can respond to a variety of chemical, mechanical, and electrical stimuli. The hyperpolarizing response in L cells differs from the responses to ACh found in a number of neuronal and other cell types (*3*). We have no evidence as to whether this hyperpolarizing response serves as a regulatory mechanism with regard to fibroblast metabolism or mitotic activity, but the more than fourfold increase in cell K^+ permeability and the probable doubling of Na^+ influx as a result of the membrane potential change (*1*) could result in appreciable changes in the ionic milieu of the cell. The recent observations with regard to changes in cell membrane permeability and potential during the onset of cell division in sea urchin eggs are indicative of a close relation between cell membrane properties and mitosis (*4*). We suggest that the HA response, capable of being elicited by different modalities of stimulation and being propagated by electrical and humoral means, could reflect some significant control mechanism for the regulation of connective tissue disposition and, hence, of organ growth.

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Social Control of Sex Reversal in a Coral-Reef Fish

Abstract. Males of Labroides dimidiatus *control the process of sex reversal within social groups. Each group consists of a male with a harem of females, among which larger individuals dominate smaller ones. The male in each harem suppresses the tendency of the females to change sex by actively dominating them. Death of the male releases this suppression and the dominant female of the harem changes sex immediately. Possible genetic advantages of the system are considered.*

Sex reversal is widespread in a number of tropical fishes included in the families Labridae, Scaridae, and Serranidae (*1, 2*). In this report I describe the pattern of protogynous sex reversal in the labrid fish *Labroides dimidiatus*. The species is a member of a small but widespread genus, the species of which are termed "cleaner fish" because they remove ectoparasites from the skin of other fishes (*3*). Choat (*2*) established that the species is protogynous, with far more females than males, and that probably all the males were secondarily derived from females.

The basic social unit is a male with a harem of usually three to six mature females and several immature individuals living within the male's territory. At Heron Island, Great Barrier Reef, detailed field records were kept on 11 groups for up to 25 months; 48 sex reversals were recorded in these and another eight groups. Individual adults were recognized by unchanging variations in their color patterns.

All individuals exhibit territoriality, but its expression varies with age and sex. The largest, oldest individual is the male, which dominates all the females in the group. Larger, older females of the group dominate smaller ones, which usually results in a linear dominance hierarchy. Thus territoriality is only fully expressed in males and is directed mainly toward other males. Usually there is one dominant female in each group, but sometimes two equal-sized females are codominant and can successfully defend their territories against each other. The dominant female lives in the center of the male's territory, with the other females scattered around. The male is socially very active. It makes frequent excursions throughout its territory both to the feeding areas of the females and to points on the territory border where the male is likely to meet neighboring males. During these excursions the male feeds in the females' areas and actively initiates aggressive encounters with them and other individuals. Females, on the other hand, are more sedentary and passive. When a male meets a female of the same group, the male frequently performs a distinctive aggressive display toward the female. This display has not been seen in encounters between males and only very rarely in encounters between females, when it was given by dominant females.

Some males and large females have maintained nearly the same territories and feeding sites for almost 2 years. Small adults and large juveniles are more mobile. Deaths of individuals high in the hierarchy result in more marked changes in the distribution of other high-status individuals than do deaths of low-status individuals. With the death of a high-status female, the vacated area may be incorporated into the territory of an individual of equal status or taken over by an individual immediately below the deceased in status, the lower status female deserts its own territory in the process. This shift can result in the immediate redistribution of three or four high-status females.

Sex reversal frequently occurs as a part of the reorganization of the group following the death of the male. The success of an initiated reversal depends upon both inter- and intragroup social pressures. Intergroup social pressures take the form of territory invasion and takeover attempts by neighboring males, and if these pressures are successfully resisted by the dominant female it changes sex. Groups with codominant females sometimes divide when both dominants change into males. In all, 26 cases of single dominant females reversing sex were observed (five naturally occurring and 21 experimentally induced by removing the male), and four cases of reversal of pairs of codominants were also seen (all induced by removing the male).

Observations of five dominant females after the removal of their males have shown that the first behavioral signs of sex reversal appear rapidly and that the behavioral changeover can be completed within a few days. For approximately half an hour after the death of the male the dominant female continues to behave aggressively as a normal female. This simple female aggression then wanes to more neutral reactions to nearby subordinate females. Approximately 1½ to 2 hours after male death, maleness appears in the form of the special male aggressive display that the new "male" starts performing to the females of its group. The assumption of the male aggressive role can be virtually completed within several hours, when the "male" starts visiting its females and territory borders. The switchover to male courtship and spawning behavior takes somewhat longer but can be partly accomplished within 1 day and completed within 2 to 4 days. Other individuals also respond within a couple of hours to the altered social situation created by male death; low-status females take over vacant female territories, and neighboring males invade and attempt to take over the territory and harem.

The death of a male does not necessarily lead to a sex reversal within the group. In 11 cases intergroup pressures were apparently too great, and neighboring males invaded the territory, taking it and the female group over. In four of these cases the dominant female had started to behave like a male before the invasion but reverted to female behavior after the completion of the takeover and remained as a fully functional female. In all these successful takeovers the invading male was considerably larger than the incumbent dominant female and was able to dominate relatively easily. In the one interrupted sex reversal observed, the dominant female was under the control of a slightly larger invading male for about 2 weeks after the death of the original male. During this period the female behaviorally went through the series ♀ → ♂ → ♀ → ♂, the final change being a successful one.

Five observed sex reversals were not associated with male death. Before reversal all five individuals were medium-large females of high status; four were subdominants and one was a codominant. The area of each individual was away from the main areas of social activity of the dominant male, which visited the female relatively infrequently. Consequently each female had much less social contact with the male than did females of comparable status within the same group.

Histological examinations were made of the gonads of 29 females and 35 males. The ovaries of 28 of the 29 females contained small spermatogenic crypts located close to sites of early oogenesis in the ovarian lamellae, and in 15 of these 28 females some crypts contained sperm or spermatids. Free sperm were not detected, and the spermatogenic crypts appeared to be completely enclosed. The gonads of 28 males of known "age" (age from the start of reversal) have been examined. From the small series of "young" males examined, it appears that sperm can be released 14 to 18 days after the start of reversal.

Table 1. Aggressive acts by males against three hierarchical classes of females [three types of aggressive acts—simple attacks (SA), high-intensity male aggressive display (HD), and low-intensity male aggressive display (LD)]. The data represent eight males and their harems. Hierarchy subdominants have been arbitrarily divided into two classes. The distribution of aggressive acts did not differ significantly between the eight social groups [goodness-of-fit test, *G* (*5*)]. The data from all groups were therefore pooled. The same method demonstrated significant heterogeneity among the three classes of females ($G = 69.085$, d.f. = 4, $P < .01$).

Females	Male aggressive acts		
	SA	HD	LD
Dominant	54	94	371
Large subdominant	36	8	48
Small subdominant	20	1	22

These data demonstrate social control of sex reversal in this species, with males regulating the production of males. Probably all females are capable of changing sex, and most (possibly all) have testicular elements within perfectly functional ovaries. The tendency of any female to change may be actively suppressed by more dominant individuals in the hierarchy. Nondominant females have aggression by both sexes directed at them; the dominant female is the object of only male-type aggression and is dominated by only a single individual. Death of the male means that the female of highest status becomes totally dominant with the group, and the tendency to change sex is no longer suppressed. The rapidity with which a new male behaviorally assumes its role is a reflection of the presence of male elements in all females and the necessity for a new male to consolidate its position quickly in the face of constant intra- and intergroup pressures. Subdominant females are also potential males and must be inhibited if the group structure is to be maintained. Neighboring males must be excluded if a harem is to be maintained. Males direct their aggression differentially toward females of different status in their hierarchies. The male is more aggressive toward those females most likely to change sex and threaten his position—that is, larger females, especially the dominant one (Table 1). The aggression directed at these higher status females is also more characteristically male. Incomplete control of high-status females such as those most peripheral in the male's territory, can result in sex reversal. High-status females probably suppress females lower in the hierarchy; the latter evidently need less male control.

Field experiments with seven isolated females (the other members of naturally isolated groups were removed) indicate that the presence of a harem is not necessary for sex reversal to be accomplished, although the process may be slower. Experiments with six males similarly isolated without harems demonstrated the continuance of sperm production for up to 26 days in functional males.

Many Labridae and Scaridae are protogynous hermaphrodites with female-biased sex ratios (*2*), and in some species social control of sex reversal may operate in a similar manner to that in *Labroides dimidiatus*. In other species, especially schooling forms, a well-defined social structure based on individual relationships might not be possible, and sex reversal may be controlled more by endogenous factors. Male control of the production of males has been demonstrated in the laboratory in a protogynous serranid fish, *Anthias squamipinnis* (*4*).

At the present, discussion of the biological significance of protogyny remains speculative. Arguments have been put forward to explain protogyny and the biased sex ratio in terms of population growth, with the predominance of females increasing fecundity (*4*). Choat (*2*) advanced the idea that the biased sex ratio, maintained by protogyny, could be considered as an inbreeding mechanism because it reduced the number of genotypes available for recombination, and this would permit adaptation to specific local conditions.

My observations on the pattern of sex reversal in *L. dimidiatus* support this idea of genetic advantages for the system. The genotypes of the males are those which are maximally recombined, because each male spawns regularly with the females of its group and each female spawns, in the main, with the dominant male only. The male genotype is the genotype best adapted to local conditions because the male is derived from the oldest female of the group. Individuals enter the group and gradually move up within it, with only the best adapted females eventually being able to reverse sex. Thus the social organization is a framework within which the selective process works. The social group is a self-perpetuating system which ensures the maintenance of the biased sex ratio by controlling sex reversal. Social control of sex reversal both maximizes the genetic advantages of the process and imparts considerable flexibility to it. Males are produced only when they are needed, and this method overcomes the possible precariousness of a strongly biased sex ratio maintained by endogenously controlled sex reversal.

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Conditioned Approach and Contact Behavior toward Signals for Food or Brain-Stimulation Reinforcement

Abstract. *When presentation of a retractable lever always preceded food delivery, rats licked or gnawed the lever. They also approached but seldom orally contacted a lever signaling brain-stimulation reinforcement; instead, subjects sniffed, pawed, or "explored" the lever. Therefore, a Pavlovian conditioned stimulus evoked directed skeletal responses whose specific form depended on the forthcoming unconditioned stimulus.*

In their experiments on "autoshaping," Brown and Jenkins (*1*) found that hungry pigeons will consistently peck a small lighted disk whose illumination signals the imminent presentation of grain, even though the pecks never affect the delivery of grain. Furthermore, Williams and Williams (*2*) showed that such pecking persists even if it actually prevents scheduled grain deliveries. These results are difficult to incorporate within the framework of operant conditioning or other types of learning in which responses are assumed to be strengthened by their consequences.

However, the results do parallel several phenomena of Pavlovian conditioning, which involves pairings of an originally irrelevant event, the conditioned stimulus (CS), with some biologically significant event, the unconditioned stimulus (UCS). In autoshaping, as in Pavlovian conditioning, the CS (illumination of a disk) comes to elicit a conditioned response that anticipates and resembles the unconditioned response to the UCS (pecking at grain), and response-produced omission of the UCS often does not eliminate or even greatly weaken the conditioned response (*3*). On the other hand, the conditioned response in autoshaping is directed toward a particular external stimulus (the lighted disk), whereas the responses typically studied in Pavlovian conditioning (for instance, visceral or glandular responses) cannot be directed at some environmental object or location. However, Pavlov and others (*4*) did notice and describe in detail a variety of motor behaviors that accompanied the conditioned responses under study (such as salivation).

If we assume, as Pavlov did, that the CS eventually comes to serve as a substitute or surrogate for the UCS, then the form of the motor behavior directed at the CS in the autoshaping situation ought to be strongly controlled by the particular UCS that follows it. Our experiments with rats, reported here, provide one test of this hypothesis, because we compared conventional food UCS with reinforcing electrical stimulation of the brain (*5*); brain stimulation, unlike the food UCS used in most prior autoshaping studies, does not involve an external object that must be approached, contacted, and consumed. In addition, we wished to determine whether the results for pigeons represent a relatively general phenomenon of animal learning; would rats also "autoshape," that is, approach and contact a signal for an appetitive UCS?

A well-illuminated Skinner box had a food chute centered on the front wall (width, 27.9 cm). Two identical stainless steel retractable levers (3.2 cm wide and 1.3 cm thick), one in the center of each of the two side walls (width, 23.2 cm) were 4.4 cm above the floor and protruded 1.6 cm when inserted into the chamber. Whenever a lever was inserted, light from four miniature lamps (6 volts, 0.2 amp, type 328) inside the lever was visible through four 2-mm holes in the front of the lever and two 2-mm holes on top.

Illumination and insertion of a lever lasted 15 seconds and occurred independently of presentations of the other lever. The interval between successive presentations of a given lever ranged from 45 to 135 seconds (mean, 90 seconds). Lever depressions and all contacts of the levers with bare skin (such as the palms of forepaws, or nose or mouth) were recorded separately. Videotape records enabled us to examine various qualitative characteristics of the conditioned responses.

All rats, whether trained with food or brain-stimulation UCS, were exposed to the same five successive experimental treatments. Each daily session consisted of 40 presentations of each lever. First, the rats received a baseline (operant level) session during which the levers were presented without any food or brain stimulation. In the second phase (acquisition), presentations of one lever, designated the positive stimulus (CS+) for a particular rat, were immediately followed by delivery of a food pellet in the food group and by intracranial stimulation in the other group. The second lever (CS^0) was presented randomly with respect to presentations of food, brain stimulation, or CS+.

In the third phase (extinction), each lever was still presented 40 times daily, but no food or brain stimulation was delivered. In the fourth phase (reac-