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The garibaldi, *Hypsypops rubicundus*, is a sexually monochromatic pomacentrid found in rocky subtidal areas of Southern and Baja California. During the spawning season, males attempt to attract females to a nest of red algae located within individually defended territories. Females were observed to enter the nests of several males before selecting one for spawning and were significantly more likely to spawn in nests that contained eggs in the early stages of development than nests with no eggs or with late stage embryos. Among empty nests, the density of red turf algae and the number of nesting males surrounding the nest were inversely related to the amount of time elapsed until a nesting male acquired the first clutch of a brood. The percentage of long algae in the nest was positively related to this measure. These results demonstrate active female choice of spawning site by female garibaldi and suggest that certain characteristics of the male-defended nest influence this choice.

Factors Influencing Spawning Site Choice by Female
Garibaldi, Hypsypops rubicundus (Pisces:Pomacentridae)

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INTRODUCTION

One of the major areas of focus in behavioral and evolutionary biology deals with how animals choose their mates. In particular, it is important to ascertain which phenotypic characters are preferred in one sex by members of the opposite sex (reviewed by Halliday, 1983).

Substrate-spawning fish species in which spawning occurs on male-established egg deposition sites are particularly convenient subjects for studying mate choice. Because eggs are "expensive" to produce, causing females to entrust a large fraction of their reproductive output to a single male, there are theoretical reasons to expect females to be choosy. This should be particularly true if males vary in individual qualities or the quality of their defended resources (e.g., Trivers, 1972; Parker, 1983). Similarly, if male parental investment is extensive, egg - deposition space is limited, and females vary in expected fecundity, then males may also be expected to be selective in their choice of mates (Parker, 1983). Since females must visit males to spawn, and since reproductively active males are often found in close proximity to one another, the opportunity exists for females to sample a number of available males with seemingly little search cost (though this will vary among populations). Female visitation,

coupled with spatially structured colonies of reproductive males, provides a means by which rejection:acceptance sequences can be predictably observed. Finally, because fertilization is external and the demersal eggs are usually visible, a means of quantifying female choice without having to observe the actual spawning act is available.

A number of workers have provided evidence that such species do exercise choice of mates based on assessable characteristics. Most studies have focused on female choice and evidence exists for preference based on male characteristics (Downhower and Brown, 1980; Schmale, 1981; Myrberg et al., 1986; Noltie and Keenleyside, 1986) territory characteristics (Ridley and Rechten, 1981; Sargent, 1982) or aspects of both (Kodric-Brown, 1983; Thompson, 1986).

In this study, I use a correlative approach to address two questions as part of a continuing study on mate choice in *garibaldi*, *Hypsypops rubicundus*, at Santa Catalina Island. Do female *garibaldi* choose among available males, thus mating nonrandomly? If so, what are the criteria used in making those choices? As potential choice criteria I considered male size, the number of courtship acts performed in the presence of a female, the distance between neighboring nesting males, the number of surrounding nesting males, and characteristics of the egg deposition-site (including the presence of eggs). I also considered

the potentially confounding factor of differential female distribution.

THE BREEDING SYSTEM

The garibaldi is a large (up to 36 cm total length), pomacentrid fish common in the rocky subtidal zone of Southern and Baja California. Adults are monochromatic and bright orange while juveniles are red-orange with iridescent blue spots. Males in at least some populations obtain slightly greater (up to 3 cm) maximum lengths. Clarke (1970) attributed this to their greater longevity.

The breeding biology of the garibaldi has been described previously (Limbaugh, 1964; Clarke, 1970, 1971) and is summarized below. Both sexes defend year-round feeding territories of 10 to 15 m, although some non-territorial adults (floaters) exist (Clarke 1970; pers. obs.). Beginning in March, males selectively remove certain algal species and debris from a nest site located on a rocky substrate within the territory boundaries. This activity promotes the growth of several species of filamentous red algae that are used as an egg attachment site (see Foster, 1972 for species composition). The same nest site is used by the same individual in successive breeding seasons, and by successive territory holders following the disappearance of a resident (Clarke, 1970). Nests of this type and permanence are rare among fishes.

Spawning activity may begin as early as May and end as late as October and appears to vary both within and among populations (Clarke, 1970). During spawning, the female skims over the nest and deposits eggs on the algal turf,

while the male hovers near the nest and periodically enters, fertilizes and fans the eggs. Male entry is often preceded by his ejection of the female, who then hovers in the water column until the male performs a courtship act (pers. obs.). After spawning, the female returns to her territory. At Santa Catalina, females spawn more than once during a given season; precisely how often is not known. Spawning may occur anytime between sunrise and sunset (pers. obs.).

When first deposited, the elliptical eggs are bright yellow, 1 mm in diameter x 2 mm long, and have filaments that facilitate their attachment to the algae (Limbaugh, 1964). Egg color changes from yellow to gray after approximately four days and hatching occurs after 12 to 23 days (Limbaugh, 1964; pers. obs.). Male parental care involves nipping and fanning of the eggs and defending them against egg predators.

METHODS

Study Population and Data Collection. - This study was conducted between 9 June and 30 August, 1986, in Big Fisherman Cove, Santa Catalina Island, California. The study population was defined by the locations of 48 nesting males that occupied contiguous territories or that were separated by territories of females and non-nesting males. All territories were located at depths of less than 9 m (at low tide), and 90% were at depths of 5:m or less.

Data were collected using SCUBA or by free diving. Approximately eight diver-hours per day were spent during the course of the study (640 hrs total).

All nesting males were captured with a 0.5:m diameter landing net, measured with a metric ruler, and marked in situ using color-coded t-tags (Floy Tag and Manuf. Inc. Seattle, WA) inserted between the dorsal pterygiophores. Nesting males ranged in size from 16.5 to 21.9 cm standard length (SL) (\bar{X} = 19.28, SD = 1.42.). An additional 70 non-nesting individuals (females and bachelor males) were also marked and others could be recognized on the basis of scar patterns and/or territory locations. Nests were labeled with numbered plastic flagging tape anchored to the substrate with rocks or tied to algae. The flags were positioned such that they did not appear to interfere with courtship or nest-tending activity.

The location of each territory was mapped by recording inter-nest distances (measured to the nearest 0.10 m from the center of each nest) and compass bearings. As a means of estimating female density, I estimated the number of non-nesting adults surrounding each nesting male by outlining contiguous 10 x 10 m grids and counting the number of individuals whose territories were at least partially included in this area. When an individual occurred in more than one grid, it was assigned to the grid where most of its time was spent during the counting period.

This means of estimating female density was necessary since non-nesting garibaldi could not be sexed in the field if not engaged in reproductive activity (i.e. spawning females). Territories of known females occurred throughout the study site. For analysis, I used the number of nesting and non-nesting individuals whose territories resided at least partially within 20 m of each nest. A radius of 20 m was selected since it was the greatest distance for which accurate counts were made for all 40 nesting males.

I measured nest area by sketching nests on waterproof paper, recording the appropriate dimensions, and drawing detailed maps of them on fine-grid graph paper. Dimensions of sub areas within the nest that were covered by red turf algae, a mixture of red and other algal species (i.e. chlorophytes and phaeophytes) or bare spots were also recorded. Areas of red turf algae were further classified

as dense, if the substrate could not be seen through the turf, and sparse if it could. Finally, I measured the length of red turf algae at representative locations within the red turf areas. I classified red turf algae as short (1-4 mm), medium (5-8 mm) or long (>8 mm). For analysis, I multiplied the percentage of each nest that was covered by dense red turf, sparse red turf, mixed turf, and bare spots by weighting factors of 1, 0.5, 0.25, and 0 respectively. These weighting factors subjectively reflected the frequency with which the four substrate types were used as egg-deposition sites and the density of red algal growth. The sum of these products was an index representing the percent high quality nest cover. For example, a nest covered entirely with dense red turf would receive a value of 1.00 (= 100 %) whereas a nest composed of half sparse red turf and half mixed turf would receive a value of 0.375. Total high quality nest cover was estimated by multiplying percent high quality nest cover by the area of the nest.

Each nest was ranked for concealment (inaccessibility to potential egg predators). Five paths of entry (top, bottom, left, right, and front) were considered. A half point was assigned to a path if an egg predator (a fish measuring 30 cm or less) could approach the nest from that direction but only gain access to a limited portion of the nest without having to circumnavigate a barrier or change direction. A full point was assigned if the predator could

make an effective beeline for the nest. Points were summed over all paths to obtain the concealment score. For example, a score of one might be given to a nest in a hole, and a five to a nest on a pier piling.

Forty of the 48 nests were surveyed daily and form the basis of the analysis. During surveys, I recorded the presence or absence of eggs, the color of the eggs, their position in the nest, and the major and minor axes of the area covered by eggs. Since females deposit their eggs among the most recent of previously deposited eggs, it was not possible to count the number of individual clutches present in a brood. During surveys, I also determined male reproductive readiness (as evidenced by nest-tending activity and/or courtship) and opportunistically recorded any social interactions. When courted females were seen, they were followed until they either spawned or became lost from sight. For courting males, I counted the number of Dips (as defined by Myrberg, 1972) performed in the presence of a given female as she passed the nest. I did not attempt to measure Dip amplitude or record sounds associated with courtship (see results). I recorded the response of females to courting males as either 1) ignore (the female did not swim toward the nest), 2) approach (the female approached the nest but did not enter), 3) enter (the female entered the nest but did not spawn), and 4) spawn. I also recorded male chases of females. Since the entire site was covered during surveys, males were observed

for an approximately equal amount of time.

Analysis. - All behavioral data were analysed using G (contingency and goodness-of-fit) and Mann-Whitney U-tests. A stepwise multiple regression was used to analyse the non-behavioral data collected during nest surveys. For the dependent variable, I used the inverse of the number of days elapsed until a nest received the first clutch of eggs for a given brood. For those nests that received additional broods following the hatching of the first, I used the inverse of the mean latencies. For example, if a nest received the first clutch of a brood after two days of being empty, and then four days following the hatching of that brood received the first clutch of a second brood, it would receive a value of 0.333. This measure was termed the "preference index" and assumes that the most preferred males (nests) will receive eggs before the least preferred. Thus, low values indicate low preference by females and high values high preference. It also avoids the complications associated with the influence of pre-existing eggs on female choice (see results).

Eleven nests contained eggs on the first day of the study and were counted as having been open for one day. Ten of these received a second brood, and three a third. In all, 13 fish received two, and four three broods. Empty days were counted only as long as a male tended his nest. Male receptivity length varied during the spawning season,

and once nest tending stopped it was never resumed. Due to changes in the values of some independent variables (the distance and number of active males and algal length) and the apparent decline in female spawning activity late in the season, any third broods were excluded from the analysis. In the three cases where nest quality appeared to decrease markedly following the hatching of a brood, subsequent data were also excluded from the analysis.

The independent variables were male standard length, nest size (area), percent high quality nest cover, total high quality nest cover, percent long algae, percent medium algae, percent short algae, concealment, distance to nearest nest, number of nests within 20 m, number of non-nesting individuals within 20 m, and ratio of nesting to non-nesting individuals within 20 m.

To maximize homoscedasticity with respect to the independent variables and reduce the positive skew, the dependent variable was transformed using a natural log ($x+1$) transformation (Zar, 1984). Additional transformations, as needed, were performed on some of the independent variables.

Since the assignment of an initial value of one to those nests that possessed eggs at the beginning of the study may have artificially inflated their preference index (although their subsequent success suggests otherwise), I repeated the analysis using only those 29 nests that were empty at the beginning of the study, and counted only the

number of days elapsed until they received the first clutch of their first brood. As in the previous analysis, those nests that received no clutches were assigned a value of zero.

RESULTS

Female Searching Behavior and Male-Female Interactions. -

Prior to spawning, a female would leave her territory and swim in an erratic manner with all fins strongly erected ("Fin Erect"). Females displaying this behavior elicited courtship behavior from nesting males. In contrast, when a swimming female's fins were not erect, she was either ignored or chased by males.

Females travelled considerable distances while encountering courting males and did not simply spawn with the nearest available male. Females were frequently observed making several excursions prior to spawning, separated by 5 to 15- min feeding bouts within their territories. The distance from a female's territory to her selected nest, the farthest nest encountered, and the distance travelled per excursion all increased significantly (Mann-Whitney U-test, $p < 0.05$) between early (9-30 June) and later (after 30 June) periods of the spawning season when some males began to discontinue nesting activity (Table 1).

Males only courted when Fin Erect females passed within visible range. Male courtship behavior consisted of a series of Dips ($\bar{X} = 2.72$, $SD = 1.17$, $n = 83$) accompanied by thumping sounds, audible to the observer, as first described by Limbaugh (1964). Dipping was followed by a rapid return to the nest where the male fanned and nipped

at the algae. Females either ignored the male, approached the nest but did not enter, entered the nest but did not spawn, or entered the nest and spawned. Female entrance to the nest was accompanied by circular skimming movements in which the female rubbed her ventrum against the algal substrate. These activities occurred throughout the day.

On some occasions, males whose nests already contained eggs chased females from their territories even after performing courtship displays. Such chases were observed 12, 7, and 8 times for males with gray, yellow/gray, and yellow eggs respectively. Four of the chases by males with yellow eggs involved males that already had spawning females in their nest. In another case, the female bit the eggs.

Males did not interact among themselves during courtship, and rarely interacted at all except for an occasional threat display along a common border. Furthermore, males rarely moved through neighboring territories while courting females. Thus, females were free to choose among available nests (or males) without interference from male-male aggression.

Female response to courting is presented in Table 2, summarizing 72 observations of 61 females and 43 males. Eleven females were observed on two occasions. Sequences ranged from 1 to 18 courting males encountered by a female during an observation ($\bar{X} = 5.33$, $SD = 5.02$). The 27 cases in which the male chased the female away from the nest are

TABLE 1. Distances travelled by females while selecting spawning sites ($\bar{X} \pm SD$).

Portion of Breeding Season	Distance Travelled (Meters)		
	To Selected Nest	To Farthest Nest	Total
Early (6/9-6/30)	19.67 \pm 17.63 (n=9)	33.11 \pm 45.99 (n=9)	69.22 \pm 96.78 (n=9)
Late (7/1-8/30)	39.17 \pm 12.92 (n=6)	102.38 \pm 80.14 (n=8)	158.04 \pm 57.13 (n=9)

not shown and were not included in the analysis. A highly significant spawning preference existed for those nests which contained yellow (< 5 d old) eggs (G including spawn column = 39.31, $p < 0.001$; G without spawn column = 0.88, $p > 0.75$). These spawns involved 13 different females (one female spawned in two nests, both containing yellow eggs) and 10 different males. If cases in which the female ignored the male are excluded from the analysis, further accounting for the possibility that yellow-egg nests were simply approached more frequently, the result remains highly significant (G = 62.93, $p < 0.001$).

Additionally, of 34 cases in which spawning was observed while in progress, 25 spawns occurred in nests containing yellow eggs. This was highly disproportionate to the availability of such nests summed over those days in which spawning was observed (G = 66.16, $p < 0.001$).

An insufficient number of spawns were observed in empty nests to allow comparison of features associated with selected versus rejected nests or males. Nevertheless, female response data can be used to examine those qualities that can be evaluated by the female at a distance and thus might determine her initial response (approach or ignore). Among those qualities considered were male standard length, nearest distance to another nesting male, the number of other nesting males within 20 m, and the number of Dips performed during a given male-female encounter. Only empty nests were included to avoid possible bias associated

TABLE 2. Observed female responses to courting males compared to egg presence and coloration. See text for definition of responses. Yellow/Gray and Gray were combined for statistical analysis.

	Ignore	Approach	Enter	Spawn	TOTAL	%SPAWN
Empty	35	10	63	1	109	0.9
Yellow	6	2	7	12	27	44
Yellow/ Gray	2	1	6	1	10	10
Gray	7	1	9	0	17	0
TOTAL	50	14	85	14		

with the presence of eggs.

Only one variable produced a significant result. Males who were below the median distance to their nearest neighbor were ignored significantly less than males who were above the median distance ($G = 7.37$, $p < 0.01$).

Regression Analysis.- The results of the stepwise regression for all 40 nests are presented in Table 3. Clearly, percent high quality nest cover accounted for the greatest amount (30%) of the variation in the preference index (Fig.1). The best fit for this variable was obtained using an X-cube transformation. Two other variables, percent long red turf and number of nests within 20 m added significantly to the model, while nest size was marginally non-significant. None of the remaining variables added significantly to the model.

Reanalysis of the data using only nests that were empty at the beginning of the study, and counting only the number of days elapsed until a nest received its first clutch, produced similar results (Table 4). Total high quality cover, and percent short red turf (with natural log (x+1) transformation) however, provided a slightly better fit than percent high quality cover and percent long red turf. Note that percent short adds positively whereas percent long adds negatively in the previous analysis. The number of nests within 20 m remained a significant variable.

Again, none of the remaining variables added significantly to the model.

Although male standard length was not significant in the stepwise regression, it was positively correlated with the transformed preference index and percent high quality nest cover ($r = 0.35$; $p = 0.03$; and $r = 0.36$, $p = 0.02$ respectively). Its correlation with total high quality and percent short turf was marginally non-significant ($r = 0.30$ and -0.30 respectively, $p = 0.06$). Thus, females selecting high quality nests frequently spawned with larger males as well.

TABLE 3. Results of stepwise multiple regression for all nests (N=40). See text for complete list of independent variables and definitions.

Variable	Order	t	p	R ²	
				Sequential	Simple
* % High Quality Cover	1	4.83	<0.001	0.30	0.30
% Long Algae	2	-2.31	0.03	0.37	0.0009
Nests Within 20 m	3	2.59	0.02	0.46	0.07
Nest Size	4	1.83	0.08	0.51	0.09

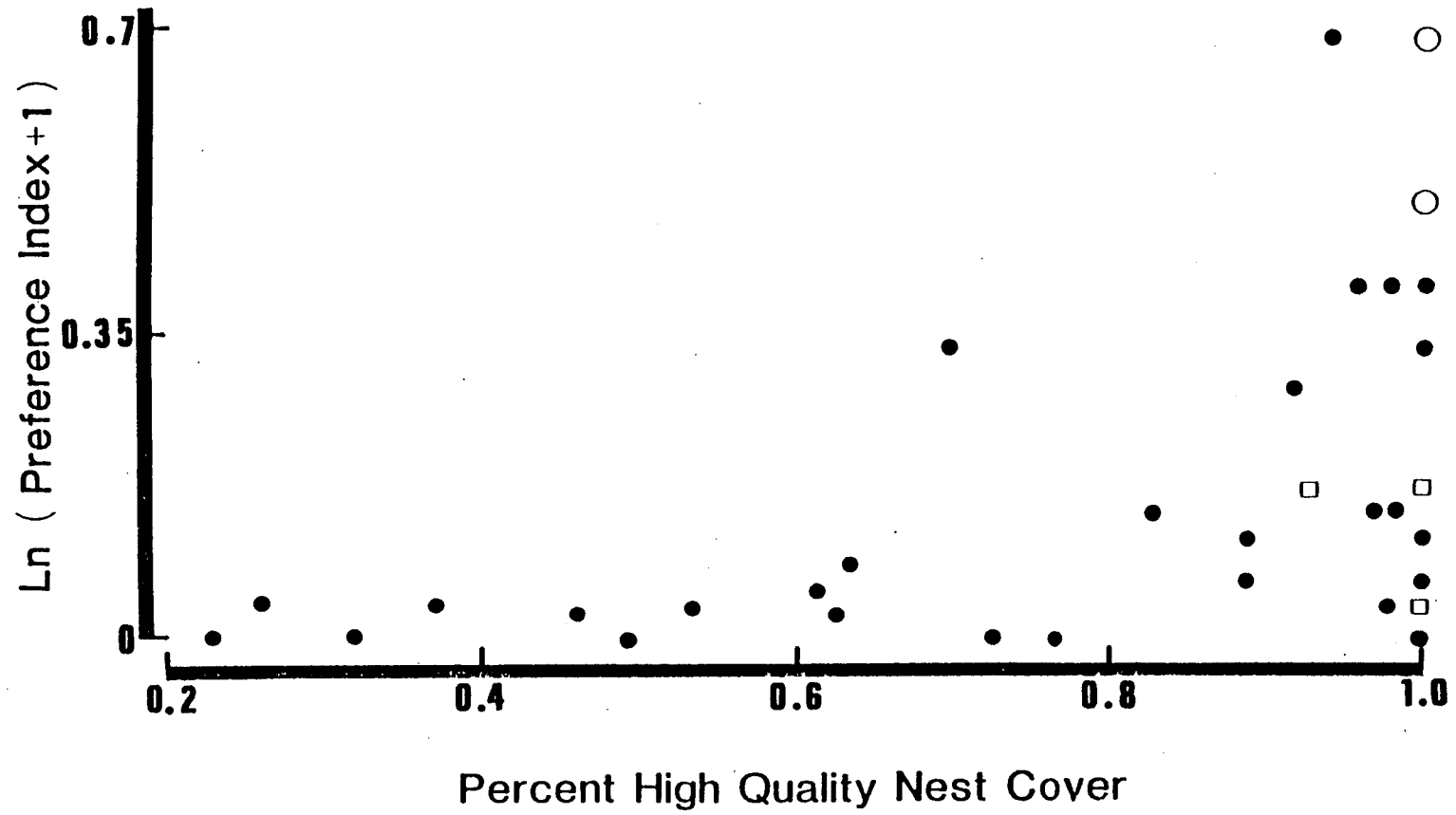
* X-cube transformed

TABLE 4. Stepwise multiple regression for nests empty at beginning of study (N=29).

Variable	Order	t	p	R ²	
				Sequential	Simple
Total High Quality Cover	1	4.28	<0.001	0.32	0.32
% Short Algae*	2	2.24	0.03	0.46	0.03
Nests Within 20 m	3	2.16	0.04	0.54	0.16

* Ln (x+1) transformed

Fig. 1. Plot of transformed preference index against percent high quality nest cover (in fraction form) for all 40 nests. Solid circles = 1 observation, open squares = 2, open circles = 3.



DISCUSSION

Parker (1983) and Partridge and Halliday (1984), among others, have made the distinction between active female choice and passive attraction. The former is a product of selection on female behavior, whereas the latter results from male exploitation of female perceptual makeup and need not involve actual preference for a particular characteristic. To demonstrate active choice, it is necessary to show that females reject certain males in favor of others, and that these rejection:acceptance sequences result in nonrandom matings, since females may simply require a certain minimal amount of courtship before any mating can occur (e.g., Crews, 1980; De Boer, 1981).

A strong preference was found for nests which already contained eggs in the early stages of development. Such nests are visible (to the human observer) from a greater distance than are empty nests, and the presence of yellow eggs may increase both the probability that a female will see the nest and that she will spawn once there (Table 2). Females were observed to approach yellow-egg nests before the male initiated courtship. Further circumstantial evidence for such preference is provided by the following observations. First, in 52 of 54 cases recorded, males receiving an initial clutch received at least one subsequent clutch, and usually reached approximately 75% of their nest capacity, within four days following the

acquisition of the first clutch. Second, as many as four females could be seen simultaneously hovering in the Fin Erect posture near nests that contained yellow eggs. This was not observed near empty or gray-egg nests. Third, females always deposited eggs among or around the pre-existing eggs, even when much nesting space remained available. This observation conflicts with Clarke's (1970) report that females deposit eggs in separate, distinct batches.

Although these data indicate female preference for nests with yellow eggs, they cannot be used to determine the mechanisms by which females choose such nests, or whether yellow eggs are preferred over gray eggs. Rejected gray-egg nests (from Table 2) were significantly more full than accepted yellow-egg nests (Mann-Whitney U-test, $z = 2.09$, $p = 0.04$) and thus may not have had sufficient available nest space. While females may in fact prefer the eggs themselves, the observed pattern may also have resulted from strong unanimity of choice for other nest (or male) features or from certain females copying the choice of others who selected nests on the basis of these other features (e.g., Bradbury, 1981; Losey et al., 1986). Distinguishing among these alternatives will require experimental procedures.

Field observations suggestive of female preference for nests with eggs have been made for several other substrate spawning fish species (Hunter, 1963; De Martini,

1976; Marconato and Bisazza, 1986). Such preference has been demonstrated experimentally in the laboratory for threespine sticklebacks, Gasterosteus aculeatus (Ridley and Rechten, 1981) and river bullheads, Cottus gobio (Marconato and Bisazza, 1986). Rohwer (1978) addressed the subject theoretically, concluding that females should prefer to spawn in nests that contain eggs in the early stages of development since brooding males would be more likely to consume eggs deposited later during the brood cycle or the entire batch if only a small number of eggs were deposited. This phenomenon might favor bright coloration of early stage eggs as occurs in garibaldi since severe penalties may exist for being the only clutch in the nest. Ridley and Rechten (1981) extended Rohwer's argument, suggesting that an overall dilution effect, independent of the source of predation, would favor choice for nests with eggs. An additional advantage to spawning in nests with eggs is that male parental investment may increase with increasing brood size (e.g., Coleman et al., 1985).

Certainly these do not represent an exhaustive, mutually exclusive list of alternatives. In light of these hypotheses, it should be restated that females were observed consuming eggs while in nests. Furthermore, in the only two cases in which males did not receive additional clutches after receiving an initial clutch, all eggs disappeared immediately after turning gray. Finally, I commonly observed mouth-shaped gaps in nests with eggs.

These gaps measured 1.5 - 2.0 cm in diameter, approximately the gape width of an adult *garibaldi*. I further observed (though rarely) egg predation attempts by small heterospecifics. Thus, eggs appear to be subject to both con and heterospecific predation.

Other nest qualities associated with algal growth appear to be important criteria at least in choosing among empty nests. Although empty nests can be seen at a distance, it is not likely that females can assess most algal characteristics without approaching or entering the nest. The skimming behavior exhibited by females following entrance to the nest may provide them with both visual and tactile means of evaluating nest characteristics. The regression analyses (Tables 3 - 4) suggest that females prefer those nests that contain the highest percentage or greatest amount of dense turf algae, especially those with short or medium length growth.

Three hypotheses can be offered to explain the apparent female preference for these particular nest features in *garibaldi*. First, the species of red algae that predominate in the nest may simply be more effective as anchoring sites for eggs than other forms of algae or bare areas and short growth may be more effective than long growth. An effective anchoring mechanism is important because *garibaldi* often inhabit areas of high wave action and are too large to spawn in small crevices or on other protected substrates. Furthermore, male fanning activity

is vigorous, involving the entire ventral portion of the body. Such water motion might easily dislodge eggs attached to an open rock face. Although I have no data to compare the efficacy of different lengths or types of algae, eggs deposited on sparse growth appeared to disappear more readily than eggs deposited on dense growth, and eggs deposited on bare areas invariably disappeared.

Second, the behaviors used in nest tending activity (nipping and fanning) should promote short, dense growth of red filamentous algae (Foster, 1972). These behaviors are also used in the tending of eggs. Thus, the length, density and purity of the nest may be a reflection of the amount of energy a male devotes to nest tending and may thus be indicative of his ability to invest in parental care and/or his experience as a parent. Nest size may also be assessed in this manner, although it is largely limited by the size of its substrate. Environmental factors may play an additional role in determining nest condition, and nest condition may thus reflect the overall conditions to which eggs would be subject. The third is that nests may be a sexually selected feature which simply appear "attractive" to females.

Neither male size nor the number of Dips performed during courtship were correlated with the initial female response (approach or ignore). Although male size was correlated with the preference index, this appeared to be due to its correlation with nest quality. Clarke (1970)

noted that new nests required several years before they became well established. New, and thus sparse, nests are more likely to be occupied by smaller, younger males. However, smaller males also obtain vacated, well established nest-sites (Clarke, 1970; pers. obs.) which may account for the poor relationship between male size and nest quality ($r = 0.36$). However, in the absence of experimental data, the role of the male in determining female spawning-site choice cannot be accurately assessed. This is particularly true since other male characteristics that were not examined (e.g., male physical condition, Dip amplitude, and sounds associated with courtship) may well be used as cues. Myrberg et al. (1986) have shown that female bicolor damselfish, Pomacentrus partitus, are preferentially attracted to particular features of male courtship sounds. Attractive sounds in this species however are associated with larger males.

Two factors associated with the density of nesting males, nearest neighbor distance and the number of nesting males within 20 m, were significantly related to female approach probability and first clutch acquisition latency (once nest algae characteristics were corrected for) respectively. The density of nesting males may influence female choice in a number of ways. First, females may actively seek high densities of males because there are more males from which to choose (Bradbury, 1981), and/or because eggs may suffer less predation (Dominey, 1981).

Second, higher densities of nesting males may simply be easier to locate, or may expedite female receptivity (De Boer, 1981). Third, this pattern may result from an overflow effect which would be greatest in areas of high male density. For example, a female who is rejected from a nest with yellow eggs may simply go to the nearest acceptable empty nest. On the only occasion in which the events immediately preceding a spawn in an empty nest were observed, the female was rejected by a male with yellow eggs and then spawned with his nearest neighbor.

In conclusion, although the data in this study are correlative, they serve to expose those features of males and their nest sites which are likely most important in determining female spawning site choice in *garibaldi*. Although passive factors may play a role in the initial attraction of the female to the nest, active female choice appears to exist for particular nest characteristics (including the presence of eggs). These data provide a foundation for future experimental work which will seek to further establish the relative role of each of these factors in determining female spawning site choice, as well as the selective forces that favor and decision rules which mediate them.

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