADEMIC PRESS

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Published by
LOGOS PRESS LIMITED
in association with
ELEK BOOKS LIMITED
2 All Saints Street, London, N.1.

Distributed by
ACADEMIC PRESS INC.
111 Fifth Avenue, New York, N.Y. 10003
and

ACADEMIC PRESS INC. (London) LIMITED
Berkeley Square House, Berkeley Square, London, W.1.

Library of Congress Catalog Card Number 65-27403

Paper supplied by A. H. James and Company Ltd.
London
Printed in the Republic of Ireland by Hely Thom Limited, Dublin

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EDITOR'S FOREWORD

This is the second in a series of review volumes. In such a series, the editor is faced always with a dilemma: whether to group the contents of each volume around a single integrated theme, or to spread them over the entire field so as to achieve as balanced a treatment as possible.

A glance at the list of contents will make it evident that this volume, like the last, is neither balanced nor integrated. The most that can be said for it is that certain articles complement other articles. The behavioural aspects of the subject, not always taken sufficient account of by reproductive physiologists, are represented by two articles, one, by Margaret Bastock, on courtship, the other, by Martin Richards, on maternal behaviour. Psychosocial, on implantation, follows naturally from Emmens, on the action of oestrogens. Restall considers the mammalian gametes in relation to the maternal reproductive tract; Gilbert considers the life-history of the hen's egg, again in relation to the reproductive tract. Gruenwald concerns himself with the growth of our own species before birth, while Tanner, writing on puberty, is also largely concerned with problems of growth.

As with any anthology, the choice of topics cannot but reflect, at least in part, the predilections of the editor. We hope that this volume will nonetheless prove of interest and use to a wide range of workers, both within the field of reproduction and in neighbouring fields.

ANNE McLAREN

Edinburgh
Summer 1966

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ERRATUM

ADVANCES IN REPRODUCTIVE PHYSIOLOGY VOLUME I

Readers are requested to make the following corrections in the article "Intersexuality in Domestic Mammals" by Professor J. D. Biggers and Dr. R. A. McFeely in *Advances in Reproductive Physiology*, Volume 1.

Table V, page 41:

- (1) Line 1, column 3, male yellow cat. The genotype should be X^vY and not X^vX^v .
- (2) Line 2, column 3, male tortoiseshell cat. The genotype should be (X^vX^v+Y) and not (X^vX^vY) .

ANN McFEELY

Philadelphia
Summer 1966

THE PHYSIOLOGY OF COURTSHIP AND MATING BEHAVIOUR

MARGARET BASTOCK

Present Address: Department of Zoology, University of Edinburgh, Scotland

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Of all animal behaviour, courtship has perhaps unique interest. This apparently anthropomorphic activity is widespread in the animal kingdom, occurring among many invertebrates as well as vertebrates. It is distinctive and often bizarre in form and appearance and, while its usefulness in facilitating mating may be obvious, its origins and its mechanisms are often obscure.

A. ORIGINS OF COURTSHIP

This article will concern itself mainly with mechanisms of courtship: their nature and their mode of operation. However, a preliminary consideration of the origins of courtship is by no means

irrelevant to this problem for it concerns the circumstances of courtship and its relationship with mating behaviour.

It seems certain that courtship has evolved independently in many groups of animals. It is almost universal among birds and mammals, and sporadic among reptiles, amphibia, fish and invertebrates. Often there are large groups of related species all with displays (like the fruit-flies) and other similar groups all lacking them (like the house-flies). And within the groups which do possess them it is apparent that the displays of closely related species resemble one another in detail more closely than do those of distantly related ones (Hinde and Tinbergen, 1958; Lorenz, 1941; Spieth, 1952; Tinbergen, 1959). In these groups, displays must have arisen early in evolutionary history and diverged as the species diverged. But in other groups circumstances do not seem to have favoured displays.

One important question which can be asked about the evolution of any character concerns its advantages and the circumstances which promote them. Sometimes the advantages of courtship are obvious. Fiddler crabs live together in large communities, often many species together, on a muddy or sandy shore in the Indo-Pacific or in America. Males, each on their separate territories, wave their brilliantly coloured claws and move their bodies as if in a dance (Fig. 1). The movements are very distinctive and those of the different

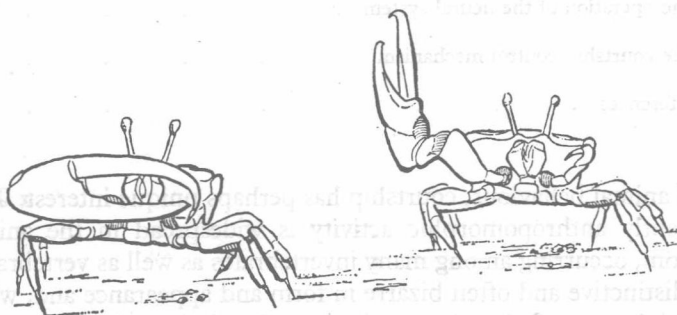


Fig. 1. Two stages in the display of the fiddler crab (*Uca pugnax rapax*). The enlarged claw is stretched out, then raised and lowered jerkily with accompanying body movements. Both the form and the tempo of the wave vary between species. In this species the tempo is unusually slow; sometimes 13 seconds per wave. (Crane, 1957).

species are clearly distinguishable (Crane, 1957). Hence females who can only be induced to mate by specific stimuli from the displays of their own males, are likely to get the 'right' mates. So are the males which provide those stimuli most unambiguously. In other words,

circumstances in which there is danger of cross-mating give advantage to 'coy' females and to displaying males.

Other advantages are equally apparent. When male and female grasshoppers answer each other's calls, or fireflies respond to one another's flashes, they are being guided to potential mates; the specificity of the flashes and the calls at the same time ensures that they are the 'right' mates. And when whitefish display over a particular type of sea bottom (suitable for their eggs), or fighting fish males display beneath a specially constructed bubble nest (Fig. 2), or

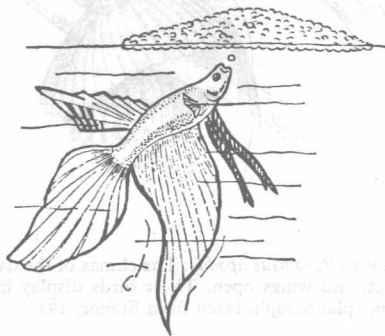


Fig. 2. The male fighting fish (*Betta splendens*) displays beneath his bubble nest. After courting a female, he catches the eggs and blows them into the nest. (Lorenz, 1952).

male birds display on their territories, they are attracting females both to themselves and to suitable places for breeding.

These considerations suggest that wherever there are difficulties about mating or about male and female meeting at the right time and place, then displays will evolve.

Sometimes, particularly when animals are gathered together at display time (fiddler crabs, peacocks, lek birds, fruit-flies), males will compete with one another to attract females. This may be of enormous advantage in polygamous species, enabling the most attractive males to fertilise many more females than normal: it leads to the evolution of elaborate and fantastic displays and adornments as each male 'tries' to outdo his rival (Figs. 3 and 4). Darwin believed that displays arose for this reason alone (Darwin, 1890), but it is likely that there are always mating difficulties which the males compete to overcome (Huxley, 1938; Maynard Smith, 1958). House-fly males are polygamous and must compete for females, yet they have no displays.

A second question concerning evolution is more relevant to problems of mechanism. We may ask how the displays arose in the first place. It is easy to see that distinctive and stimulating males might be selected in certain circumstances, but what causes them to



Fig. 3. Great bird of paradise (*Paradisae apoda*): The climax of the dance with body beautifully curved, plumes erect, and wings open. These birds display in groups. (N.Y. Zool. Soc. photograph, taken from Stonor, 1940).

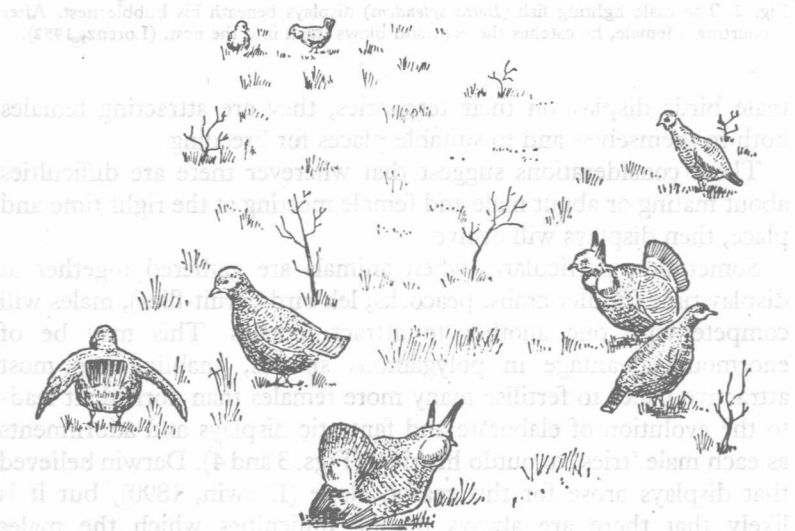


Fig. 4. Another example of an elaborate group display. Male prairie hens (*Tympanuchus cupido*) gather in a lek in the early morning for display. Display features include a tail fan, head tufts which look like horns, and two orange-covered air sacs in the neck which can be used to produce a loud booming noise. (Pycraft, 1914, taken from Etkin, 1964).

do distinctive things or indeed to do anything at all other than seek out a female and attempt to mate with her? More detailed studies of the situation and behaviour of the male when he courts offer some clues here. A male stickleback (*Gasterosteus aculeatus*), visited by a female on his territory, alternates between attacking her (because she is an intruder) and attempting to lead her to his nest (to spawn there). His zig-zag display dance appears to be a rhythmic alternation of these two tendencies, formalised into a dance (Fig. 5). The zig is an



Fig. 5. The zig-zag dance of the male three-spined stickleback (*Gasterosteus aculeatus*), high intensity (left) and low intensity (right). (Tinbergen, 1951).

incomplete attack (it sometimes ends in a bite) and the zag is an incomplete excursion to the nest (which is eventually completed) (Pelkewijk and Tinbergen, 1937; Sevenster, 1961; Tinbergen, 1942, 1951). The spectacular circle flight displays which occur early in the courtship of the green heron (*Butorides virescens*) occur in similar circumstances. The female has only recently entered the male's territory and the male still tends to attack her on occasions. But he also has a nest or nest-site in his territory which he guards and makes conspicuous to his mate. The circle flights, which are performed with huge ritualised wing beats, again appear to formalise these two tendencies (Fig. 6). The flight seems to start as an attack; it is launched from the nest-site directly towards the female with many indications of aggression (in posture and plumage); it ends as a