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EYE COLOUR AND AGGRESSION IN JUVENILE GUPPIES, *POECILIA RETICULATA* PETERS (PISCES: POECILIIDAE)

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Abstract. A series of four related experiments on guppy, *Poecilia reticulata*, juveniles indicates that eye colour is related to motivational state. In juveniles of this species two distinct eye colour states are easily discernible, with a transient intermediate state infrequently seen. These states are dark, light, and intermediate. In aggressive interactions involving both both dark- and light-eyed fish, dark-eyed fish won 98.6% of the encounters ($N = 222$ encounters). Eye colours are significantly correlated with bout lengths of certain behaviours (aggressive encounters, swimming, substrate biting); total time spent in certain behaviours (swimming, aggressive encounters); and type and intensity of aggressive encounters. Eye colour appears to be related to motivational state and may serve a signal function.

Baerends et al. (1955) and Gorlick (1976) reported detailed studies on the reproductive and dominance behaviour of adult guppies, *Poecilia reticulata* Peters. While Gorlick (1976) reported a correlation between dominance and eye colour, neither study reported a consistent relationship between eye colour and specific sexual or aggressive behaviours. The relationship between eye colour and dominance has been reported for other species of fishes. In the family Cyprinodontidae such a correlation has been noted by Cox (1966) and by Barlow (1961), who report that in desert pupfish, *Cyprinodon macularius* Baird and Girard, the dominant male has a dark iris. Echelle (1973) reports that dark eye colour in Red River pupfish, *C. rubrofluviatilis* Fowler, is associated with breeding males, aggressive females, aggressive non-breeding males, and fish resting in dark areas and that silvery eye colour is associated with extremely frightened breeding males and the less aggressive females and non-breeding males. Kingston (1980) reported a relationship between eye colour and aggressiveness in 17 species of goodeid (Cyprinodontiformes) fishes. In these fishes dark eye colour is correlated with fright and losing encounters, while aggressiveness is correlated with a barred eye pattern. Light eye colour is correlated with normal activity without aggressive encounters. Barlow (1963) reports an association between aggressiveness and eye colour in dwarf chameleon fish, *Badis badis* (Hamilton) (family Nandidae), and Greenberg (1947) reports this association for green sunfish, *Lepomis cyanellus* Rafinesque (family Centrarchidae).

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Gorlick (1976) noted aggressive behaviour in guppies as young as three days old. Incidental to other studies, we too noted that guppies are highly aggressive from an early age and that winners of encounters were highly predictable based on eye colour of combatants. The studies presented here were undertaken to verify and quantify our early observations and to establish whether eye colour was an indicator of motivational state as it seems to be in the four previously mentioned species, or an attack inhibitor as reported for body colour by Barlow & Wallach (1976) for *Cichlisoma citrinellum* (Gunther) (family Cichlidae).

Methods and Materials

General

Four separate but related sets of observations were initiated. In all studies the fish of any given aquarium were from one litter and were housed in 38-litre aquaria measuring 28 cm × 51 cm × 27 cm. Fish used in these studies came from two different stocks. One stock, referred to hereafter as Indiana fish, were fourth and fifth generations produced by brother × sister crosses. The progenitors were obtained from an aquarium shop in Martinsville, Indiana, and each generation was parented by fish from a single litter. The second stock, hereafter referred to as Puerto Rico fish, were litters from wild-caught pregnant females taken from a moat around the greenhouse on the Puerto Rico Nuclear Center grounds in Mayaguez. All observations on Indiana fish were done in 1971 while the senior author was an employee of Indiana University, Bloomington, Indiana. All observations on Puerto Ricc fish were done in 1971 and 1972 at the Frontier Laboratory of the University of Puerto Rico, Colegio de Agricultura y Artes Mechanicas in Mayaguez.

Litters selected for observations had a minimum number of five fish, and for Indiana fish the observed maximum was 21. Some of the Puerto Rico fish were removed on the first day after birth so that the maximum number in a tank was 11. Observations were limited to the period from the sixth day after birth, when the fish had grown to a more easily observable size, to an age six days younger than that when the most precocious fish in the most rapidly growing litter showed the first traces of secondary sexual characters. No data were retained for Indiana fish beyond day 46 and for Puerto Rico fish beyond day 36. Observations were limited to afternoon and late morning. No observations were made within an hour after feeding. We suspended observations for one day or more after moving fish to a new aquarium or adding large amounts of water.

Fish were fed daily with (R) Tetra Min. The only things in the aquaria besides the fish were 5 to 10 snails, *Physa* sp., and a small clump of a stonewort, *Nitella* sp. Accumulations of mulm were siphoned out of the aquaria at irregular intervals.

There were three basic methods of sampling: event sampling, scan sampling, and focal sampling. Event sampling involved recording all aggressive encounters occurring in a tank during a 5-min period. Scan sampling involved scanning the tank every 10 s during a 5-min period to determine proportions of time spent in each scored activity. Focal sampling involved continuously observing a single individual for 5 min and recording all its activities. Specific details of these procedures follow.

Event Samples

The first set of observations were termed '5-min event samples'. The objectives of these observations were to determine the relationship between eye colour and both outcome of aggressive encounters and type of aggressive encounters. During a 5-min period every aggressive encounter was scored and the following information noted: eye colour of both participants; eye colour of winner (if there clearly was a winner); type of aggressive encounter; and activity of the winner immediately prior to the encounter.

Eye colour was usually either definitely dark or definitely light and was scored as intermediate in the rare cases where it was not immediately obvious.

There were four basic types of encounters noted. Mutual Display ('side-by-side' of Gorlick 1976) involved two individuals holding their bodies in rigid *c*-curves with fins spread and bodies quivering. Display involved one individual going through the motions of the mutual display but usually perpendicular to and in front of its opponent with the opponent usually ignoring or fleeing these attentions. Nip involves mouth or head contact with the opponent and is equivalent to Gorlick's (1976) 'nip'. Chase involves one fish rushing at another, usually with the second one fleeing. This behaviour is very similar to the 'rapid approach' of Gorlick (1976) and may be equivalent. Many encounters involved combinations of these four and were scored separately as such.

Six types of activity were scored. Feeding occurred only if some object was actually seen to be ingested. Substrate Biting was scored if the fish tilted its body and contacted the bottom of the aquarium or some other solid object while opening and closing its mouth. Swimming and Stationary were as the names imply. Surface Skimming was scored differently between stocks observed because of observer differences. Indiana fish were scored as engaging in this activity if they consistently kept within 2 mm of the surface while swimming rapidly. Puerto Rico fish were scored thus only if they touched the surface film.

This study consists of 36 event samples using Indiana fish and 214 using Puerto Rico fish. All Indiana fish observations were made by Martin, and all Puerto Rico fish observations were made by Hengstebeck. Before beginning the Puerto Rico studies it was established that there was a 76% reliability between observers on encounter type, eye colour, location, and pre-encounter activity. Most of the errors (92%) were of omission as opposed to 8% errors of disagreement. This prevented the possibility of pooling data for the two populations.

Scan Samples

The second set of studies was termed '10-s scan samples'. The objectives of these studies were to determine whether eye colour correlated with selected specific activities and to provide baselines for other studies.

Every 10 s during a 5-min period the observer would score every fish visible in the aquarium as to eye colour and type of activity. A 10-s interval was chosen because the observer was

90% confident that within this limit no fish was scored twice. During the study there was never an interval when the number of scores recorded exceeded the number of fish. Activities and eye colours were as previously defined. Sixty 5-min observations were made for this series of studies. All observations were of Puerto Rico fish.

Focal Studies

Two sets of focal studies were undertaken. The first focused on behaviours of a particular individual. While watching the fish the observer scored the behaviours on a paper chart recorder with the chart speed set at 7.6 cm/min. This method gave both frequency and duration of behaviours during the 5-min observation period. Eye colour was recorded simultaneously with the behaviours. The behaviours considered were Swimming, Substrate Biting, Surface Skimming, Initiating and Involved in an Aggressive Encounter, Involved in an Aggressive Encounter, and Fleeing. A fish was scored as Initiating an Encounter if it obviously changed direction to become involved in an encounter. Fleeing was considered to be a sudden cessation of an aggressive encounter by leaving rapidly, whether or not pursuit was involved.

The objectives of the first focal study were to determine constancy of eye colour, and to determine whether there were differences between light- and dark-eyed fish in frequency, bout length, or total time spent in a given activity.

Selection of the focal fish was not random. Before each observation period the observer located an easily visible fish having the eye colour to be observed. Initial eye colour was alternated so that the final sample would contain an equal number of light- and dark-eyed individuals. This usually meant that the fish was in the half of the aquarium nearest the observer. An effort was made to vary choice of fish according to behaviour. That is, if a fish chosen to be observed was Substrate Biting prior to the beginning of the observations, the next focal fish should, if possible, be engaged in some other behaviour before starting. Two fish from the same aquarium were not observed on the same day.

The second set of focal studies were termed proximity studies. The objective of these studies was to establish how often fish come near each other without having overtly aggressive interactions. The general technique was that of the previous focal samples except that the following were substituted for the previous list of behaviours: Initiates Proximity; Other Fish Initiates Proximity; Proximity; Initiates and Is Involved in an Aggressive Encounter; Involved in an Aggressive Encounter; and Flees. A fish that swam within 1 cm of another fish was considered to Initiate Proximity. If initiation was mutual or if it was uncertain as to which initiated proximity, the category was simply given as Proximity. The other categories are as previously defined. The focal individual of the previous focal study was followed for an additional 5 min for the proximity observations. For both focal studies, when a fish was being observed but its exact behaviour could not be determined for any reason it was so noted on the chart. There were 37 each of focal behaviour and focal proximity samples taken for fish that were initially either dark- or light-eyed, and all of these involved Puerto Rico fish.

Results

Based on the 10-s scan samples, at any given time most fish have light-coloured eyes (see Table I). Spearman rank analysis of these data indicates that light-eyed and dark-eyed fish engage in the same activities for roughly the same proportion of time ($r_s = 0.86$, $N = 7$, $P < 0.05$).

During the focal samples it was noted that most of the total number of fish observed changed eye colour during any given 5-min period. The number of changes during a 5-min observation period ranged from 0 to 19. There

Table I. Percentage of Time Spent in Each Activity by Fish with Dark or Light Eye Colour Based on 10-s Scan Samples*

	Activity	% Total	% for that eye colour
Dark eye	Swimming	5.49	43.2
	Substrate Biting	4.46	35.2
	Surface Skimming	1.86	14.7
	Stationary	0.02	0.2
	Aggressive Encounters	0.88	6.9
Light eye	Swimming	40.01	45.8
	Substrate Biting	32.43	37.1
	Surface Skimming	13.61	15.6
	Stationary	0.27	0.3
	Aggressive Encounters	1.00	1.2

Total % of Time Spent by All Fish in Each Eye Colour State

Dark 12.71
Light 87.32

*$N = 60$ 5-min observations of Puerto Rico stock.

were 74 sets of observations in these studies, 37 each of initially light-eyed and initially dark-eyed fish. During the observational period 22 of the light-eyed fish did not change colour, whereas only 8 dark-eyed fish did not change colour ($\chi^2 = 6.5$, $df = 1$, $P < 0.02$). Only two fish made a single change of colour. If an individual changes colour at all during the period of observation, there will usually be multiple changes.

A one-way analysis of variance indicated that activity bout lengths in the focal studies were significantly different between eye colour types for aggressive encounters. Mean bout lengths of aggressive encounters were 10.3 s for dark-eyed fish, 7.2 s for intermediate fish, and 1.8 s for light-eyed fish (F (2, 17) = 3.80, $P < 0.005$). Since intermediate fish were involved in very few encounters, data for them may be misleading. Mean bout lengths of Swimming were 12.6 s for light, 8.9 s for dark, and 5.7 s for intermediate ($F(2,370) = 5.54$, $P < 0.005$). Mean bout lengths of Substrate Biting were 22.2 s for light, 11.7 s for dark, and 8.3 s for intermediate ($F(2,265) = 8.29$, $P < 0.005$). Despite these differences in activity bout lengths, total time spent in any particular behaviour was significantly different only for aggressive encounters. Since there were few intermediate fish involved in aggressive encounters, the analysis of variance was limited to light- and dark-eyed fish. The mean total time spent in aggressive encounters for light-eyed fish was 1.2 s, and for dark-eyed fish 40.2 s ($F(1,53) = 10.32$, $P < 0.002$).

Table II shows that for all combinations of eye colour types, Substrate Biting was engaged in immediately prior to an aggressive encounter more frequently than would be expected from the 10-s scan observations. The difference between observed and expected frequencies is more noticeable in encounters involving light-eyed fish.

Both stocks were compared for similarity of pre-encounter behaviour and encounter types using Spearman rank correlation analysis. Pre-encounter behaviours were significantly correlated between stocks only for encounters where both fish were light-eyed ($r_s = 0.950$, $P < 0.05$).

Contingency analysis was used to test for differences between stocks in pre-encounter behaviour and encounter types, but was limited to encounters between light- and dark-eyed fish due to sample sizes. Table III shows that the two stocks were significantly different for both pre-encounter behaviour ($\chi^2 = 14.54$, $df = 3$, $P < 0.005$) and encounter type ($\chi^2 = 147.44$, $df = 3$, $P < 0.001$).

In aggressive encounters between light- and dark-eyed fish, the winner was the dark-eyed fish in 98.7% of the encounters ($N = 148$) among the Puerto Rico fish and in 98.4% of the encounters ($N = 64$) among the Indiana fish. The null hypothesis would assume a 50% probability that the winner would be a dark-eyed fish. Both stocks vary significantly from this null hypothesis (Puerto Rico, $\chi^2 = 74.0$, $df = 1$, $P < 0.001$; Indiana, $\chi^2 = 60.0$, $df = 1$, $P < 0.005$).

While there is no clear indication of a particular type of aggressive encounter occurring frequently or infrequently for light-eyed versus light-eyed or light-eyed versus dark-eyed, the dark-eyed versus dark-eyed encounters have a high incidence of mutal displays (see Table IV).

When initiation of aggressive encounters could be determined, dark-eyed fish initiated encounters proportionately more frequently than light-eyed fish. Dark-eyed fish initiated 51 of 71 encounters while light-eyed fish initiated 6 of 71 encounters ($\chi^2 = 4.63$, $df = 1$, $P < 0.05$).

Eye colour was noted to change occasionally during aggressive encounters. Dark-eyed fish were found to be less likely than the light-eyed fish to change eye colour during aggressive encounters. Using focal observation data, we noted

Table II. Pre-encounter Behaviour versus Eye Colour, Puerto Rico Data Only*

	Dark	vs	Dark
	Observed		Expected
Swimming	17		15.1
Surface Skimming	1		2.1
Substrate Biting	16		12.3
Previous Encounter	1		2.4
Other	0		3.1
$\chi^2 = 5.8$	$df = 4$	$P < 0.20$	
	Light	vs	Light
Swimming	28		33.9
Surface Skimming	2		5.6
Substrate Biting	42		27.4
Previous Encounter	2		1.0
Other	0		6.1
$\chi^2 = 18.2$	$df = 4$	$P < 0.001$	
	Light	vs	Dark
Swimming	57		68.7
Surface Skimming	7		11.1
Substrate Biting	86		55.7
Previous Encounter	1		2.8
Other	0		12.7
$\chi^2 = 33.8$	$df = 4$	$P < 0.001$	

*Expected values are based on 10-s scan samples.

that of 71 encounters involving dark-eyed individuals 67 did not change eye colour, while of 13 encounters for light-eyed individuals 8 did not change eye colour ($\chi^2 = 6.74$, $df = 1$, $P < 0.01$).

An incidental observation that came from these studies was that under nearly identical conditions the highly inbred aquarium trade fish matured more slowly than did fish obtained from wild stocks. This may be an indication of large genetic differences between stocks. Because of this possibility and because of observer differences, grouping of data between stocks was not attempted.

Discussion

Gorlick (1976) indicates that dark eye colour in adult guppies may be related to dominance. He further hypothesizes that alpha individuals are each dominant over small subgroups so that there might be several alpha individuals in any large group of fish. The idea that dark eye colour

Table III. Contingency Analysis of Puerto Rico versus Indiana Stocks for Pre-encounter Behaviour and Encounter Type*

	Pre-encounter behaviour		
	Puerto Rico	Indiana	Total
Swimming	57 (63.2)	33 (26.8)	90
Surface Skimming	7 (9.8)	7 (4.2)	14
Substrate	86 (75.1)	21 (31.9)	107
Other	1 (2.9)	3 (1.1)	4
Total	151	64	215
$\chi^2 = 14.54$	$df = 3$		$P < 0.005$
	Encounter type		
Mutual Display	33 (14.3)	10 (28.7)	43
Display	12 (10.4)	2 (3.6)	14
Display and Chase	12 (27.4)	25 (9.6)	37
Nip	64 (55.5)	11 (19.5)	75
Chase	61 (74.4)	16 (2.6)	77
Total	182	64	246
$\chi^2 = 147.44$	$df = 3$		$P < 0.005$

*Parenthetical numbers are expected values. Sufficient data for this type of analysis were only obtained for aggressive encounters between light-eyed and dark-eyed fish.

Table IV. Eye Colour Compared for Aggressive Encounter Types*

	Puerto Rico stock			
	Dark vs Dark	Dark vs Light	Light vs Light	Total
Mutual Display	30 (12.6)	33 (42.9)	16 (23.5)	79
Display	4 (4.3)	12 (14.7)	11 (8.0)	27
Chase	6 (17.1)	61 (58.1)	40 (31.8)	107
Nip	10 (16.0)	64 (54.3)	26 (29.7)	100
Total	50	170	93	313
$\chi^2 = 21.30$		$df = 6$	$P < 0.01$	
	Indiana stock			
Mutual Display	16 (9.2)	10 (17.6)	6 (5.2)	32
Display	7 (10)	27 (19.3)	1 (5.7)	35
Chase	6 (7.5)	16 (14.3)	4 (4.2)	26
Nip	4 (6.3)	11 (12.8)	8 (3.9)	23
Total	33	64	19	116
$\chi^2 = 18.18$		$df = 6$	$P < 0.01$	

*Parenthetical numbers are expected values.

is related to dominance is not contradicted by the fact that over 98% of all encounters involving fish of each eye colour were won by the dark-eyed individual and, in the few cases where eye colour changed during or immediately following an aggressive encounter, the winner darkened his eye colour or the loser lightened his. These ideas and data are also consistent with the observations of Echelle (1973) for *Cyprinodon rubrofluviatilis* and of Cox (1966) for *C. macularius*. In these fish dark eye colour is associated with dominance and aggressiveness while light eye colour is associated with non-aggressiveness and fright. This similarity is expected as the families Cyprinodontidae and Poeciliidae either had a common ancestor or Poeciliidae is derived directly from Cyprinodontidae (Rosen & Bailey 1963).

The family Goodeidae is closely related to the Poeciliidae and likewise has a common ancestor with the Cyprinodontidae. Kingston (1980) has shown for 17 species in that family that eye colour is correlated with winning or losing aggressive encounters. Unlike the Poeciliidae, these fish display the eye colours related to aggressiveness and fright only during and immediately after encounters. Normal eye colour is light. Aggressiveness is correlated with a barred pattern, while fright is correlated with complete darkening of the eye. In this case, eye colour clearly seems to serve a signal function.

Rasa (1969) found eye colour of a damselfish, *Pomacentrus jenkinsi* (family Pomacentridae), to be correlated with dominance, but the correlation is not simple. She found that eye colour is a measure of aggressiveness while fin position is a measure of fright. She also found that while eye colour of pairs of fish that were engaged in encounters is highly negatively correlated and therefore usually different, fin position has no such correlation. Thus for *Pomacentrus* the two motivational states are partially independent. Dominance is a summation of aggressive and fright motivation, with aggressiveness perhaps being more important than fright in determining outcome of pairings.

Our data support the idea that eye colour in juvenile guppies is a measure of motivational state rather than simply a measure of dominance. Eye colour changes rapidly and often. While an individual is dark-eyed it has a 98% probability of winning over a light-eyed fish. Any individual when light-eyed has only a 2% probability of winning over a dark-eyed fish. Were there a stable hierarchy and were eye colour simply a measure of dominance, then one would expect that when two dark-eyed fish met and one recognized the other as dominant, it should blanch its eyes rather than risk an encounter. This was never seen to happen, though changes in eye colour were noted on several occasions following encounters.

Fish having either eye colour type were found to engage in the scored activities in roughly the same proportions ($r_s = 0.86$). Despite this, dark-eyed fish have both longer mean bout length and greater total time spent in aggressive encounters, while light-eyed fish have significantly longer bout lengths for Substrate Biting and Swimming. The longer bout lengths and greater total time spent in aggressive encounters in dark-eyed individuals suggests that that state is a measure of aggressiveness. Drewry (1962, 1967) and Foster (1967) reported a behaviour similar to Substrate Biting as a part of courtship in several species of the genus *Fundulus*. In these fish the female responds to the initial aggressive display of the male by tilting the body so that the head is downward and then biting the substrate. This seems to be redirected behaviour or a displacement behaviour that serves to develop the next stage of courtship. If Substrate Biting in guppies is a redirected activity, then light eye colour is probably a measure of fright since the light-eyed fish Substrate Bite before aggressive encounters more often than do dark-eyed fish. If the hypotheses presented here are correct then perhaps fright and aggressiveness are not as loosely linked as Rasa (1969) found for *Pomacentrus*.

Eye colour might be hypothesized to serve as an attack inhibitor, as body colour does in the midas cichlid, *Cichlisoma citrinellum* (Gunther) (Barlow & Wallach 1976). Since fish of either eye colour attack fish of both eye colours, it does not seem to be effective if it serves that role. Before that hypothesis can be completely discarded, further testing is needed; however, the hypothesis that best fits our data is that eye colour is an indicator of motivational state. All behaviour patterns that we noted are consistent with this latter hypothesis.

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