

SEXUAL SIZE DIMORPHISM IN SURGEON FISHES DIMORPHISME SEXUEL CHEZ LES POISSONS CHIRURGIENS

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ABSTRACT

Sexual size dimorphism in 11 surgeonfishes ranges from macroandry (male larger) through isomorphism to macrogyny (female larger). These patterns are examined in relation to three hypotheses that often are used to account for the evolution of different sexual size dimorphisms: 1. Agonistic competition for mates selects for increased size and results in large relative size. 2. Intersexual resource competition selects for sexual size differences that reduce intersexual niche overlap. 3. Selection favours investment in non-agonistic mechanisms of mate-competition that results in reduced growth and longevity and in small relative size. It is concluded that macroandry may result from agonistic competition among males to form harems and/or obtain high quality mates; that macrogyny may result when reduced male size decreases intersexual competition; and that isomorphism may occur in species in which, due to sperm competition, males invest heavily in sperm production, because energetic costs of gamete production are sufficiently high in both sexes to minimize differences in their growth rates.

RÉSUMÉ

Le dimorphisme sexuel dans les tailles de 11 acanthurides va de la macroandrie (mâle plus long) en passant par l'isomorphisme jusqu'à la macrogynie (femelle plus longue). Ces caractéristiques sont analysées par rapport à trois hypothèses qui souvent sont utilisées pour expliquer l'évolution des différents dimorphismes sexuels des tailles: 1. La compétition agonistique pour les mâles sélectionne des tailles plus grandes, le résultat étant des tailles relatives plus grandes. 2. La compétition intersexuelle pour des ressources produit une tendance vers la différence des tailles entre les sexes. 3. La sélection favorise l'investissement dans des mécanismes non agonistiques de compétition pour des couples ce qui a comme résultat un grandissement et une longévité réduits et une taille relative petite. On conclut que: la macroandrie peut être à l'origine d'une compétition agonistique parmi les mâles afin de former des harems et/ou pour obtenir des mâles de haute qualité; que la macrogynie peut avoir pour origine une taille réduite de mâles qui diminue la compétition intersexuelle; et que l'isomorphisme peut survenir chez des espèces dont les mâles investissent largement dans la production de sperme, parce que les coûts énergétiques de la production des gamètes sont assez élevés dans les deux sexes pour minimiser les différences de leur taux de croissance.

INTRODUCTION

Degree of sexual size dimorphism (SSD) is a consequence of complex interactions of sexual and natural selection. Such selection may operate either directly on size or it may operate on some other character that indirectly affects maximum size by affecting growth and longevity. Although in some instances the size of each sex varies independently, in others the relative size difference between the sexes may itself be a factor that selects for the absolute size. Further, although selection for size sometimes reflects a dependency of reproductive success on relative size, in other cases reproductive success depends on absolute size (Darwin 1874; and e.g., Ghiselin 1974; Ralls 1976; Clutton-Brock 1983).

Here I describe patterns of SSD in 11 acanthurids from four genera (Acanthurus, Ctenochaetus, Naso and Zebrasoma) living at two widely separated sites, and present data that bear on three hypotheses that have been used to account for variation in SSD: (A). Agonistic competition for mates selects for increased size and produces large relative size in the competing sex (Darwin 1874). (B). Size differentiation reduces intersexual competition for resources (Selander 1966). (C). The amount and life-history scheduling of investment in non-agonistic adaptations for mate-competition at the expense of growth and longevity determine the absolute and relative size of the competing sex (Ghiselin 1974; Warner and Harlan 1982). Due to a lack of relevant data, other hypotheses (e.g. female choice) will not be considered here.

PATTERNS OF SEXUAL SIZE DIMORPHISM

In five of the species, males grew to a larger size than females (macroandry) (Table 1). One other species (A. nigrofuscus) was macroandrous at one site and isomorphic at another. Two species were isomorphic. In two other species females reached a larger size than males and were larger than their mates (macrogyne), while another species (Z. veliferum) was macrogyne at one site and apparently isomorphic at the other. The greatest extremes of SSD were reached among the macrogyne species (Table 1).

SOCIAL AND MATING SYSTEMS

Details of methods, study areas and social grouping patterns and mating systems of the study species are presented elsewhere (Robertson et al. 1979; Robertson 1983). For the purposes of this paper the information on social and mating systems can be summarized as follows. Surgeonfishes may live in (1) temporally stable, territorial harem groups composed of 1 male and several females, (2) temporally stable, territorial heterosexual pairs, (3) territorial or non-territorial groups of unpredictable composition, (4) solitary territories (individuals of either sex) or (5) large, mobile feeding schools. Spawning takes two basic forms, pair-spawning and group-spawning, although intermediate states occur. Pair-spawning involves 1 male and 1 female; it may occur in the pair's normal feeding territory or in a temporary spawning territory to which both fish have migrated. In a group-spawning act, a

cluster of up to 20 males spawns simultaneously with (apparently) one female. Group-spawnings often occur en masse when hundreds or thousands of fish aggregate at a spawning ground. Pair-spawning males are territorial and attempt to prevent other males from interfering in their spawnings. Group-spawning males are non-territorial and do not agonistically compete for females.

EVOLUTIONARY HYPOTHESES

A. Agonistic mate-competition produces large sexual size: This hypothesis predicts several correlations between patterns of SSD and mating system structure. 1. Macroandry should occur in species in which males agonistically compete for mates in various ways - (a) to form harems, (b) to pair with a female if females are in short supply, (c) to acquire a high quality mate (Price 1982), or (d) to acquire a temporary spawning territory if they do not form pairs or harems. 2. Macrogyne should occur in species in which females compete for mates and male mating success is either independent of size or a negative function of size. 3. Isomorphism should occur in species in which neither sex competes for mates in this manner.

The data show the following: 1. Macroandry. The majority of macroandrous species do form harems (Table 1), and males defend their harems against male conspecifics. However data are lacking to show whether (a) harem formation depends on male-male agonistic interactions and (b) large males are more successful than small males at forming harems. There are no data that indicate whether females were in short supply in any macroandrous species, and in none of those species was pair or harem formation absent. The major apparent exception to the expectation that harem forming species will be macroandrous is A. leucosternon, which is strongly macrogyne, but in which a few males form harems (Table 1). This apparent contradiction resolves when it is seen that harem formation in A. leucosternon probably results from a sex-ratio imbalance rather than male-male competition: the adult sex-ratio was 1:1.15 and, because many of the "excess" females were not living with males, (Robertson et al. 1979) it seems that males were not competing to form harems.

In fishes in general, female fecundity increases with body size (e.g. Wootton 1979). As estimated from ovary sizes (Table 2) this relationship probably holds for female surgeonfishes. In many species that form relatively long term male/female associations and in which female quality (i.e. fecundity) increases with size, males compete to pair with large females and large males are more successful at doing so (Ridley 1983). The available data show that such size-assortative pairing occurs in harem forming macroandrous surgeonfishes (Table 3). Thus agonistic competition for high quality mates may produce macroandry in surgeonfishes. The relative importance of such competition versus competition to form harems remains to be determined.

2. Isomorphism. The data conform to expectations since the species that definitely are isomorphic have mating systems characterized by a lack of agonistic mate-competition (Table 1). The situation with Z. veliferum at Palau is not clear, because quantitative data are lacking

Table 1. Relative sexual size, social groupings, spawning patterns, levels of sperm competition and testis size in surgeonfishes.

Species	Relative Size of Sexes \bar{X} of ♂ weight / ♀ weight		Individuals per Social Group ⁵	Predominant Spawning Types ⁶	Amount Sperm Competition	Testis Weight		nd/nq
	as % of body wt	Relative to ovary wt ⁷						
	Macroandry					\bar{X} (SE)		
<i>Z. scopas</i> (A) ¹	1.34(14)**2	2.2	p	p	very low	0.3(.05)	.30	14/13
<i>Z. scopas</i> (P)	1.74(19)**	2.7	p	p	very low	0.2(.03)	.18	20/25
<i>C. strigosus</i> (A)	1.47(9)**	2.7	p	p	very low	0.5(.05)	.33	8/15
<i>C. striatus</i> (P)	1.63(12)**	3.1	p+g	p+g	low to high	0.9(.12)	.69	31/20
<i>C. striatus</i> (A)	1.25(8)**	2.8	p+g	p+g	low to high	2.1(.30)	.31	7/12
<i>N. lituratus</i> (A)	1.44(4)**	2.0	nd	nd	nd	0.3(.30)	.14	10/15
<i>A. nigricaudus</i> (A)	1.06(9)* ³	2.1	nd	nd	nd	0.7(.01)	.18	7/10
<i>A. nigrofuscus</i> (P)	1.15(14)**	2.2	p+g	p+g	med to high	2.0(.32) ⁸	.63	14/39
	Isomorphism							
<i>A. nigrofuscus</i> (A)	1.0 ns	(upg)	g	g	high	1.7(.36)	.47	16/19
<i>A. triostegus</i> (A)	1.0 ns	(upg,sc)	g	g	high	3.7(.76)	.88	42/19
<i>A. lineatus</i> (A)	1.0 ns	(sol)	nd	nd	nd	1.9(1.12)	1.72	10/8
<i>A. lineatus</i> (P)	1.0 ns	(sol)	g	g	high	3.2(.32)	1.52	34/24
<i>Z. veliferum</i> (P)	1.0 ⁴	1.7(sc)	p	p	very low	0.2(.05)	nd	6/nd
	Macrogyne							
<i>Z. veliferum</i> (A)	0.68(9)**	2.0	p	p	very low	0.5(.08)	.27	9/9
<i>A. leucosternon</i> (A)	0.46(16)**	2.05	nd	nd	nd	0.6(.19)	.25	11/10
<i>A. glaucoparicus</i> (P)	0.38(13)**	2.0	nd	nd	nd	0.4(.05)	.20	13/12

1: A=Aldabra, P=Palau. 2: Intragroup \bar{X} for (n) pairs or harems. upg = unpredictable groups, sc = schooling, sol = solitary territories. Median test for 10 largest fish of each sex:** p < .01, * p < .05, ns=not significant. 3: error in Robertson et al. 1979 - ♂ 6.3% (not 63%) > ♀. 4: Tentative - based on observations only. 5: Palau data for groups at high population density. Numbers are for heterosexual pairs or harems. 6: p = pair spawn, g = group spawn - see text for descriptions; nd=no data. 7: \bar{X} testis weight as % of body weight/ \bar{X} ovary weight as % of body weight (using active gonads only). 8: Harem forming males only.

Table 2: Correlation between body weight and gonad weight in each sex of five surgeonfishes¹

Species	Spearman correlation coefficients	
	Male (n)	Female (n)
<i>Z. scopas</i> (P)	0.22 ns (20)	0.49* (25)
<i>A. nigrofuscus</i> (P)	0.79*** (25)	0.72*** (43)
<i>C. striatus</i> (P)	0.42* (31)	0.41ns ² (20)
<i>A. lineatus</i> (P)	0.61*** (37)	0.66*** (36)
<i>A. triostegus</i> (A)	0.82*** (43)	0.72*** (27)

P = Palau A = Aldabra. 1: species for which there are samples of ≥ 20 of each sex. *p < .05, ***p < .001; ns = not significant (2: .10 > p) .05).

on the precise degree of dimorphism. There were two major elements in its mating system at Palau - (a) the formation of macrogynous pairs and (b) the defense of temporary spawning territories by the larger males. The occurrence of (near?) isomorphism in *Z. veliferum* at Palau may represent the result of opposing selection pressures for size change in males, i.e. selection to decrease male size when pairs are formed (see below) and selection to increase male size when there is competition for spawning territories.

3. **Macrogyne.** The macrogynous species conform to only one of the two predictions of the hypothesis: (i) Assuming relative gonad size is a reliable indicator of female quality (see above), then the data indicate that large males are not more successful than small males at pairing with high quality females (Table 3). (ii) However,

Table 3: Size-assortative pairing in surgeonfishes.

Species ¹	Correlation for intrapair weights ²		Male size differential ³
	n		
Macroandrous			
<i>Z. scopas</i> (P)		.64(*)	13
<i>Z. scopas</i> (A)		.60(*)	12
<i>A. nigrofuscus</i> (P)		.51	13
		(.10 > p > .05)	
Macrogyne			
<i>A. leucosternon</i>		.38(ns)	15
<i>A. glaucoparicus</i>		-.11(ns)	12

1: Adequate samples not available for other species. A = Aldabra. P = Palau. 2: Spearman r (*p < .05, ns = not significant). 3: weight largest ♂ / weight smallest ♂ in sample.

there was no evidence that a size advantage gives an advantage to females competing for mates. In only one of the three macrogynous species (*A. leucosternon*) was there a shortage of males (see above); but females with mates were not larger than females without mates (Mann-Whitney $U_{19,6} = 62$, p > 0.20). Consequently there is no indication that agonistic mate-competition would select for increased female size in this species, and it does not appear to be involved in producing macrogyne in any of the surgeonfishes.

4. **Intraspecific variation.** In two species there were differences in patterns of SSD that correlated with differences in mating system

structure as predicted by the hypothesis. First, at Aldabra A. nigrofuscus was isomorphic and its mating system was characterized by an absence of agonistic mate competition. At Palau this species was macroandrous and a major component of its mating system (harem formation) involved male-male agonistic mate competition. Second, at Aldabra, Z. veliferum only formed pairs and was macrogynous. At Palau, small males of this species formed macrogynous pairs while larger males defended temporary spawning territories. The latter class of males attained approximately the same size as females. Barlow (1974) reported that elsewhere this species forms harems in which the male is larger than his females. Thus, as predicted by the agonistic-competition hypothesis the occurrence of harem formation and defense of spawning territories in both these species is associated with increased male size.

B. Intersexual competition produces size differentiation: Increasing size difference between the sexes usually is thought to reduce competition between them by decreasing niche overlap (Selander 1966). Increased SSD could be selected for on this basis if the species formed small, stable, heterosexual groups, since the reproductive success of individuals of both sexes would then depend directly on each others resource intake (Selander 1966; Ghiselin 1974). Such a situation obtains in surgeonfishes that form pairs and harems, with each such group living in a shared feeding territory that it defends against a variety of food competitors. Species for which this hypothesis has been invoked use relatively large food items, and the ability to obtain and process such items depends on consumer size (Selander 1966). Most of the acanthurids considered here eat foods (microalgae

or detritus - Robertson and Gaines, unpublished data) that are so small that consumer size seems unlikely to affect processing ability. However, size-dependent access to feeding microhabitats could affect what the sexes of such fishes eat and affect intersexual niche overlap.

I examined two predictions that derive from the "competition reduction by niche differentiation" hypothesis: (1) the ratio of the degree of similarity of diets of members of the same sex to the degree of similarity of diets of members of the opposite sex should be greater in dimorphic species than in isomorphic species, and (2) in the absence of such differences in the sexes' diets, dimorphic species that form pairs or harems should show substantial intersexual differences in usage of different feeding microhabitats (data on isomorphic species that form pairs or harems are not available for comparison). The data show the following. First, there is no evidence of a relationship between the pattern of SSD and levels of intrasexual versus intersexual diet overlap (Table 4). Second, in two dimorphic species there were statistically significant differences in usage of feeding microhabitats by the sexes, but such differences were minor, and overall intersexual similarity of microhabitat usage was high (Table 5). Thus there is little or no evidence to support the "competition reduction by niche differentiation" hypothesis.

Increased SSD could also reduce intersexual competition by altering the proportions of shared resources that were used by each sex. Because of differences in the size of each sex's investment of energy in gamete production, an increase in the female's share and decrease in the male's share of the common resources supply is more likely to benefit both members of a group than

Table 4: Intersexual similarity of diets of surgeonfishes.

Dimorphism Pattern Species	Mean (Std. Error) percent similarity of stomach contents ¹			
	Intrasexual		Intersexual	♂/♀
	Male	Female		
Macrogynous				
<u>A. leucosternon</u>	58.1(1.8)	59.6(2.4)	57.0(1.5)	9/6
<u>A. glaucopariens</u>	69.5(2.4)	68.8(2.2)	70.1(1.7)	7/8
<u>Z. veliferum</u> (A)	39.0(7.0)	31.0(7.6)	39.0(5.6)	8/7
Isomorphic				
<u>A. lineatus</u> (P)	65.8(2.3)	69.5(1.2)	70.1(1.3)	5/7
<u>A. lineatus</u> (A)	57.7(4.4)	54.2(1.8)	56.2(1.7)	5/7
<u>A. triostegus</u>	42.5(3.1)	48.6(2.7)	45.5(2.0)	10/9
Macroandrous				
<u>Z. scopas</u> (A)	55.3(6.0)	51.5(2.7)	58.3(2.0)	6/9
<u>N. lituratus</u>	77.1(2.2)	64.1(4.4)	71.0(2.5)	9/6
<u>A. nigrofuscus</u> (P)	66.4(1.4)	73.8(2.0)	70.3(1.1)	10/5

1: χ^2 Czekanowski Index (see Bloom, 1981) - All possible combinations of individuals were compared. All species are considered for which there are data for ≥ 5 individuals of each sex. Details of these diet analyses will be given elsewhere (Robertson and Gaines, in prep.). A = Aldabra P = Palau.

Two-way ANOVA of above data (untransformed)

Source	df	SS	F value
Sex	2	125	0.19 ns
Dimorphism	2	864.7	1.33 ns
Interaction	4	179.5	0.14 ns
Error	18	5848.5	

would the reverse pattern of sharing. Macrogyne could be produced if decreased male size reduced intragroup competition in this manner. It could develop if (i) there was little or no mate-competition among males that would select for increased male size, and (ii) males were unable to reduce intragroup competition by increasing the size of the shared resource supply e.g., by increasing territory size. The data presented above indicate that in macrogynous surgeonfishes there is little male-male competition to form harems and no size dependency on the ability of males to pair with high quality females; i.e. the first condition appears to be met. The second condition remains to be examined with further field work. Further field work also is needed to determine not only whether there is real potential for intersexual competition in pair-forming surgeonfishes but also whether reduction in male size is the most efficient or only way to minimize such competition.

Table 5: Use of feeding microhabitats by members of pairs of two Aldabran surgeonfishes.

Micro-habitat ¹	Mean (Std. Error) percent of bites taken in each microhabitat by			
	<i>A. leucosternon</i>		<i>Z. scopas</i>	
	Males	Females	Males	Females
1	35.6(3.6)	30.1(3.5)	7.7(1.5)	9.9(1.5)
2	26.5(3.1)	31.0(3.6)	31.2(2.4)	31.6(2.2)
3	16.7(2.4)	16.8(3.0)	22.6(2.9)	19.2(2.9)
4	13.3(2.0)	12.2(2.3)	3.3(1.5)	4.5(0.9)
5	2.5(0.6)	2.1(0.5)	5.4(0.9)	7.5(2.2)
6	1.3(0.5)	0.9(0.3)	1.9(0.8)	2.1(0.7)
7	1.1(0.6)	0.9(0.4)	2.7(1.1)	2.9(2.1)
8	0.9(0.3) * ²	2.2(0.6)	18.6(2.6)	15.5(1.3)
9	0.2(0.1) *	2.2(0.6)	2.0(0.5)*	4.2(1.1)
10	0 **	0.6(0.3)	3.6(1.0)	3.4(0.7)
No. pairs observed	34		16	
Percent Similarity ³	91.8		92.4	

1. These microhabitats incorporated all substrates used by individuals of both sexes. 2. T test; Null hypothesis: within pair $\Delta = 0$, * $p < .05$, ** $p < .001$, other values not significant. 3. Czekanowski Index - see Bloom, 1981.

C. Investment in mating adaptations at the expense of growth and longevity: Competition for mates can take various forms besides agonistic contests in which size directly conveys a competitive advantage. Competitive ability in males may be based on factors such as courtship activity, mate-finding activity or sperm production. Growth and longevity of males that so compete may be affected by the size and life-history scheduling of such investments; large, early investments may limit male growth and longevity sufficiently to produce extremes of macrogyne in fishes (Ghiselin 1974; Warner and Harlan 1982).

The only data I have that relate to the potential influence of investment in such competitive mechanisms on SSD in surgeonfishes concern the size (but not the life-history scheduling) of males' investments in sperm production. Sperm competition (Parker 1970)

appears to have selected for increased sperm production and enlarged testes in various fishes (Robertson and Choat 1973; Warner and Harlan 1982). In surgeonfishes in which sperm competition is prevalent, due to a predominance of group spawning, testis sizes are substantially larger than in species in which such competition is rare (Table 1, Mann-Whitney U Tests for pair-spawner versus group and group+pair-spawner species: for \bar{X} testis weight/body weight, $U_{5,6} = 30$, $p < .01$; for testis weight relative to ovary weight, $U_{4,6} = 23$, $p < .05$).

If the effect on male growth rates of the size of their investments in sperm production were sufficient to produce the observed differences in SSD patterns in surgeonfishes, then we would expect that the relative size of such investment would be greatest in macrogynous species, intermediate in isomorphic species, and least in macroandrous species. The data conform to only part of that prediction. Males of macrogynous species do not have large testes but, except for *Z. veliferum*, testes reached the largest sizes among isomorphic species (Table 1). Thus, although the development of macrogyne does not represent a response to investment in sperm production, such investment may be involved in the production of isomorphism, as follows. First, high metabolic costs of gamete production in both sexes are likely to minimize intersexual differences in growth rates. Second, in such species large size may give a competitive advantage to males during group spawning because testes size is positively correlated with body size in species in which group spawning commonly occurs (Table 2). Thus, since fecundity in females also appears to increase with size (Table 2), selection would tend to increase size in both sexes, while growth would be limited to a similar extent in both. This combination of factors may result in isomorphism.

CONSTRAINTS ON SIZE CHANGE IN THE SEXES

In acanthurids in which there is little or no sperm competition, growth constraints deriving from the energetic requirements of gamete production probably affect the sexes quite differently. First, in fishes in general (Wootton 1979) and probably in acanthurids (see above) female fecundity is a positive function of body size. Equivalent male fecundity, i.e. the ability to produce sufficient sperm to fertilize one female's eggs (in the absence of sperm competition) probably is much less size dependent, since testes in pair-spawning species are small (Table 1) and testis size does not correlate with body size in the one pair-spawning species for which data are available (Table 2). Second, the metabolic costs of such equivalent fecundity levels probably are much higher in females because ovaries are so much larger than testes in pair-spawning species (Table 1). The intersexual differences in energy requirements for gamete production may determine the extent to which maximum size in each sex can be influenced by various selection pressures. Because of these different size/fecundity relationships, natural selection will tend to maintain or increase female size more than male size, while growth limitations deriving from gamete production will restrain increases in female size more than male size. In acanthurids in which there is much

sperm competition, male size and growth probably are subject to similar selection pressures and metabolic limitations as operate on female size. Overall in acanthurids, male size may be freer than female size to vary in response to a variety of selection pressures, the degree of SSD may mainly reflect changes in maximum male size rather than maximum female size, and SSD differentials may be maximized in macrogynous rather than macroandrous species (see Table 1).

CONCLUSIONS

1. None of the three hypotheses alone satisfactorily accounts for all three patterns of SSD in surgeonfishes. 2. The "agonistic mate-competition" hypothesis accounts for macroandry and isomorphism but not for macrogyny. 3. The "reduction of intersexual competition" hypothesis can account for macrogyny and isomorphism but not for macroandry. However, it seems unlikely that any reduction in intersexual competition results from intersexual niche differentiation. 4. The "growth limitation due to energetic investment in gamete production" hypothesis accounts for isomorphism and macroandry but not macrogyny. 5. Different patterns of SSD may primarily reflect change in maximum male size in response to different selection pressures associated with a variety of mate-competition mechanisms rather than change in maximum female size.

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