

Sexual selection and the potential reproductive rates of males and females

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PRONOUNCED sex differences in mating competition are a prominent feature of many animal breeding systems. These differences are widely attributed to sex differences in parental investment^{1,2} which bias the ratio of sexually receptive females to males³ (the operational sex ratio), generating more intense competition between members of one sex, usually males³⁻⁵. Unfortunately, relative parental investment¹ is usually impossible to measure in species where both sexes invest in their offspring^{6,7} and there is currently no empirical basis for predicting the pattern of mating competition in these species. In contrast, the potential rate of reproduction by males and females (measured as the maximum number of independent offspring that parents can produce per unit time) is both more directly related to the operational sex ratio and more easily estimated in natural populations⁷. Here we show that among species where males care for the young, the sex with the higher potential reproductive rate competes more intensely for mates than the sex with the lower potential rate of reproduction.

In animals without parental care or where females are responsible for all care, the potential reproductive rate of males usually exceeds that of females. As a result, the operational sex ratio is biased towards males and males are the predominant competitors for mates^{1,7,14}, (except in a few cases where males contribute resources used in the production of zygotes⁸⁻¹¹). In contrast, in species where males are responsible for all parental care while females pay the costs of egg production (which include some teleost fishes¹⁴⁻¹⁶, anurans¹⁷, urodeles¹⁸, invertebrates^{19,20} and a few birds^{21,22}), the direction of mating competition differs between species. In some, females compete intensely for mates, males are choosy in selecting partners and females are brighter than males²³⁻²⁶. In others, males compete intensely for females, females are choosy in selecting partners, and males are brighter than females^{27,28}. An explanation of these differences could be that only in some of these species does the involvement of males in parental care depress their potential reproductive rate below that of females⁷.

To test whether differences in the direction of mating competition depend on which sex has the higher potential rate of reproduction, we extracted data on the maximal reproductive rates of males and females for 29 species where males were responsible for parental care, there was a clear sex difference in the intensity of mating competition, and data were available (Tables 1 and 2). With only two possible exceptions, males had potentially higher reproductive rates than females in all 'predominant male competitors' (Table 1). The most highly developed examples of predominant male competition combined with male parental care are found in fish and frogs where males can care for multiple clutches simultaneously or in quick succession²⁷⁻²⁹. For example, in the three-spined stickleback, *Gasterosteus aculeatus*, males can guard 10 or more clutches of eggs at a time and do so for about 2 weeks, whereas females can lay one clutch every 3-5 days²⁸. Consequently, the potential reproductive rate of males is higher than that of females, the operational sex ratio is male-biased and males compete intensely for mates.

By contrast, in all species that we identified as 'predominant female competitors', females were able to achieve higher rates of reproduction than males. The clearest examples occur in small polyandrous shorebirds, where the potential reproductive rate of males is low because incubation is prolonged and brood

TABLE 1 Relationship between reproductive rates and mating competition for species in which males are responsible for parental care

	Competition for mates more intense in males	Competition for mates more intense in females
<1	Fish <i>Cottus</i> (2 spp) <i>Oxylebius pictus</i> <i>Chromis notata</i> <i>Chrysiptera cyanea</i> <i>Badis badis</i> <i>Pimephales promelas</i> <i>Etheostoma olmstedii</i> <i>Gasterosteus aculeatus</i> <i>Forsterygion varium</i> Frogs <i>Alytes obstetricans</i> <i>Hyla rosenbergii</i> <i>Eleutherodactylus coqui</i>	
Female rate		
Male rate		
>1	Fish <i>Hippocampus</i> spp Birds ? <i>Rhea americana</i>	Fish <i>Apogon notatus</i> <i>Nerophis ophidion</i> <i>Syngnathus typhle</i> Birds <i>Actitis macularia</i> <i>Phalaropus</i> (2 spp) <i>Eudromias morinellus</i> <i>Jacana</i> (5 spp) <i>Rostrathula benghalensis</i> <i>Turnix sylvaticus</i>

Males compete more than females for access to mates in all but two of the species in which a male has a higher potential reproductive rate than a female (mainly ectotherms). Females are the more competitive sex (sex roles are 'reversed') in species where the potential reproductive rate of females exceeds that of males (primarily endotherms).

size is small²¹. For example, in the polyandrous spotted sandpiper *Actitis macularia*, where females compete intensely for mating partners, males do not raise more than one clutch of four eggs during the breeding season, whereas females can produce an egg a day and lay clutches for up to four different males in the course of the season^{23,30}. Predominant female competition also occurs in some fish where males carry eggs or young for lengthy periods and their reproductive rate is constrained by the number of eggs they can carry, including the pipefishes, *Nerophis ophidion* and *Syngnathus typhle*^{25,26,31,32}, and some cardinal fishes³³. Further examples can be expected in other animals where males bear eggs or young.

Both possible exceptions in Table 1 are instructive as they illustrate the need to calculate reproductive rates over different periods in different species. In the greater rhea, *Rhea americana*, males incubate broods of 20-30 eggs laid by several females and compete vigorously for mating access to female groups³⁶. The potential reproductive rate of females calculated over the entire breeding season may be higher than that of males. During the period of mating and brood production however, males can fertilize and accept eggs faster than females can lay them and the operational sex ratio is probably male-biased. In seahorses (*Hippocampus* spp.), the operational sex ratio is biased towards males despite a prolonged male gestation period because the reproductive rate of females is constrained by monogamous pair bonds and by limited periods of receptivity¹².

The potential rates of reproduction by males and females thus provide a basis for predicting the direction of mating competition in the two sexes and thus the direction of sexual selection. Several other factors, however, can bias the operational sex ratio and influence the relative intensity of mating competition. These include behavioural adaptations to competition in the sex with the potentially higher reproductive rate, such as precopulatory guarding of multiple mates and earlier eclosion, emergence or arrival times^{24,37-40}. Conversely, biases in the operational sex

TABLE 2 Maximum observed reproductive rates in species where males are responsible for parental care

Dominant male competitors		Male care duration	Clutch (C) and brood (B) size	Interclutch interval	Max. F/max. M rate of reproduction	Competing sex	Ref.
<i>Alyce: oostetricans</i> (Dicroglossidae: Midwife toad)	2-3 weeks	M can carry > 1 clutch at a time	FF breed 2-4 times per summer at monthly intervals	<1	M	45-47	
<i>M: rosenbergii</i> (Dicroglossidae)	4 days	B=2-350	23 days	<1 (0.25)	M	27	
<i>L. therodactylus coqui</i> (Leptodactylidae)	17-26 days of care 8-9 month season	B=up to 5 x C at once C=16-43	up to 6 clutches per season	<1	M	29	
<i>C. hangiongensis</i> (Cottidae: river sculpin)	4 weeks	B=3.4-5.3 x C up to 13 x C	2 per season	<1	M	49	
<i>C. gobic</i> (Cottidae: river bullhead)	4 weeks	B=2.15 x C C=75-200	2 per season	<1	M	50	
<i>A. pictus</i> (Atherinidae: greenling)	2.5-3.5 weeks 30 days between spawnings up to 7.5 x C per season	B=0-10 x C per cycle B=0-22 x C per season C=1,500-5,000	3 per season	<1	M	51, 52	
<i>Crom: s notata</i> (Pomacentridae: damselfish)	4-12 days (depends on temperature) 8.2-17.8 days between spawnings	B=1-4 x C 2.8-4.6 nests per season C=10,000-27,500	7.2-18.4 days	<1	M*	15, 53	
<i>Dryoptera cyanea</i> (Pomacentridae: damselfish)	4 days MM spawn continuously	B=up to 12,255 eggs per cycle C=900-2,500 eggs per cycle	4 days	<1	M	54	
<i>Sals beds</i> (Lundidae)	2 days egg/3-4 days larvae 7-8 days between spawnings	B=2-3 x C	4-7 days	<1	M	55, 56	
<i>Pnephales promelas</i> (Pryniidae)	4-8 days males spawn continuously for 3-5 weeks	B=max. 6,000 eggs per nest C=200-700 eggs	3-4 days	<1	M	57, 58	
<i>Eth: tome olmsted</i> (Percidae: tessellated darter)	4 days	B=max. 2,000 eggs C=19-324 (season 1=727)	5-16 days (1=7.6)	<1	M*	15, 59	
<i>Gasterosteus aculeatus</i> (Gasterosteidae: stickleback)	2 weeks at 21 °C	B=up to 10 x C B>C=51-150	3-5 days	<1	M	28	
<i>Fersterygion varium</i> (Pterygidae)	7-10 days spawn up to 15 times per season	B=20-7,080 (1=2,245) eggs C=20-1,680 (1=796) eggs	100% spawn once 31% spawn > once never > 5 times per season	<1 (0.3)	M	60	
<i>Hippocampus fuscus</i> (Syngnathidae: Seahorse)	13-14 days	C>B	<13-14 days	>1	M	12	
<i>Rea americana</i> (Greater Rheal)	Incubation 36-37 days plus care one brood per season	B=26.5 C=2-3	up to 12 MM per year	eggs per season > 1 eggs per laying period < 1	M	34-36	
Dominant female competitors		Male care duration (including incubation)	Clutch (C) and brood (B) size	Interclutch interval	Max. F/max. M rate of reproduction	Competing sex	Ref.
<i>Actitis macularia</i> (Spotted sandpiper)	Incubation 21 days max. 8.1 eggs per season usually one brood per season	C=B=4 1 egg per day	max. 11 eggs per season	>1	F	23, 30	
<i>Phalaropus lobatus</i> (Red-necked phalarope)	Incubation 17-21 days male care=33 days usually one brood per season	C=B=4 1 egg per day	10 days up to 2 clutches per season	>1	F	24, 61	
<i>Phalaropus fulicarius</i> (Grey phalarope)	Incubation 18-20 days male care=37 days usually one brood per season	C=B=4	up to 2 per season	>1	F	61, 62	
<i>Eudromia morinellus</i> (Dotterel)	Incubation 24-28 days male care=61 days usually one brood per season	C=B=3	5-11 days up to 3 clutches per season	>1	F	61	
<i>Jacana spinosa</i> (American jacana)	about 60 days*	C=B=4	up to 3 MM per year (≥4 clutches in few weeks) minimum=2-4 days up to 6 clutches per season (up to 2 MM)	>1	F	63	
<i>Jacana jacana</i> (White-necked jacana)	about 60 days*	C=B=4 1 egg per day	several MM per F at same time several MM per F at same time up to 4 MM per F at same time up to 4 MM per F at same time	>1	F	64, 65	
<i>Hydrophasianus chirurgus</i> (Common rail)	about 60 days*	C=B=4	several MM per F at same time several MM per F at same time up to 4 MM per F at same time up to 4 MM per F at same time	>1	F	66, 67	
<i>Actophilornis africana</i> (African jacana)	Incubation 24 days male care > 60 days	C=B=4	up to 4 MM per F at same time up to 4 MM per F at same time	>1	F	68, 70	
<i>Rostadula benghalensis</i> (Parted snipe)	Incubation 15-19 days 1-2 months care (62 days)	C=B=4	up to 4 MM per F at same time	>1	F	69	
<i>Lanius sylvaticus</i> (Blue button quail)	Incubation 12-15 days/care 18-20 days male cycle=53 days total	C=B=3.5	not known but estimated that F can brood with up to 5 MM per year 10-19 days (1=13.8)	>1	F	69, 71	
<i>Apogon notatus</i> (Apogonidae: cardinalfish)	8 days care plus 8-15 days =14-23 days between spawning	C=B	up to 12 MM per year	>1	F	33	
<i>Arenigobius ophiodon</i> (Syngnathidae: pipefish)	28-37 days	C=1.8 x B M=204 eggs per season F=386 eggs per season C=1.9 x B M=91 eggs per season F=219 eggs per season	>1 (1.8)	F	25, 31		
<i>Syngnathus typhle</i> (Syngnathidae: pipefish)	28-45 days	C=1.8 x B M=204 eggs per season F=386 eggs per season C=1.9 x B M=91 eggs per season F=219 eggs per season	>1 (1.9)	F	26, 31		

Species shown are allocated to two categories on the basis of reports of mating competition: predominant male competitors (a) and predominant female competitors. (b) Although both sexes may compete for particular mating partners, most species could be allocated to the groups without difficulty. Records of reproductive rate ignore the possibility of 'stolen' copulations by males. Abbreviations: M, male; F, female; MM, males FF, females. Columns show the best available estimates of: (1) the duration of male care of eggs (incubation) and/or young and of the time between successive broods where remating does not follow immediately on independence of the previous brood; (2) average clutch size laid by females (C) and the average brood size cared for by males (B). Where males are known to care for several clutches simultaneously, the maximum recorded rate of reproduction by females or the maximum number of successful breeding partners per season; (4) maximum recorded female reproductive rate (eggs per unit time) divided by the maximum recorded rate of reproduction by males (independent young reared per unit time). For most species, estimates of reproductive rate were only adequate to indicate whether the potential reproductive rate of males exceeded that of females or vice versa; (5) whether males or females are recorded as the primary competitors for mates or breeding territories. * In congeners/other *Jacana* spp.

ratio may be reduced by sex differences in life expectancy⁴¹, which can reflect the costs of increased competition in the potentially faster sex⁷. Variation in the time necessary to find mates may constrain mating competition in some species⁴² (G. Parker, personal communication), while the form of competitive behaviour may be affected by variation in the costs and benefits of particular tactics to the two sexes. Finally, where the potential rate of reproduction is similar in the two sexes, the relative benefits of acquiring qualitatively superior mates^{43,44}, rather than the operational sex ratio, may determine the comparative intensity of mating competition in the two sexes. □

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1. Trivers, R. L. in *Sexual Selection and the Descent of Man* (ed. B. Campbell) 136-179 (Aldine, Chicago, 1972).
2. Trivers, R. L. *Social Evolution* (Cummings, California, 1985).
3. Emlen, S. T. & Oring, L. W. *Science* **197**, 215-223 (1977).
4. Thornhill, R. in *Evolution of Animal Behaviour: Paleontological and Field Approaches* (eds Nitecki, M. H. & Hitchell, J. A.) 113-135 (Oxford University Press, Oxford, 1986).
5. Krebs, J. R. & Davies, N. B. *An Introduction to Animal Ecology* (Blackwell Scientific, Oxford, 1987).
6. Knapton, R. W. *Can. J. Zool.* **62**, 2673-2674 (1984).
7. Clutton-Brock, T. H. *The Evolution of Parental Care* (Princeton University Press, New Jersey, in the press).
8. Gwynne, D. T. *Trends Ecol. Evol.* **6**, 118-121 (1991).
9. Gwynne, D. T. *Behav. Ecol. Sociobiol.* **16**, 355-361 (1985).
10. Gwynne, D. T. & Simmons, L. W. *Nature* **346**, 172-174 (1990).
11. Thornhill, R. & Gwynne, D. T. *Am. Scient.* **74**, 382-389 (1986).
12. Vincent, A. C. J. thesis, Univ. Cambridge (1990).
13. Baylis, J. R. *Nature* **276**, 278 (1978).
14. Baylis, J. R. *Envir. Biol. Fish.* **6**, 223-251 (1981).
15. Breder, C. M. Jr & Rosen, D. E. *Modes of Reproduction in Fishes* (Natural History Press, New York, 1966).
16. Thresher, R. E. *Reproduction in Reef Fishes* (T. F. H. Publications, Neptune City, New Jersey, 1984).
17. Wells, K. D. in *Natural Selection and Social Behavior* (eds Alexander, R. D. & Tinkle, D. W.) 184-197 (Chiron Press, New York, 1981).
18. Nussbaum, R. A. *Misc. Publs Mus. Zool. Univ. Mich.* **169**, 1-50 (1985).
19. Wilson, E. O. *Insect Societies* (Harvard University Press, Cambridge, Massachusetts, 1971).
20. Thornhill, R. & Alcock, J. *The Evolution of Insect Mating Systems* (Harvard University Press, Cambridge, Massachusetts, 1983).
21. Erckmann, W. J. thesis, Univ. Washington (1981).
22. Handford, P. & Mares, M. A. *Biol. J. Linn. Soc. Lond.* **25**, 77-104 (1985).
23. Oring, L. W., Lank, D. B. & Maxson, S. J. *Auk* **100**, 272-285 (1983).
24. Reynolds, J. D., Colwell, M. A. & Cooke, F. *Behav. Ecol. Sociobiol.* **18**, 303-410 (1986).
25. Rosenqvist, G. *Anim. Behav.* **39**, 1110-1115 (1990).
26. Berglund, A. *Evolution* (in the press).
27. Kluge, A. G. *Misc. Publs Mus. Zool. Univ. Mich.* **160**, 1-170 (1981).
28. Kynard, B. E. *Behaviour* **67**, 178-207 (1978).
29. Townsend, D. S., *Am. Nat.* **133**, 266-272 (1989).
30. Oring, L. W. & Knudson, M. L. *Living Bird* **11**, 59-73 (1972).
31. Berglund, A., Rosenqvist, G. & Svensson, I. *Am. Nat.* **133**, 506-516 (1989).
32. Berglund, A., Rosenqvist, G. & Svensson, I. *Mar. Ecol. Prog. Ser.* **29**, 209-215 (1986).
33. Kuwamura, T. *Envir. Biol. Fish.* **13**, 17-24 (1985).
34. Bruning, D. F. *Nat. Hist.* **82**, 68-75 (1973).
35. Bruning, D. F. *Living Bird* **13**, 251-294 (1974).
36. Bruning, D. F. thesis, Univ. Colorado (1974).
37. Iwasa, Y., Odendaal, F. J., Murphy, D. D., Ehrlich, P. R. & Launer, A. E. *Theor. Populat. Biol.* **23**, 363-379 (1983).
38. Gregory, P. T. *Can. J. Zool.* **52**, 1063-1069 (1974).
39. Michefer, G. R. *Behav. Ecol. Sociobiol.* **14**, 29-38 (1983).
40. Myers, J. P. *Can. J. Zool.* **59**, 1527-1534 (1981).
41. Breitwisch, R. *Curr. Ornithol.* **6**, 1-50 (1989).
42. Sutherland, W. J. *Anim. Behav.* **33**, 1349-1352 (1985).
43. Burley, N. *Proc. natn. Acad. Sci. U.S.A.* **74**, 3476-3479 (1977).
44. Burley, N. *Am. Nat.* **127**, 415-445 (1986).
45. Duellman, W. E. & Trueb, L. *Biology of Amphibians* (McGraw-Hill, New York, 1986).
46. Crespo, J. thesis, Univ. Lisbon (1979).
47. McDiarmid, R. W. in *The Development of Behavior: Comparative and Evolutionary Aspects* (eds Burghardt, C. M. & Bekoff, N.) 127-147 (Garland, New York, 1978).
48. Smith, B. G. *Biol. Bull. Mar. Biol. Lab. Woods Hole* **13**, 5-39 (1907).
49. Goto, A. *Copeia* **1987**, 32-40 (1987).
50. Marconato, A. & Bisazza, A. *J. Fish. Biol.* **33**, 905-916 (1988).
51. DeMartini, E. E. *Anim. Behav.* **35**, 1145-1158 (1987).
52. DeMartini, E. E. *Copeia* **1985**, 966-975 (1985).
53. Ochi, H. *Envir. Biol. Fish.* **17**, 117-123 (1986).
54. Gronell, A. M. *Ethology* **81**, 89-122 (1989).
55. Barlow, G. W. *Copeia* **1962**, 346-360 (1962).
56. Barlow, G. W. *Z. Tierpsychol.* **21**, 99-123 (1964).
57. Unger, L. M. *Behav. Ecol. Sociobiol.* **13**, 125-130 (1983).
58. Sargent, R. C. *Behav. Ecol. Sociobiol.* **25**, 379-385 (1989).
59. Galé, W. F. & Deutsch, W. G. *Trans. Am. Fish. Soc.* **224**, 220-229 (1985).
60. Thomson, S. *Anim. Behav.* **34**, 580-589 (1986).
61. Cramp, S. et al. *Handbook of the Birds of Europe, the Middle East and North Africa* Vol. III (Oxford University Press, Oxford, 1983).
62. Ridley, M. W. *Ibis* **122**, 210-226 (1980).
63. Jenni, D. A. & Collier, C. *Auk* **89**, 743-765 (1972).
64. Osborne, D. R. *Wilson Bull.* **94**, 206-208 (1982).
65. Osborne, D. R. & Bourne, G. R. *Condor* **79**, 98-105 (1977).
66. Hoffman, A. *Scop. Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* **78**, 367-403 (1949).
67. Hoffman, A. *Orn. Ber.* **2**, 119-126 (1950).
68. Matthew, D. N. *J. Bombay nat. Hist. Soc.* **61**, 295-301 (1964).
69. Urban, E. K., Fry, C. H. & Keith, S. *The Birds of Africa* Vol. II (Academic, New York, 1986).

70. Vernon, C. J. *Ostrich* **44**, 85 (1973).
71. Wintle, C. C. *Honeyguide* **82**, 27-30 (1975).

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Construction of a pattern-generating circuit with neurons of different networks

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RHYTHMIC motor behaviours are generated within the central nervous system by neuronal circuits called central pattern generators (CPG)¹. Although a CPG can produce several forms of the same behaviour²⁻⁵ and several circuits may interact to generate different behaviours⁶, it is generally assumed that a given CPG consists of a predefined assemblage of neurons that is functionally distinguishable from other circuits. However, recent studies on the stomatogastric nervous system of crustacea have suggested that CPGs may not be immutable functional entities⁷⁻¹⁰. We now report that under an identified neuromodulatory stimulus, the CPG that produces swallowing-like behaviour of the foregut in lobsters is constructed *de novo* from neurons belonging to other CPGs. Consequently neurons operating independently as members of different circuits may be reconfigured into a new pattern-generating circuit that operates differently from the original circuits. This not only challenges the concept of the CPG being a discrete functional entity, but also demonstrates that a modulatory input can specify an appropriate CPG from a pool of individual neurons of diverse origins.

We performed our experiments on preparations *in vitro* of the stomatogastric nervous system (STNS) of the lobster *Homarus gammarus*. The STNS consists of four interconnected ganglia (Fig. 1a) that together generate well described motor rhythms of the four regions of the foregut¹¹. These independent foregut rhythms control oesophageal ingestion of food, and its storage in the cardiac sac, trituration by the gastric mill system and filtration through the pylorus on the way to the midgut (Fig. 1b). We describe here a new distinct motor activity of the STNS which transfers food between these different foregut compartments. We show that this swallowing-like behaviour arises first from the rhythmic opening of a valve situated between the oesophagus and the cardiac sac (OCS valve) (Fig. 1b), and second from a massive reorganization of all other foregut rhythms (Figs 2 and 3).

In STNS preparations with the anterior part of the foregut left attached, the three dilator muscles (ocsv1-3; Fig. 1b) of the OCS valve are generally inactive and the latter remains closed. We have found that opening of the valve is driven from the commissural ganglion (Fig. 1a) by OCS dilator motoneurons, which in turn are controlled by two equivalent interneurons arising in the inferior ventricular nerve (Fig. 1a). These cells have been previously identified and named 'pyloric suppressors'¹² (PS). Intracellular depolarization of either PS neuron to evoke firing strongly activates ocsv dilator muscles (Fig. 1c). Although PS is generally silent *in vitro*, we believe the neuron has endogenous bursting properties that drive rhythmic dilation

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