

Courtship displays and coloration as indicators of safety rather than of male quality: the safety assurance hypothesis

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Male courtship displays and bright coloration are usually assumed to provide information to females about some aspect of the male's value as a mate. However, in some species, courtship may serve another function—namely, indicating the current predation risk at the mating site and assuring the female that it is safe to mate there at this time. We developed this safety assurance hypothesis (SAH) and tested its predictions in the bluehead wrasse (*Thalassoma bifasciatum*), a Caribbean reef fish. Females in this species come to males' territories to spawn, and males court each arriving female. Males with larger white flank patches court less intensely than less bright males. We show that such males are probably more visible to predators and thus need not court so intensely to provide the same degree of safety assurance to a female. When model lizardfish predators are presented at spawning sites, males habituate to them quickly, but newly arriving females who see the predator are expected to demand more assurance of site safety. Accordingly, and consistent with the SAH, males court females more intensely (longer average courtship bout length) under such circumstances, but males with bright flank patches do not increase their courtship as much as duller males do. Despite this relatively low intensity of courtship, the spawning rate of bright males does not decline relative to that of duller males in the presence of a predator, suggesting that bright coloration conveys a differential benefit. Females of species like the bluehead wrasse, who spawn repeatedly over the course of their life, are expected to be more concerned with their own risk of mortality during each spawning bout than with the quality of a particular male. It is in such species that we expect the SAH to be most applicable. *Key words*: bluehead wrasse, coral reefs, courtship behavior, fish, risk aversion, safety, *Thalassoma bifasciatum*. [*Behav Ecol* 11:444–451 (2000)]

Courtship displays and coloration have traditionally been viewed as means for the male to convey information about himself to the female (Alcock, 1998; Andersson, 1994; Hamilton and Zuk, 1982). This may include information on species identity and individual quality. In species where the male subsequently provides care for the young, courtship intensity has been shown to correlate strongly with quality of care (e.g., Greig-Smith, 1982; Knapp and Kovach, 1991; Sikel, 1995), and brightly colored males in some species have been shown to be in better condition than less brightly colored ones (Milinski and Bakker, 1990). Even in species without male parental care, there is some evidence that courtship may convey information about indirect benefits accruing to mates (e.g., Reynolds and Gross, 1992).

However, courtship occurs in some situations where it would appear that females would not require further information about a prospective mate. Consider the bluehead wrasse (*Thalassoma bifasciatum*), a common fish inhabiting shallow water over coral reefs throughout the Caribbean. Mating takes place year round, and individual females mate several times per week. These females tend to be highly faithful to particular mating sites (Warner, 1987, 1990), where the same brightly colored male will be present for an average of about 90 days and sometimes much longer (Hoffman et al., 1985). Individual males are easily distinguished by variability in a distinctive black-white-black marking on their flanks, and it has been shown that females respond to this coloration

character (Warner and Schultz, 1992). Yet, each time the female arrives on the site to mate, the male courts her assiduously. There is no parental care in this species. Why must the male court the female? A proximate ethological explanation is that courtship and coloration are necessary to stimulate and otherwise prepare a female for mating (e.g., Crews, 1975, 1992). Such is not the case for the bluehead wrasse: at other mating sites large males are displaced by group-mating aggregations of smaller, less brightly colored males, and females mate readily at these sites without benefit of courtship (Warner and Hoffman, 1980a).

Here we propose and test a hypothesis about an alternative function of courtship and bright male coloration: the safety assurance hypothesis (Warner, 1987; see also Uzendoski et al., 1993). We suggest that under certain circumstances the information conveyed concerns safety of the mating site rather than some characteristic of the male himself. That is, females may still require information before mating, but their mating decisions may be based more on current site safety (a transient quality) than on the relative quality of the male. We tested the safety assurance hypothesis (SAH) by manipulating female perceptions of local safety and observing male courtship responses.

The SAH suggests that bright coloration and intense courtship convey more information to a female precisely because they are dangerous. If a brightly colored male is more detectable by a predator than a dull male, then all else being equal, the presence of the bright male conveys relatively greater assurance of current local safety to the female. A similar argument can be made for courtship: if longer or more intense courtship is more dangerous, then a male conducting such a bout will convey more information about current safety to an observing female than would a male conducting a shorter, less

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intense courtship bout. If both coloration and courtship serve to convey safety information, a brightly colored male will be able to court less than a dull male and still convey safety assurance information, while a dull male will be required to court more. We tested this corollary of the SAH by examining male courtship in relation to their coloration and by measuring the response of differently colored males to changes in female perception of local safety.

To illustrate this idea and to introduce the research setting, we continue with our example of the bluehead wrasse. Courtship by brightly colored males is conspicuous and occurs in the area (high in the water column) where mating will occur. Release of gametes from high in the water column can aid in conveying fertilized eggs away from reef-based predators and may aid dispersal as well (Randall and Randall, 1963; Robertson and Hoffman, 1977; Thresher, 1984). However, the risk of predation on adults increases with distance from the protection of the reef (Hobson, 1975), and the mating act itself reduces vigilance. Mating in many animals increases predation risk (Endler, 1983; Gwynne, 1989; Lima and Dill, 1990; Magnhagen, 1991; Ryan, 1985), and courtship is often performed near where mating will occur. Bright coloration may also increase predation risk (Endler, 1991), both for the bright male and the attending female (Pocklington and Dill, 1995). Thus females may mate with certain males because doing so reduces the predation risk cost of mating (Clutton-Brock et al., 1993; Deutsch and Weeks, 1992). Here we extend this idea by suggesting that courtship and coloration can provide females with information about current predation risk, even after mate choice has occurred.

In the bluehead wrasse, the qualities of the courting male are not likely to change over the course of several days: size, coloration, behavior, and sperm output are relatively invariant (Hoffman et al., 1985; Warner and Hoffman, 1980b; Warner et al., 1995a). However, the current safety of the mating site can change dramatically. Predators such as lizardfish, groupers, and snappers tend to range widely, and an element of surprise is often essential to their success (Hobson, 1975). The fact that a predator was not present at some previous time may have no information value as to the present safety of a mating site. For a female, a simple demonstration of the current safety of a mating site could be much more important to fitness than information about a particular male, and male displays could provide such a demonstration. The SAH predicts that the addition of obvious potential predators should alter the apparent quality of the site and induce females to require more assurance of safety, perhaps through more courtship or other conspicuous behavior. However, if courtship or coloration is simply a means to convey information about the male, there should be no change in behavior, or activity should decline because of the risk to males. In the following experiments, we attempted to disentangle male and female interests by temporally separating the apparent predation threat to the two sexes.

To be applied to the bluehead wrasse, the SAH encompasses a series of assumptions and predictions, each of which were tested: (1) Males designated as conspicuous are indeed easier for predators to detect visually. (2) Courtship behavior is dangerous. Males under predation threat will curtail courtship. (3) Females require safety assurance before mating. Given an existing amount of information about the male, females under greater predation threat will require more courtship. (4) If both conspicuousness and courtship are effective at conveying safety information to a female, then under normal conditions females will require less courtship from bright males. Thus, courtship intensity and coloration will be inversely related. Under predation threat (perceived by females, but not

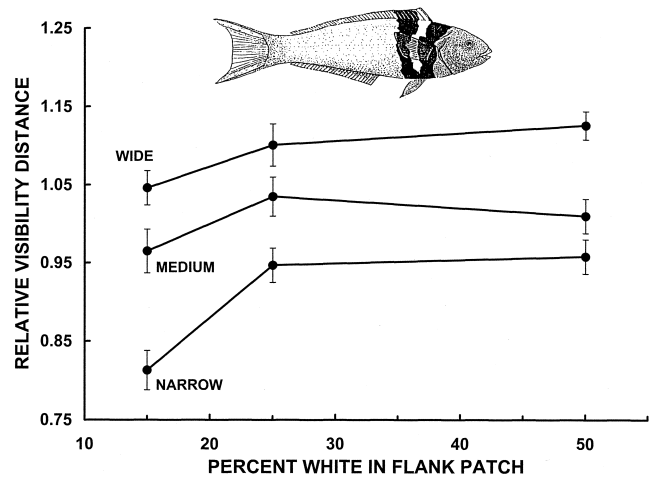


Figure 1

Relative conspicuousness of nine different models of terminal color phase male bluehead wrasse to a human observer under field conditions. Total flank patch width was 10 mm (narrow), 15 mm (medium), or 20 mm (wide); the white area within each patch series was set at 10, 25, or 50%. Relative visibility distance is the maximum distance (in meters) at which a particular flank patch could be seen on a day divided by that day's average sighting distance. Error bars are ± 1 SE.

males), less conspicuous males will increase courtship activity more than bright males.

METHODS

This study took place on patch reefs in Tague Bay, St. Croix, U.S. Virgin Islands (17°45' N, 64°35' W), May–July 1995 and 1996. *Thalassoma bifasciatum* is dichromatic: large males are in the terminal color phase (TP), easily distinguished from the less conspicuous initial color phase (IP) of females and smaller males. On Tague Bay patch reefs, most females feed on plankton on the upcurrent ends of reefs during the day and migrate to specific downcurrent mating sites for a single, brief visit (Warner and Schultz, 1992). Individual TP males each occupy a spawning site (Hensley et al., 1994; Warner, 1988) and defend the site against smaller, younger IP males (Warner, 1984; Warner and Hoffman, 1980b). Mating takes place daily during a discrete afternoon period of about 3 h, throughout the year. For the following experiments, a critical aspect of the mating system is that females arrive sequentially at the mating site so that the brief individual visits are spread over the mating period, with few or no interactions occurring among females. Fertilization is external and the eggs are pelagic, so neither males nor females have any further contact with the young. Previous studies of tagged individual females indicate that, on average, they spawn 2 out of every 3 days and strongly tend to return to the same mating site (Warner, 1984, 1986, 1995). This fidelity leads to consistent differences between TP male sites in average daily spawning rates, from less than 5 to more than 80 matings per day (Warner et al., 1995a).

As mentioned above, TP males have a distinctive black-white-black flank patch on their sides (see vignette in Figure 1). The proportion of white in this flank patch has been shown to be positively correlated with both female preference for particular males and with successful TP male defense against smaller males; the overall size of the patch had a much weaker effect (Warner and Schultz, 1992). This flank patch is variable between individuals but cannot be modified in size by an individual except through scale replacement, which can

take several weeks. Predictions of the SAH would be more complex if bright coloration were correlated with a male's intrinsic ability to escape predation. In the bluehead wrasse, however, the proportion of white in the flank patch is not correlated with morphometric variables in territorial TP males, including depth of body, overall length, or relative pectoral fin length (Warner and Schultz, 1992).

To gauge the contribution of the flank patch to conspicuousness of the male, we constructed nine two-dimensional models of TP males. These models were the size of an average-length TP male [90 mm standard length (SL)] and differed in the overall size and percent white of the flank patch. The total width of the patch varied from narrow (10 mm), to medium (15 mm), to wide (20 mm). In nature, the average width of flank patches at the lateral line is 16.2 mm. Within each width category, the percent white was either 15%, 25%, or 50%; average percent white in nature is 23.3% (Warner and Schultz, 1992). Conspicuousness was judged by a human observer as the maximum distance (in meters) at which the flank patch could be seen under water. All models were tested 5 times on each of 5 different days. Visibility naturally varied between days, and we normalized each day's results relative to the daily mean sighting distance for the set of nine models. We do not assume that marine predators have the same visual abilities as a human being with a facemask, but rather seek to estimate the relative conspicuousness of different intensities of the flank patch markings.

We attempted to distinguish between alternative functions for courtship and coloration by observing the relationship between these two variables in a natural setting. We also manipulated perceived predation risk through controlled presentation of a model predator. At the beginning of the presentation, both the male and any females present presumably perceive the model as a threat. As the spawning period progresses, the male gains information that this particular predator is not a threat (i.e., the male habituates). In contrast, females are present sequentially at the spawning site for only short periods of time, and thus each female perceives the threat anew.

For each of 17 experiments, two mating sites on the same large reef were chosen as a pair. Members of the pair were closely matched as to average daily mating success, rate of intrusion by smaller males, and physical characteristics of the spawning site (see Warner, 1988). During the experiment, each site of the pair was observed for the same 2 days for the entire spawning period (approximately 3 h). The observer at each site continuously recorded all spawning and courtship behaviors. Bluehead wrasse courtship was consistent and stereotypical. The male positioned himself in the water column 0.5–1.5 m above the spawning site and the waiting female. He would then swim in very tight circles, rapidly vibrating his pectoral and caudal fins (Dawkins and Guilford, 1994). During courtship, the tips of the vibrating pectorals were black (normally they were clear). We defined a courtship bout by continuous fin vibration; if a male paused for more than 1 s, we considered the bout terminated. The initiation time and duration of every courtship bout was recorded. In most cases, courtship was eventually followed by spawning: the female would begin to rise in the water column and would be joined by the male as she rapidly accelerated toward the surface. At the apex of the rapid spawning rise, the female released all of her eggs simultaneously with sperm release by the male, and both fish then moved quickly back to the substrate. The entire spawning sequence took less than 1 s, and fertilization was completed in the water column in less than 15 s (Petersen et al., 1992; Warner et al., 1995a). Courtship was occasionally accompanied by repeated upward dashes of the male ("loops") that mimic the spawning rush.

Courtship intensity can be expressed as a rate (number of courtship bouts per spawn) or as a duration (average courtship bout length). Although courtship duration changed dramatically in the presence of the model (see below), there was no discernable effect of the predator addition on overall courtship rate (mean \pm 1 SE courts per spawn in control series, 2.80 ± 0.22 ; experimental series, 2.74 ± 0.25 ; paired t test, $n = 34$ pairs, $t = 0.19$, $p = .85$). Thus only courtship duration is discussed below.

On the first day of an experimental series, one of a pair of mating sites was randomly designated as the experimental site. At the base of this mating site we placed a Plexiglas cylinder (12.8 cm diam, 61 cm long) containing a preserved lizardfish (a sand diver *Synodus intermedius*, 39 cm standard length) on a 2 cm bed of sand. Lizardfish (Synodidae) are sedentary, benthic predators that attack from positions on the bottom. They account for the majority of the attacks on blueheads during spawning (174 of 256 predation events witnessed in Panama and St. Croix since 1974; Warner RR, personal observation). The lizardfish was coated with clear epoxy resin and positioned in a realistic posture. When presented with the model predator inside the cylinder, blueheads at the experimental sites showed cautious behavior (see Results). The cylinder prevented close inspection of the model and resulted in a measurable habituation period (see below). At control sites (the other member of the pair), we deployed an identical but empty Plexiglas cylinder. On the second day of the experimental series, the deployments were reversed. Thus in half of the comparisons, the control presentation preceded the experimental one, while in the other half the experimental presentation was done first. Subsequent analysis revealed no effect of the order of presentation.

After half of the 2-day experimental series, TP males were captured, measured, and photographed. We recorded standard length, body depth, tail length, and pectoral length from the fish themselves (see Warner and Schultz, 1992). From digitized images, we recorded the relative area of white in the flank patches. For any paired structure, the two measurements were averaged. Because of logistical difficulties, measurement and recapture were not initiated until late in the 1995 series. Of the 34 males used in the experiments, 17 were captured for these measurements (4 of 20 in 1995 and 13 of 14 in 1996).

RESULTS

Conspicuousness as a function of coloration

Our observations of fish models revealed that, in general, conspicuousness of the flank patch increased with the overall width of the patch and with the percent of white within the patch (Figure 1, Table 1). While visibility increased consistently with the total width of the patch, the percent white in the patch strongly affected visibility only when increased from 15% to 25% (Figure 1). There was little or no additional contribution to visibility due to increases of percent white from 25% to 50% (individuals in the experimental series naturally ranged between 16% and 28% white; see Figure 2). The interaction between patch width and percent white was not significant (Table 1), indicating that an increase in percent white had a similar effect regardless of the actual size of the flank patch. The overall average maximum distance at which flank patches could be seen by a human was 9.4 m, which is substantially larger than the radius of a typical TP male mating territory (Warner and Hoffman, 1980b).

Table 1
Two-factor analysis of variance of the effect of total flank patch width and percentage white area in the flank patch on visibility distance

Source	df	SS	MS	F	p
Patch width (A)	2	0.255	0.127	17.948	.0001
Percent white (B)	2	0.079	0.040	5.577	.0078
Interaction (AB)	4	0.017	0.004	0.608	.6592
Error	36	0.255	0.007		

SS, sum of squares; MS, mean square. Data are the daily mean sighting distances (in meters) of five replicates run for each of nine models (narrow, medium, or wide; 15, 20, or 25% white), normalized to the average visibility distance for that particular day. Observations were made on 5 different days.

Relationship of courtship duration to male coloration

Under control conditions, males varied in average courtship duration, and there was a clear relationship of this duration with the percent of white in the flank patch (Figure 2). Males with a greater percentage of white in their patch tended to court for shorter durations ($r = -.742$, $p < .001$).

This result is consistent with the idea that courtship and coloration may both serve to convey information to a female and that one may substitute for another. However, the basis for variation among males could be due to another causal variable. The most obvious candidate is daily mating rate because this varies greatly between males (Hoffman et al., 1985; Warner and Schultz, 1992). Daily mating rate is known to affect sperm output per spawn (Warner et al., 1995a), so it was quite possible that it could affect courtship intensity as well. Increases in mating success are also known to be associated with large amounts of white in the flank patch of the TP male (Warner and Schultz, 1992). However, there was no relationship between the total number of spawns accrued by a male on the control day and his mean courtship duration ($r = .13$, $p > .50$). In a related study using many more males, Warner and Schultz (1992) also found no correlation between average daily mating success and mean courtship duration. There was also no relationship between mean courtship duration and any of the morphometric variables ($n = 17$, $p > .05$ for standard length, body depth, tail length, and pectoral length).

General effects of predator addition

The presence of the model predator at the mating site resulted in a strong initial reaction by both male and female bluehead wrasses. The same behavior was shown by males before habituation (see below) and by females subsequently arriving at the mating site. Individuals would remain quite near the substrate, oriented head-on toward the model. Fish would often slowly approach the model, swimming in a characteristic up-and-down motion as they came closer to the model (see Godin and Davis, 1995, for an example of how such behavior reduces predation risk). Blueheads react in an identical fashion under normal situations when a predation threat is present (Warner RR, unpublished observations). The presence of the cylinder without the model elicited no such reaction. Bluehead wrasses are opportunistic feeders, and the addition of the empty cylinder resulted in immediate inspection. Subsequently it was ignored.

While there was no question that the model was treated with caution, there was only a slight overall effect of predator addition on overall spawning rate at a particular site (Figure 3). The mean spawning total on predator-addition days was 91% of that on control days, indicating that most females did

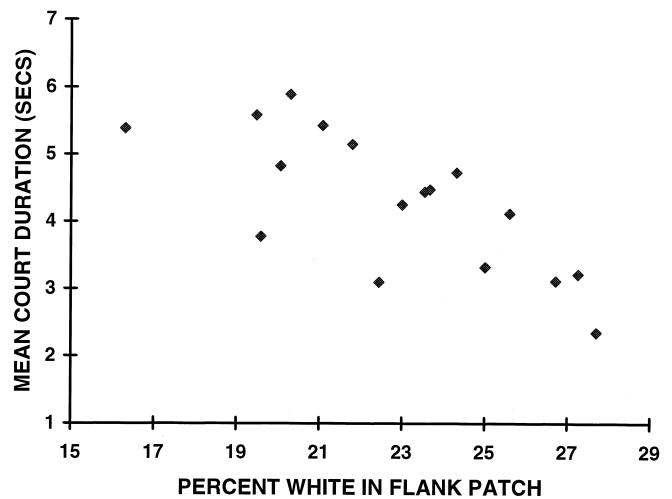


Figure 2
Mean courtship duration (averaged over the entire spawning period) as a function of percentage white area in the flank patch of terminal color phase male bluehead wrasse.

not simply abandon mating at a site with predation threat. As suggested by the results presented above, there was no relationship between losses of mating and male coloration, morphometric, or behavior variables. While between-site variation is considerable, spawning rates at a particular site normally remain rather constant from day to day, with an average coefficient of variation of 26% (Warner and Schultz, 1992). The fact that females detected the predator but continued to spawn at the site allows an investigation of male response to females, as presented below.

Effects of predator addition on courtship

Initial responses of males

There was a strong initial response of courtship duration to predator addition. For all males, courtship duration was ini-

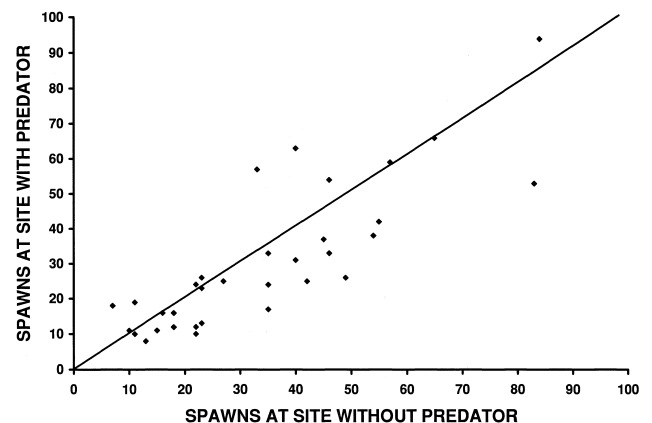


Figure 3
Comparison of the spawns accrued over the course of the mating period for terminal color phase males under control conditions versus spawns during the mating period by that same male with a predator added. A 1:1 line is provided for reference. The correlation between control and experimental data is 0.837 ($p < .001$). There is a trend for number of spawns during the experimental period (mean \pm 1 SE, 29.9 ± 3.5) to be lower than the number of spawns during the control period (33.6 ± 3.4), but the difference is not significant [t test for paired data, t (two-tailed) = 1.85, $p = .072$].

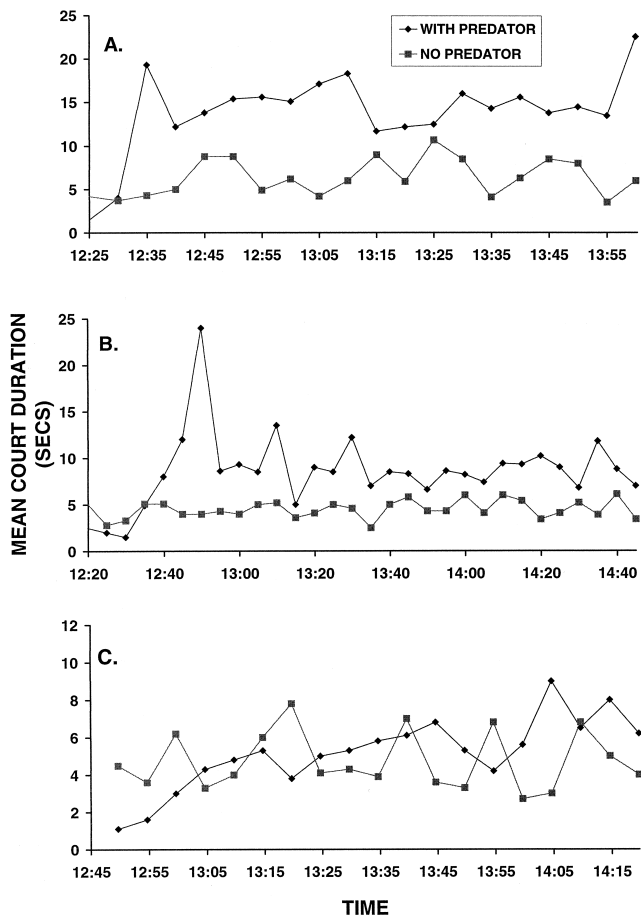


Figure 4
 Mean courtship durations (in seconds) over successive 5-min periods for terminal color phase males with and without the experimental predator present. The origin represents the start of the mating period, and the initial low values in the predator-present trials indicate the prehabituating period. (A) Male 2F1, 8 and 11 June 1995, (B) Male 13C1, 13 and 14 June 1995, (C) Male 15I1, 26 and 27 June 1995.

tially short, averaging less than 45% of the duration of courtship in the initial periods of the control observations for the same males (mean \pm 1 SE courtship duration in first 10 min of spawning: control, 4.2 ± 0.2 s; with predator, 1.9 ± 0.3 s; $p < .001$). Courtship responses are most easily visualized as average courtship durations for successive 5-min periods over the course of the spawning period (examples in Figure 4). Courtship duration remained depressed for an average of 2.4 5-min periods before it returned to control levels (or greater, see below), showing a clear pattern of habituation. Thus we did not use the first two time periods in the calculation of post-habituating responses, either in the controls or the experimental presentations (below).

Subsequent responses of males

After the habituation period, males varied considerably in their courtship responses. For many males (e.g., Figure 4a and 4b), the courtship durations increased after habituation to levels much higher than in the control situation and remained high during the entire spawning period. For other males, however, courtship durations only returned to control levels (e.g., Figure 4c).

Overall, the posthabituating courtship response had a distinct pattern relative to control levels of courtship duration

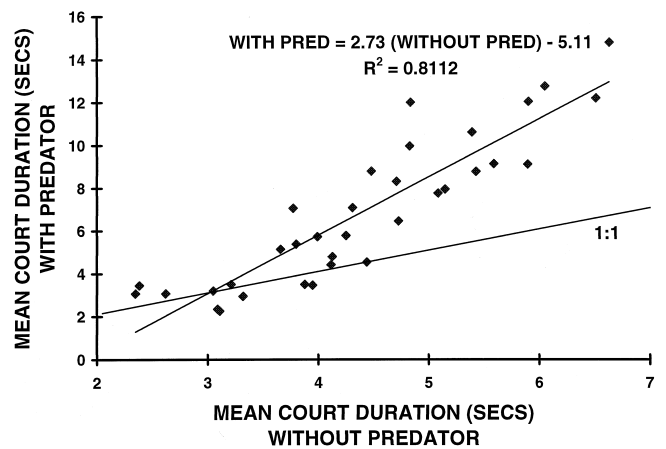


Figure 5
 Mean posthabituating courtship durations (averaged over successive 5-min period means) for terminal color phase males, comparing the spawning periods with an added predator versus control periods (no predator present). The 1:1 line represents the expectation that the presence of a predator does not affect courtship duration. The regression slope is significantly different from 1.0 (see text).

(Figure 5). Males with relatively short average courtship durations on control days showed little or no posthabituating response to predator addition, whereas males with long mean courtship durations in the control tended to be those who increased courtship duration in the presence of a predator. The regression relationship between control mean courtship durations (CC) and mean courtship durations with a predator present (PC) was $PC = (2.73)CC - 5.11$. The 95% confidence interval for the slope was between 2.25 and 3.20, indicating a strong tendency for larger responses by males with longer control courtship durations. The regression crosses the 1:1 line at a mean courtship duration of approximately 3 s; thus males with average control courtship durations less than this value showed little or no post-habituating response to the model's addition.

Response to predator addition as a function of coloration

Once habituated, males tend to increase courtship durations in the presence of a predator, if they respond at all. The males that do respond are those that have relatively long courtship durations in the absence of a predation threat. These are the males with relatively small amounts of white in their flank patches (Figure 2). Given this relationship between coloration and courtship duration, the pattern of posthabituating response to the addition of the predator model becomes more clear. Males with larger percentages of white in their flank patches not only tend to court for shorter durations, but they also tend not to respond to the addition of the predator model (Figure 6). In contrast, males with less white in their flank patch court for relatively long durations and respond to predator additions by lengthening courtship durations still further in the posthabituating period. Despite the fact that brightly colored males had relatively lower courtship than dull males in the presence of predators, they did not suffer any greater losses of mating.

DISCUSSION

The results and their interpretation can be summarized as follows:

1. Models of males with relatively large white flank patches are more conspicuous, at least to human observers.

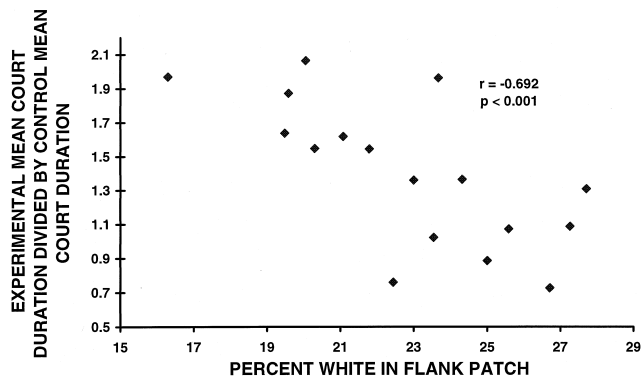


Figure 6

Responses of terminal color phase males to predator addition in relation to percentage white area in the flank patch. Responses are expressed as a proportional change in mean courtship duration, experiment divided by control; thus 1.0 would represent no change (see Figure 5) ($r = -0.692$, $p < 0.001$).

2. All males initially court less in the presence of a predator, and thus courtship intensity is a reliable signal indicating site safety.
3. After a short period of habituation, some males increase average courtship durations in the presence of a predator, while other males simply return to control levels; this suggests that females may require more intense courtship in dangerous situations.
4. Males that increase courtship duration are those with relatively long average courtship durations during control periods.
5. Males with relatively large white flank patches have relatively short control courtship durations and respond less strongly to the predator additions. Thus females may require more courtship from less conspicuous males.

In other words, conspicuous males courted for shorter periods under normal conditions and did not tend to change their posthabituation courtship duration when females at the mating site were presented with an apparent predation threat. In contrast, less conspicuous males courted for longer durations under control conditions and increased those courtship durations dramatically (after habituation) when a predation threat was added. These results are consistent with our predictions based on the SAH, and lend themselves to the following interpretation: Females require information about the current safety of the mating site before mating. If this information comes from courtship activity, males must court more if a site appears dangerous to the female. Courtship activity is particularly reliable information when it comes from a conspicuous male because he is more at risk to predation. These males need to court less for the same effect. For the same reason, in the presence of predators, less conspicuous males must increase their courtship duration more than conspicuous males (cf. Reynolds, 1993).

Note that our interpretation of courtship and coloration implies a basic sexual conflict rather than a strictly beneficial exchange of information (Rowe et al., 1994). The SAH suggests that long courtship bouts and bright coloration are inherently dangerous, raising the risk of predation on the participating male. Because of this risk, they convey valuable and truthful information to the female, and this in turn increases her probability of mating. The male is willing to incur risk because of this increased probability of mating, but his optimal strategy would be to mate without courting or displaying bright coloration. In the sense that bright coloration and extended courtship are risky to the male, they are handicaps

(sensu Zahavi, 1992). However, handicaps supposedly convey information to the female about the quality of the male, while the SAH suggests that the information concerns local safety. It is important to note that courtship is not required at group spawn sites. In these circumstances, there are often hundreds of other individuals present at the mating site, and the per capita risk of predation is substantially reduced due to dilution (Krause and Godin, 1995). In other words, where the risk is lessened, courtship is not required.

We stress that the predictions based on safety indicators are exactly opposite to those based on more traditional interpretations of courtship and color. In this latter view, females should be less discriminating (and thus require less courtship or display coloration) in the presence of a predator (reviewed in Sih, 1994; see also Hedrick and Dill, 1993; Godin and Briggs, 1996).

An alternative explanation for the intensification of courtship in the presence of a predation threat would be that females are simply more reticent to spawn and become more willing to mate after a period of no attack. This would be a plausible explanation if the response were uniform across all sites (i.e., if courtship were extended at all sites in the presence of the model), or varied randomly across sites (perhaps reflecting variation between sites in the effectiveness of presentation of the model). Instead, the courtship response varied nonrandomly between sites, depending on the conspicuousness of the attending male. Thus male–female interactions under a predation threat are not independent of the male's appearance and activity at the mating site. Simple female reticence cannot explain the apparent trade-off between coloration and courtship in attending males.

Working with guppies (*Poecilia reticulata*), Reynolds (1993) also noted a difference in the courtship response of attractive and unattractive males to a perceived predation threat. Large male guppies, which are preferred by females, decreased their courtship more than did small ones when light levels were increased. Although the overall response was the opposite to that seen in the bluehead wrasse (where courtship increased under predation threat), Reynolds's hypotheses about the reasons behind the guppies' differential response offer an interesting alternative to the SAH. For bluehead wrasse males, Reynolds's differential-cost hypothesis would suggest that conspicuous males cannot afford to increase courtship because it is more dangerous for them to do so. The prediction from this hypothesis is that attractive males would then lose relatively more matings under predation threat than would small males. In contrast, the bluehead version of Reynolds's differential-benefit hypothesis suggests that conspicuous males do not increase courtship under predation threat because they are already sufficiently attractive and extra courtship will not increase their mating rate. Under this hypothesis, no differential loss in mating rates is predicted.

For guppies, Reynolds found that large males lost proportionally more matings than did small males under predation threat, supporting the differential-cost hypothesis. For the bluehead wrasse, while there was a small overall decrease in mating rates when predators were present, this decrease was unrelated to male coloration or change in courtship duration. Thus this work lends support to a hypothesis based in differential benefit. In fact, Reynolds's differential-benefit hypothesis is congruent with the interaction between coloration and courtship in the bluehead wrasse, with the interesting difference that the benefits are also conveyed to the female in the form of safety assurance.

Obviously, we do not expect the SAH to apply to every situation where males are brightly colored or display intense courtship. It is useful to consider the circumstances under which survival considerations might take precedence over oth-

er benefits of careful mate assessment. Life-history theory suggests a reason that female bluehead wrasses appear more concerned with safety than with the qualities of the particular male with whom they are to mate (Warner, 1998). In this sex-changing species, individuals may expect to reproduce approximately 500 times as a female in the first 2 years of their lives, and, if they survive to become successful terminal phase individuals, to achieve another 2300 matings as a male (Warner, 1984). For highly iteroparous species (that is, species with many reproductive events over the course of their lives), each particular reproductive event constitutes a rather small proportion of an individual's total lifetime reproductive success. In such species, survival to future reproductive events is an extremely important component of fitness—much more important than a marginal increase in current reproductive success (Mertz, 1971; Schaffer, 1974; Stearns, 1976, 1992).

In other words, individuals in highly iteroparous species will be expected to avoid mortality risks and seek assurance that any current reproductive activity is safe. By the same token, such individuals will not be expected to engage in mate assessment or mate searching to the same degree as less iteroparous species, especially if these activities involve increased risk of mortality (Warner, 1998). Although a great deal of attention has been paid to the potential benefits of mate choice (e.g., Janetos, 1980; Reynolds and Gross, 1990), we have only recently begun to appreciate the effects of costs (Hedrick and Dill, 1993; Pocklington and Dill, 1995; Real, 1990, 1991; Sih, 1994; Warner et al., 1995b). These costs will be overwhelmingly important to species such as the bluehead wrasse.

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REFERENCES

- Alcock J, 1998. Animal behavior: an evolutionary approach, 6th ed. Sunderland, Massachusetts: Sinauer Associates.
- Andersson M, 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.
- Clutton-Brock T, Deutsch JC, Nefdt RJC, 1993. The evolution of ungulate leks. *Anim Behav* 46:1121–1138.
- Crews D, 1975. Psychobiology of reptilian reproduction. *Science* 189:1059–1065.
- Crews D, 1992. Behavioural endocrinology and reproduction: an evolutionary perspective. *Oxford Rev Reprod Biol* 14:303–370.
- Dawkins MS, Guilford T, 1994. Design of an intention signal in the bluehead wrasse (*Thalassoma bifasciatum*). *Proc R Soc Lond B* 257:123–128.
- Deutsch JC, Weeks P, 1992. Uganda kob prefer high-visibility leks and territories. *Behav Ecol* 3:223–233.
- Endler JA, 1983. Natural and sexual selection on color patterns in poeciliid fishes. *Environ Biol Fish* 9:173–190.
- Endler JA, 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Res* 31:587–608.
- Godin J-GJ, Briggs SE, 1996. Female mate choice under predation risk in the guppy. *Anim Behav* 51:117–130.
- Godin J-GJ, Davis SA, 1995. Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proc R Soc Lond B* 259:193–200.
- Greig-Smith PW, 1982. Song-rates and parental care by individual male stonechats (*Saxicola torquata*). *Anim Behav* 30:245–252.
- Gwynne DT, 1989. Does copulation increase the risk of predation? *Trends Ecol Evol* 4:54–56.
- Hamilton DW, Zuk M, 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–386.
- Hedrick AV, Dill LM, 1993. Mate choice by female crickets is influenced by predation risk. *Anim Behav* 46: 193–196.
- Hensley DA, Appeldoorn RS, Shapiro DY, Ray M, Yurigan RG, 1994. Egg dispersal in a Caribbean coral reef fish, *Thalassoma bifasciatum*. I. Dispersal over the reef platform. *Bull Mar Sci* 54:256–270.
- Hobson ES, 1975. Feeding patterns among tropical reef fishes. *Am Sci* 63:382–392.
- Hoffman SG, Schildhauer MP, Warner RR, 1985. The costs of changing sex and the ontogeny of males under contest competition for mates. *Evolution* 39:915–927.
- Janetos AC, 1980. Strategies of female mate choice: a theoretical analysis. *Behav Ecol Sociobiol* 7:107–112.
- Knapp RA, Kovach J, 1991. Courtship as an honest indicator of male parental quality in the bicolor damselfish, *Stegastes partitus*. *Behav Ecol* 2:295–300.
- Krause J, Godin J-GJ, 1995. Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. *Anim Behav* 50:465–473.
- Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640.
- Magnhagen C, 1991. Predation risk as a cost of reproduction. *Trends Ecol Evol* 6:183–186.
- Mertz DB, 1971. The mathematical demography of the California condor population. *Am Nat* 105:437–453.
- Milinski M., Bakker TCM, 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature* 344:330–333.
- Petersen CW, Warner RR, Cohen S, Hess HC, Sewell AT, 1992. Variation in pelagic fertilization success: implications for production estimates, mate choice, and the spatial and temporal distribution of spawning. *Ecology* 73:391–401.
- Pocklington R, Dill LM, 1995. Predation on females or males: who pays for bright male traits? *Anim Behav* 49:1122–1124.
- Randall JE, Randall HA, 1963. The spawning and early development of the Atlantic parrotfish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. *Zoologica* 48:49–60.
- Real L, 1990. Search theory and mate choice. I. Models of single-sex discrimination. *Am Nat* 136:376–404.
- Real L, 1991. Search theory and mate choice. II. Mutual interaction, assortative mating, and equilibrium variation in male and female fitness. *Am Nat* 138:901–917.
- Reynolds JD, 1993. Should attractive individuals court more? Theory and a test. *Am Nat* 141:914–927.
- Reynolds JD, Gross MR, 1990. Costs and benefits of female mate choice: Is there a lek paradox? *Am Nat* 136:230–243.
- Reynolds JD, Gross MR, 1992. Female mate preference enhances offspring growth and reproduction in a fish *Poecilia reticulata*. *Proc R Soc Lond B* 250:57–62.
- Robertson DR, Hoffman SG, 1977. The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. *Z Tierpsychol* 45:298–320.
- Rowe L, Arnqvist G, Sih A, Krupa JJ, 1994. Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends Ecol Evol* 9:289–293.
- Ryan MJ, 1985. The túngara frog: a study in sexual selection and communication. Chicago: University of Chicago Press.
- Schaffer WM, 1974. Selection for optimal life histories: the effects of age structure. *Ecology* 55:291–303.
- Sih A, 1994. Predation risk and the evolutionary ecology of reproductive behavior. *J Fish Biol* 45(suppl A):111–130.
- Sikkel PC, 1995. Effects of nest quality on male courtship and female spawning-site choice in an algal-nesting damselfish. *Bull Mar Sci* 57:682–689.
- Stearns SC, 1976. Life history tactics: a review of the ideas. *Q Rev Biol* 51:3–47.
- Stearns SC, 1992. The evolution of life histories. Oxford: Oxford University Press.
- Thresher RE, 1984. Reproduction in reef fishes. Neptune City, New Jersey: TFH Publications.
- Uzendoski K, Maskymovitch E, Verrell P, 1993. Do the risks of predation and intermale competition affect courtship behavior in the salamander *Desmognathus ocoephaeus*? *Behav Ecol Sociobiol* 32:421–427.
- Warner RR, 1984. Deferred reproduction as a response to sexual selection in a coral reef fish: a test of the life historical consequences. *Evolution* 38:148–162.
- Warner RR, 1986. The environmental correlates of female infidelity

- in a coral reef fish. In: Indo-Pacific fish biology: Proceedings of the Second International Conference on Indo-Pacific Fishes. (Uyeno T, Arai R, Taniuchi T, Matsuura K, eds). Tokyo: Ichthyology Society of Japan; 803–810.
- Warner RR, 1987. Female choice of sites versus mates in a coral reef fish, *Thalassoma bifasciatum*. Anim Behav 35:1470–1478.
- Warner RR, 1988. Traditionality of mating-site preferences in a coral-reef fish. Nature 335:719–721.
- Warner RR, 1990. Male versus female influences on mating site-termination in a coral reef fish. Anim Behav 39:540–548.
- Warner RR, 1995. Large mating aggregations and daily long-distance spawning migrations in the bluehead wrasse, *Thalassoma bifasciatum*. Environ Biol Fish 44:337–345.
- Warner RR, 1998. The role of extreme iteroparity and risk-avoidance in the evolution of mating systems. J Fish Biol 53(suppl A):82–93.
- Warner RR, Hoffman SG, 1980a. Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (*Thalassoma* spp.) Evolution 34:508–518.
- Warner RR, Hoffman SG, 1980b. Population density and the economics of territorial defense in a coral reef fish. Ecology 61:772–780.
- Warner RR, Marconato A, Shapiro DY, Petersen CW, 1995a. Sexual conflict: males with highest mating success convey the lowest fertilization benefits to females. Proc R Soc Lond B 262:135–139.
- Warner RR, Schultz ET, 1992. Sexual selection and male characteristics in the bluehead wrasse, *Thalassoma bifasciatum*: mating site acquisition, mating site defense, and female choice. Evolution 46:1421–1442.
- Warner RR, Wernerus F, Lejeune P, van den Berghe EP, 1995b. Dynamics of female choice for parental care in a species where care is facultative. Behav Ecol 6:73–81.
- Zahavi A, 1992. Sexual selection—badges and signals. Trends Ecol Evol 7:30–31.