sion to induce a significant potential across the membrane. The threshold E_{th} is calculated theoretically from Eq. 1 and is shown in Fig. 2 along with measured points. The rate of increase in E_{th} is slow below 100 kHz and the agreement between the theoretical and experimental results is satisfactory. However, above 200 kHz the theoretical curve begins to rise sharply and the disagreement between the theoretical and experimental results becomes apparent. Since the erythrocyte membrane is electrically shunted at these frequencies, the field intensity in the cell would be much higher than at low frequencies. Therefore, the internal field would become sufficient to perturb the structure of gelled hemoglobin S. This may be why the observed frequency dependence of E_{th} deviates from the curve predicted by Eq. 1.

From these results and theoretical considerations, we assume that the application of RF fields causes changes in the red cell membrane that may induce water uptake into the cells. In addition, RF fields seem to perturb the structure of intracellular hemoglobin S gels.

SHIRO TAKASHIMA
Department of Bioengineering, University of Pennsylvania, Philadelphia 19104

TOSHIO ASAKURA
Departments of Pediatrics and *Biochemistry and Biophysics, Children's Hospital of Philadelphia, University of Pennsylvania*

References and Notes

1. J. Dean and A. N. Schechter, *N. Engl. J. Med.* **299**, 863 (1978).
2. I. M. Klotz, D. N. Haney, L. C. King, *Science* **213**, 724 (1981).
3. T. Asakura, S. T. Ohnishi, M. Ozguc, K. Hashimoto, M. Singer, M. O. Russell, E. Schwartz, *Proc. Natl. Acad. Sci. U.S.A.* **77**, 2955 (1980).
4. L. R. Berkowitz and E. P. Orringer, *J. Clin. Invest.* **68**, 1215 (1981).
5. W. F. Schmidt, III, T. Asakura, E. Schwartz, *ibid.*, in press.
6. A. A. Teixeira-Pint, L. L. Nejelski, J. L. Cutler, J. H. Heller, *Exp. Cell Res.* **20**, 548 (1960).
7. H. P. Schwan, *Ann. N.Y. Acad. Sci.* **303**, 198 (1977).
8. H. A. Pohl and J. S. Crane, *Biophys. J.* **11**, 711 (1971).
9. U. Zimmerman, G. Pilwat, R. Rieman, *ibid.*, **14**, 881 (1974).
10. E. Neumann and K. Rosenheck, *J. Membr. Biol.* **10**, 279 (1972).
11. K. Kinosita and T. Y. Tsong, *Proc. Natl. Acad. Sci. U.S.A.* **74**, 1923 (1977).
12. ———, *Biochim. Biophys. Acta* **471**, 227 (1977).
13. ———, *ibid.*, **554**, 479 (1979).
14. M. Kaibara and T. Y. Tsong, *ibid.* **595**, 146 (1980).
15. Z. Delalic, thesis, University of Pennsylvania, Philadelphia (1981).
16. T. Tanaka, I. Nishio, S.-T. Sun, S. Ueno-Nishio, *Science* **218**, 467 (1982).
17. H. P. Schwan, in *Advances in Biological Effects and Dosimetry of Low Energy Electromagnetic Fields* (Plenum, New York, in press).
18. We are grateful to H. P. Schwan for his valuable discussion and to J. Fithian for editorial assistance. Supported by ONR grant N00014-82-K-0321 (S.T.) and NIH grants HL-20750 and HL-18226 (T.A.).

1 November 1982; revised 11 January 1983

Female Moorhens Compete for Small Fat Males

Abstract. *Female moorhens in flocks competed with each other to obtain mates. The heaviest females won most of the agonistic encounters, and these females paired with males that had large fat reserves. Fat males tended to be small, possibly because of energetic constraints on birds of large body size. Females paired with fat males initiated more nesting attempts in a season.*

Any attribute that improves the chance of mating success should, theoretically, be subject to strong positive selection, a process that Darwin (*1*) called sexual selection. Although many field studies have led to the identification of characteristics that are likely to be responsible for success in competition for mates (intrasexual selection) (*2*), few studies have resulted in the identification of characteristics in one sex that are preferred by members of the opposite sex (intersexual selection) (*3*). A field study of the moorhen *Gallinula chloropus* has revealed a characteristic in males that is subject to intersexual selection in a situation in which females compete for access to their preferred mates.

A female's choice of mate may be a critical determinant of reproductive success in situations in which males contribute to parental care or defend critical resources (*4, 5*). Females may benefit by competing for mates when the males they acquire represent, or otherwise provide, an important scarce resource (*6*). Male American jacanas (*Jacana spinosa*) perform all of the postlaying parental care, and females that are successful in competition gain exclusive access to more than one male. They thus create a scarcity of males so that unsuccessful females sometimes fail to gain any male partners (*7*). In species in which there is no shortage of available mating partners, female competition could theoretically occur if variance in male quality resulted in a scarcity of "high quality" males (*6*). Moorhens are a species in which the male performs most of the incubation (*8*). This report provides evidence that female moorhens compete for high quality males (those with large fat reserves) and that females paired to fat males start more clutches in a season since the fat males can incubate for longer than thinner males.

The moorhens in the study area (*9*) formed small flocks (5 to 40 birds) between October and March (*10*). Pair formation occurred in these flocks before the birds left to establish territories (*11*). Females (*12*) initiated courtship (*13*) more frequently than males ($N_1 = 87$, $N_2 = 12$; binomial test, $P \sim 1.0 \times 10^{-15}$; combined observations from the winters of 1978–79 and 1979–80) (*14*). Agonistic encounters (*15*) were common and typically occurred when a female approached a courting pair (*10*). These encounters sometimes led to fighting, with the antagonists jumping into the air and striking at each other with their sharply clawed feet. Marked females in competition for males participated in more fights than marked males ($N_1 = 26$, $N_2 = 12$; binomial test, $P = .033$; combined observations from the 1978–79 and 1979–80 winters). During the 1978–79 and 1979–80 winters, the numbers of agonistic encounters observed (including fights) were 85 and 152, respectively, in encounters in which both members of a dyad were marked, and 171 and 73, respectively, in encounters in which only one bird was marked. These data were used to express each female's success in terms of the percentage of agonistic encounters won (*16*). The best predictor of the outcome of aggressive encounters in flocks was body weight (*17*). However, weights can be compared only if the birds are weighed at the same time of year since there is considerable seasonal variation in body weight (*10*). In January 1979 and February 1980, 62 and 52 percent, respectively, of the females in the study population were weighed. The weights of females that were not caught at these times were adjusted with correction factors based on mean differences in weight from month to month (differences were at most 19 g) (*10*). In both years, a higher proportion of agonistic encounters was won by heavier females than by lighter females (1979: $r_s = .63$, $P < .01$, $N = 16$; 1980: $r_s = .56$, $P < .01$, $N = 21$) (*18*).

Since females court and compete for males in flocks in which there is no shortage of available males (*19*), it seems likely that the females compete for access to high quality partners. Moreover, since heavy females win contests the heaviest females should be paired to the highest quality males. Males perform 72 percent of the incubation (*8*) so that one hypothesis is that high quality males are those that can incubate for long periods. Since incubation in the moorhen is energetically expensive (*8*) and males lose weight during the breeding season (mean January weight, 386 g; mean June weight, 357 g; $t = 2.28$; $P < .05$), energy or nutrient reserves might be an important component of male quality.

Condition, or the amount of stored fat, is difficult to measure in live birds. Weight is often used as a measure of condition (*20*), but this has the disadvantage that large animals are usually heavier although they may be thin. The "size" component of weight can be removed by dividing weight by the cube of length (length is cubed for uniform dimensionality) (*21*). The combined length of the tarsus and metatarsus was used as the length measurement because it does not change with the season as do other measures such as wing length. This condition index—weight divided by the cube of the tarsus-plus-metatarsus length (*22*)—was significantly correlated with the weight of representative fat pads (*23*) in dissected moorhens ($N = 65$, $r = .66$, $P < .001$).

If male condition is an important component of male quality, the heaviest females—those that win the majority of their interactions for males—should be paired to the males that are in best condition. Male condition and female weight were positively correlated in a sample of 25 different pairs of moorhens (Fig. 1). If females select males that are in good condition, as these data suggest, then males without mates and territories should be in poor condition. In 1979 and 1980 there were 6 and 11 marked unpaired males, respectively, compared to 15 and 13 marked paired males (*24*). In both years unpaired males were in significantly poorer condition (measured in January) than paired males (in 1979, the mean condition of paired males was 2.03×10^{-4} and of unpaired males was 1.79×10^{-4} g/mm^3, $t = 3.49$, $P < .01$; in 1980, the values were 1.99×10^{-4} and 1.82×10^{-4} g/mm^3, respectively; $t = 2.15$, $P < .05$).

Males with large fat reserves should be able to incubate for longer periods in a season than thinner males. Consistent with this hypothesis, the total number of days a male spent incubating (*25*) in a season (summed over all clutches) proved to be correlated with the condition of the male at the start of the season (measured in January) ($r_s = .57$, $P < .01$, $N = 18$). If a male's fat reserves, and therefore the ability to incubate, limit a pair's reproductive performance, then the number of clutches a pair could initiate in a breeding season might also be dependent on the male's condition at the start of the season. Differences in the amount of predation on nests (*26*) could confound a comparison between pairs. To remove this effect, I considered pairs whose nesting and renesting attempts all suffered predation (up to four clutches per pair). In this

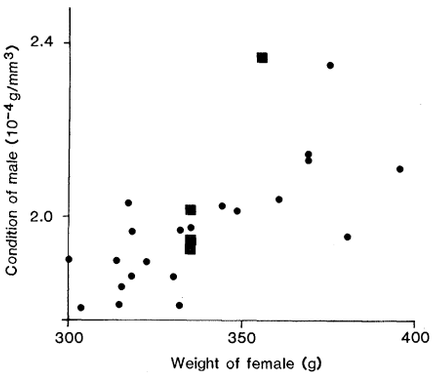

Fig. 1. Relationship between male condition and female weight for pairs of moorhens. All weights used, including those in the condition index, are based on January weights (■) or weights corrected to January weight (●) (see text). The sample considers pairs from three breeding seasons (1978 to 1980 inclusive). If a pair appeared more than once, only those data collected in the first year were included ($N = 25$, $r = .69$, $P < .001$).

sample, the number of clutches started was significantly correlated with male condition measured in January ($r_s = .73$, $P < 0.01$, $N = 14$) (*27*). Males initiate nest building (*10*) and could control the number of nesting attempts in a season by ceasing to initiate further attempts when their energy reserves are exhausted. An alternative explanation of these data is that the energy reserves of the female and her ability to lay eggs determine the number of nesting attempts and that the amount of incubation performed by a male is simply a consequence of this. However, contrary to the expectations of this hypothesis, there was no significant correlation between a female's energy reserves or condition at the start of the season and the number of clutches started ($r_s = .35$, $N = 14$, $P > .05$) (*28*).

Two factors that might influence the

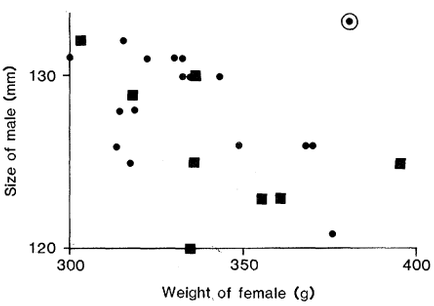

Fig. 2. Relationship between male size (the length of tarsus plus metatarsus) and female weight for paired birds. The sample is identical to that in Fig. 1. Weights were measured in January (■) or corrected to January weight (●) (see text). The outlying point (circled) represents a pair that established a territory much later than normal; this value is included in the analysis ($N = 25$, $r = -.4$, $P < .05$).

condition of males are their age and size. There was no significant difference in the January condition of three age classes [first year ($N = 14$), second year ($N = 6$), third year or older ($N = 14$); one-way analysis of variance, $F = 1.75$). However, there was a negative correlation between the condition of males and the length of the tarsus plus metatarsus ($r = -.59$, $P < .001$, $N = 47$) (*29*). This correlation suggests that small males are often in good condition (*30*) and, if this is the case, then heavy females (those that win most of their agonistic encounters) should selectively pair with small males. Figure 2 shows data that are consistent with this prediction.

A female moorhen paired to a fat male that can incubate for long periods can initiate more nesting attempts and might produce more offspring in a season. This could provide the selective advantage for females to compete for high quality fat male partners even though such males may sometimes be small.

It would be interesting to discuss the consequences of intersexual selection for small males on any genetic variance in the size of males that exists, or has existed, in the population. However, to be meaningful, such a discussion would have to include all other (as yet unknown) fitness advantages and disadvantages of small and large size in males.

MARION PETRIE*
School of Biological Sciences,
University of East Anglia,
Norwich NR4 7TJ, United Kingdom

References and Notes

1. C. R. Darwin, *The Descent of Man and Selection in Relation to Sex* (John Murray, London, 1871).
2. T. H. Clutton-Brock, S. D. Albon, R. M. Gibson, F. E. Guiness, *Anim. Behav.* **27**, 211 (1979); N. B. Davies and T. R. Halliday, *Nature (London)* **269**, 56 (1977).
3. D. T. Gwynne, *Science* **213**, 779 (1981); J. F. Downhower and L. Brown, *Anim. Behav.* **28**, 728 (1980).
4. R. L. Trivers, in *Sexual Selection and the Descent of Man, 1871–1971*, B. Campbell, Ed. (Heinemann, London, 1972), p. 136.
5. T. R. Halliday, in *Behavioral Ecology: An Evolutionary Approach*, J. R. Krebs and N. B. Davies, Eds. (Blackwells, Oxford, 1978), p. 180.
6. M. Petrie, in *Mate Choice*, P. P. G. Bateson, Ed. (Cambridge Univ. Press, Cambridge, 1983), pp. 167–179.
7. D. A. Jenni and G. Collier, *Auk* **89**, 743 (1972).
8. W. R. Siegfried and P. G. H. Frost, *Ibis* **117**, 102 (1975).
9. The moorhens were studied at a 10-hectare site near Norwich in Norfolk, United Kingdom, from December 1977 to September 1980; 245 birds were captured, marked, and weighed at intervals.
10. M. Petrie, thesis, University of East Anglia, Norwich, United Kingdom (1982).
11. Moorhens established territories after they had formed pairs. Polyandrous trios, in which a female formed pair bonds with two males, occurred at a low frequency. Such trios were established later in the season, sometimes when a neighboring female deserted her mate (*10*).
12. Individuals were sexed by applying discriminant functions derived by A. Anderson [*Wildfowl* **26**, 77 (1975)] to a series of size measurements; males are about 14 percent heavier than females. The discriminant function combining length of tarsus plus metatarsus with culmen length cor-

rectly classified 88 percent of the birds that were subsequently sexed by dissection.

13. The courtship sequence in the moorhen has been described by N. A. Wood [*Br. Birds* **67**, 104 (1974)] and by Petrie (*10*). Courtship attempts are initiated by a bird approaching another and performing a characteristic neck-arching display. The relative frequency of observations of neck-arching by marked males and females is an indication of how often each sex initiates courtship.
14. These results could be a consequence of an excess of marked females. However, of 223 marked adults, 125 were male and 98 were female. This difference was not statistically significant (binomial test, $P = .08$).
15. An agonistic encounter, as defined here, is one in which an animal, by approaching or threatening, causes another to withdraw, or one in which two animals physically fight. Chasing was the most commonly observed encounter, amounting to 75 percent of the encounters observed (*10*).
16. Almost all agonistic encounters had a clear outcome (those that did not were not included in subsequent analyses). One bird was considered dominant if it clearly elicited avoidance or withdrawal or defeated its opponent in a fight. Each individual's performance in aggressive encounters was expressed as the percentage of opponents dominated. This measure takes account of interactions between pairs of birds where only one bird was marked.
17. Relative body weight has been shown to be an important factor determining the outcome of aggressive interactions in other bird species (for example, in the dunnock *Prunella modularis* [M. E. Birkhead, *Ibis* **123**, 75 (1981)].
18. If only those females that were weighed at the same time of year are considered (that is, excluding those whose weights were estimated), the correlation between female weight and the proportion of agonistic encounters won is significant (1979: $r_s = .58$, $P < .05$, $N = 10$; 1980: $r_s = .54$, $P < .05$, $N = 11$).
19. Theoretically, competition among females could occur as a result of a shortage of available male partners in flocks. However, flocks contained approximately equal numbers of males and females. For example, the mean proportion of males and females in one flock during the 1978–79 winter was 49.7 percent and 46.5 percent, respectively (3.8 percent could not be reliably sexed as they were subadult). Moreover, agonistic encounters between females that determined access to males always occurred in the presence of other males. Most of the marked nonterritorial unpaired birds were males: 6 of 10 were males in 1979 and 11 of 15 were males in 1980. See also (*14*).
20. G. A. Clark, *Condor* **81**, 193 (1979).
21. J. A. Bailey, *J. Wildl. Manage.* **32**, 835 (1968).
22. The index involves the assumption that shape remains approximately constant over the size range considered.
23. The fat weight used was the sum of four discrete fat pads, those in the inguinal region and those covering the patella on both sides of the body. The sample was collected in November 1980; birds were dissected within 3 days of death.
24. Unpaired birds were easily identified as they formed small flocks on the area during the breeding season (*10*). The number of unpaired males cannot be expressed as a percentage of paired males in order to estimate the proportion of nonbreeding individuals in the population because the groups of nonbreeding birds may have contained birds from outside the study area.
25. Nests were found by searching the area at weekly intervals and by observation of breeding pairs. After nests were found they were visited at intervals of 1 to 3 days. It was thus possible to record the days on which clutches were started and finished, and the length of the incubation period, with an accuracy of ±3 days. The sample includes pairs for which the start of incubation and the outcome of nesting attempts (successful and unsuccessful) were known.
26. Nest predation rates can be as high as 69 percent (*10*). The following potential predators were observed on the study area: stoats (*Mustela nivalis*); rats (*Rattus norvegicus*); carrion crows (*Corvus corone*); jackdaws (*Corvus monedula*); jays (*Garrulus glandarius*); magpies (*Pica pica*); and foxes (*Vulpes vulpes*).
27. It was not possible to obtain an equivalent result for pairs that were successful in hatching eggs since the sample was too small.
28. The number of eggs that a female can lay does not appear to be a major factor limiting reproductive performance in polyandrous species [D. Lack, *Ecological Adaptations for Breeding in Birds* (Methuen, London, 1968)]. This may also be the case in moorhens; one polyandrous female laid eggs for a second male after laying three clutches for her first male (*10*).
29. Material was not available at this time of year to check this result by dissection. The sample combined 22 males measured in January 1979 with 25 males measured in February 1980. The correlation between male condition and bill length (an alternative measure of size) also gave a negative correlation ($N = 47$, $r = -.35$, $P < .02$).
30. Small males may be in better condition because they have lower absolute food requirements than larger birds. The equation derived by J. Aschoff and H. Pohl [*J. Ornithol.* **111**, 38 (1970)] provides an estimate of heat production (M) of a resting bird: $M = 0.0317\ W \exp 0.726$ where W is weight in grams and M is expressed in kilocalories per hour per bird. Substituting the weight of the smallest male moorhen measured in January ($W = 313$ g) yields $M = 2.055$, and substituting the weight of the largest male ($W = 458$ g) yields $M = 2.709$. Thus, the larger bird had a 32 percent higher heat production and a correspondingly greater energy expenditure. The higher food requirement of larger birds might become critical when the food supply, or time available for feeding, is limited. This is the case for moorhens in winter when there is a significant 12 percent decline in mean adult weight between November and January (mean November weight, 436 g; mean January weight, 386 g; $t = 4.44$, $P < .001$) (*10*).

31. I thank P. Walker for allowing me to work on his land; the Wildfowl Trust, Slimbridge, for providing dissection material; L. Huson, M. Gosling, and H. W. Norton for statistical advice and comment; A. F. G. Dixon for providing the initial opportunity to do this work and for helpful comment; T. R. Halliday, P. H. Harvey, and anonymous referees for their comments on earlier drafts; and L. M. Gosling for his continual support and for helpful discussion. Financial support was provided by the Science Research Council.

* Present address: Alder Cottage, Pilson Green, South Walsham, Norfolk, NR13 6EA, United Kingdom.

27 October 1982

Neutrophil Pseudoplatelets: Their Discrimination by Myeloperoxidase Demonstration

Abstract. *Neutrophils, especially in acute infection or the myeloid leukemias, may shed platelet-sized particles that can readily be distinguished from true platelets because they contain neutrophil myeloperoxidase. This enzyme, unlike platelet peroxidase, is not inhibited by glutaraldehyde. The myeloperoxidase and acid hydrolase levels and continuous plasma membranes of these cell-like particles suggest that they are functional cellular entities. They further differ from platelets in that they contain nuclear remnants, occur in bacteria-laden pus and inflammatory exudates, are ingested by macrophages, and do not adhere to each other or aggregate. They could be involved in the immune response to pathogens or contribute to trauma and healing by facilitating deployment of neutrophil acid hydrolase, neutral protease, and myeloperoxidase.*

While using improved cytochemical procedures for demonstrating peroxidases in granulocytic leukocytes by light and electron microscopy (*1*), we observed peroxidase-positive, platelet-sized particles in the blood of many patients. These particles differ from platelets in that they contain a glutaraldehyde-resistant myeloperoxidase (MPO) rather than platelet peroxidase, which is completely inhibited by glutaraldehyde (Fig. 1, A and B) (*2*). MPO is considered a virtual marker for the neutrophil (*3*), the most common leukocyte in peripheral blood. Unlike platelets, the newly elucidated particles may contain nuclear fragments and appear to be formed from neutrophils. We have named them neutrophil pseudoplatelets (*4*).

In most samples of blood showing such fragments, neutrophils with cytoplasmic extensions or with membranes separating their cell bodies from one of these budding moieties could readily be seen (Figs. 1 and 2). The high levels of MPO and acid hydrolases present in these particles and their continuous plasma membranes suggest that they are functional cellular entities, not merely fragments of degenerating neutrophils.

We first observed neutrophil pseudoplatelets in blood and bone marrow samples from myeloid leukemia patients, who may have many neutrophil precursors in their peripheral blood. They were more prominent in samples of blood from patients with infection-associated neutrophilia. They were most conspicuous, however, in samples of pus and inflammatory exudates, which contained large numbers of bacteria and neutrophils (Fig. 1, C to E); platelets were rarely seen in these samples. That pseudoplatelets were not present in some pus samples consisting almost entirely of neutrophils indicates that they are not merely products of dying or degenerating neutrophils.

The size range of particles classified as pseudoplatelets was the same as for platelets. In most patients, however, the median size of pseudoplatelets was considerably larger than that of platelets. Pseudoplatelets showed less of a tendency to assume dendritic or contracted forms than platelets and, unlike platelets, did not appear to adhere to each other or aggregate.

The discrimination of pseudoplatelets from platelets was rarely possible with Romanowsky-type stains such as the