

Effective Timing of Male Courtship Displays for Female Mate Choice in a Territorial Damsel Fish *Stegastes nigricans*

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Abstract The timing of female mate choice and the frequency of male courtship displays were investigated in a territorial damselfish, *Stegastes nigricans*, in Okinawa, southern Japan. Both males and females of this species held individual territories, which were distributed contiguously, forming colonies. Females visited male territories to spawn in the early morning, males subsequently tending the eggs until hatching. Females were visited by a higher number of males in the morning and evening of the day prior to spawning than on other days and received courtship displays more frequently on the morning of spawning and the previous day. Females often began spawning before male courtship displays in the morning, tending to spawn with males that had courted most frequently on the previous day. This indicates that female mate choice was usually based on the previous day's frequency of courtships. Females that were courted less frequently on the day prior to spawning began to spawn later in the morning in order to receive a greater number of courtship displays. Accordingly, males frequently courting such females on the morning of spawning as well as on the previous day, should increase their chances of mating success.

Female mate choice, one of the main subjects of behavioral ecology, has attracted a lot of interest from behavioral and evolutionary ecologists (Bateson, 1983; Andersson, 1994). Many studies of female choice have been conducted in fishes (Turner, 1993), revealing that females choose their mates on the basis of various male traits, such as body size (Rowland, 1989; Downhower and Lank, 1994), body coloration (Kodric-Brown, 1989; Bakker and Milinski, 1991; Warner and Schultz, 1992), fin length (Bischoff et al., 1985; Basolo, 1990) or the qualities of their nests or territories (Hastings, 1988; Hoelzer, 1990). Male courtship displays are also important in female mate choice, females of many species preferring males that court more frequently (Cole, 1982; Jamieson and Colgan, 1989; Knapp and Kovach, 1991). In these species, it is expected that males should conduct their courtship displays most frequently at the most effective time to be chosen by females, owing to the cost to the males of courtship behavior, e.g., loss of energy and time (Hastings, 1988), and predation risk during courtship (Endler, 1983; Magnhagen, 1991). Females may assess the

frequency of male courtships either at the time of mating or at some other time, such as on the previous day (Gronell, 1989).

The purpose of the present study was to clarify the relationship between the timing of female choice and the frequency of male courtship displays in a damselfish, *Stegastes nigricans*. This fish is widely distributed on coral reefs of the Indo-Pacific Ocean (Masuda et al., 1984), both males and females holding individual territories on dead corals or rocks and feeding mainly on algae in these territories (Sano et al., 1984). Such territories are distributed adjacent to each other, forming colonies (Karino and Nakazono, 1993). In the early morning females visit male territories to spawn demersal eggs, the males subsequently taking care of the eggs for 5–6 days until hatching. Each female spawns every two days, being the shortest interval between spawnings, usually with one male each morning, although the mate is often changed from day to day during the spawning season from June to September in Okinawa (Karino and Nakazono, 1993). Males perform two types of courtship displays, i.e., dipping in both their own and

females' territories, and caudal displays, in the latter only (Karino and Nakazono, 1993), the frequency of courtship displays being the most important factor in female mate choice (Karino, 1995). As males conduct such displays not only in the early morning, but also in the evening (Karino, 1993), this study focused on the most appropriate time for males to concentrate their courting effort so as to be chosen by a female.

Materials and Methods

From June to September 1987, I conducted underwater observations using snorkel and SCUBA on the fringing reef of Sesoko Island (26°38'N, 127°52'E), Okinawa, Japan. I chose a colony of *Stegastes nigricans* (Colony A in Karino, 1995) on the reef edge, 2.0–2.5 m below mean sea level. The colony size was 8–9 m in diameter, and the substratum, living and dead corals.

All individuals ($n=40$) in the colony could be distinguished by natural markings, such as injuries to fins and bodies. The location and range of each territory were recorded by 10–15 min observations on 6–8 June and 24–26 August. Sexual dichromatism and dimorphism were not apparent in this species, the sex of each fish being determined by its reproductive behavior (Karino, 1995): individuals that spawned in the territories of others were considered females ($n=8$) and their mates males ($n=9$). The sex of the remaining fish, which were not observed mating, was unknown ($n=23$).

The whole colony was surveyed continuously for 1.0–2.5 h in the morning, following the emergence of the fish from their shelter holes, until the end of spawning and male courtship displays ($n=64$ mornings), and for 1.5–2.5 h in the evening from the start of courtship displays until the return of the fish to their shelters ($n=48$ evenings). The spawning time of each pair, along with males that visited each female territory to court, were recorded and the numbers of dips and caudal displays performed by each male were counted. Because females of this colony chose their mates on the basis of the frequency of male displays conducted in the former's territories only (Karino, 1995), the number of displays conducted by a male in its own territory was not analyzed in this study.

I analyzed the data from 8 males, excluding one male that, following loss of his territory to another

colony member on 10 July, moved to another part of the colony and ceased spawning (Karino, 1995). Although males sometimes (17%) spawned with females from neighboring colonies (Karino and Nakazono, 1993), such inter-colonial spawnings were excluded from the present analysis.

Data from five different periods was compared, i.e., on the morning that the female spawned (MS), on the morning (MPS) and evening (EPS) of the day prior to spawning, and on other mornings (MO) and evenings (EO). On MS, most displays (310 out of 325 observed: 95.4%) were conducted before the start of spawning, the 15 displays performed subsequently being excluded from further analysis. Because most of the latter displays (14 out of 15: 93.3%) were conducted by males that were mating with the spawning females, such females usually mating with a single male on any given morning, such displays may not effect mate choice by the females on that morning. Thus the MS observation time used for further analysis was taken as that up to the onset of spawning.

For each female, the number of males that visited her territory to court in each period on different days was averaged, with the values for all females being averaged for each period. The frequencies of dips and caudal displays per 1 h were calculated for each period and averaged as above. On MS, although some females initiated spawning before receiving visits from courting males, data of the number of courting males and frequencies of courtship displays comprised those of both such females and females that began spawning after receiving courtships from males. Since the number of courting males and frequencies of displays did not follow normal distributions (Kolmogorov-Smirnov one-sample test, $p<0.05$), the differences among the five periods were analyzed by Friedman test. When a significant difference ($p<0.05$) was found, the difference between two periods for each combination was further examined by Wilcoxon signed-ranks test.

To clarify the relationship between the time spent by a female before spawning on MS and the number of courtship displays in the female's territory on the previous day, Spearman's rank correlation coefficient (r_s) between these factors was calculated. In addition, I counted the number of fish intruding into the female's territory during her spawning in a male territory, and analyzed the relationship between the frequency of intruders per 5 min and the time before spawning by calculating r_s .

To examine when females assessed male courtship displays, further analyses were performed by dividing males into two categories: spawning males that succeeded in mating with a given female on any given morning and non-spawning males that failed at that time. When a female spawned with two males in a single morning (5 cases out of 90 spawnings; Karino and Nakazono, 1993), both of the latter were treated as spawning males. The frequencies (/h) of courtship displays by a male in each category were averaged for each period for each female. The courtship frequencies of the spawning and non-spawning males were also compared by Wilcoxon signed-ranks test for each period. The difference among the five periods for each male category was analyzed by Friedman test. Whether or not each spawning male chosen by a female was that which had performed courtships most frequently on MS, MPS or EPS was also considered. Ranking of the spawning male with regard to courtship frequency was determined for each period. When no courtship displays occurred during a period, that case was excluded from the analysis.

Results

The number of males that visited a female territory to court differed significantly among the five periods (Friedman test; $\chi^2 = 14.6$, $df = 4$, $p < 0.01$, $n = 8$ female territories; Fig. 1). Females were visited and courted by a greater number of males (average about 3) on the day prior to spawning than on other days; significant differences were found between EPS and the other four periods, and between MPS and MS, MO and EO (Wilcoxon signed-ranks test, $p < 0.05$ for each combination).

The frequencies of male courtship displays also differed significantly among the five periods, both in dips (Friedman test; $\chi^2 = 11.0$, $df = 4$, $p < 0.05$, $n = 8$; Fig. 2a) and in caudal displays (Friedman test; $\chi^2 = 13.9$, $df = 4$, $p < 0.01$, $n = 8$; Fig. 2b). Females received dips most frequently on MS: significant differences were detected between MS and EPS, MO and EO (Wilcoxon signed-ranks test, $p < 0.05$ for each combination), the frequency also being higher on MPS and EPS than on MO or EO (Wilcoxon signed-ranks test, $p < 0.05$ for each combination; Fig. 2a). By contrast, females received caudal displays more frequently on the day prior to spawning than other days; significant differences were detected between

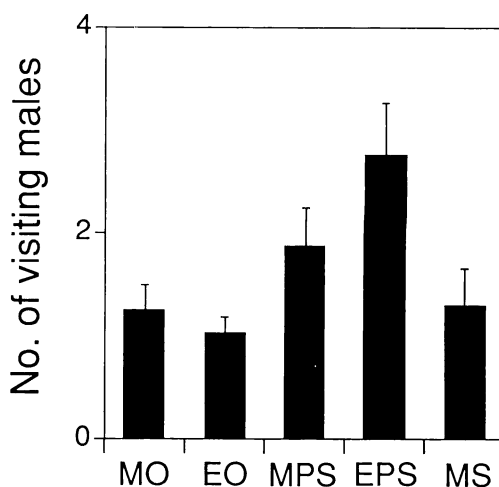


Fig. 1. Average number of males that visited a female territory to court in each period ($n = 8$ female territories). MS—morning when female spawned; MPS and EPS—morning and evening, respectively, of the day prior to spawning; MO and EO—other mornings and evenings, respectively. Vertical bar on each column indicates SE.

EPS and MS, MO and EO, and between MPS and both MO and EO (Wilcoxon signed-ranks test, $p < 0.05$ for each combination; Fig. 2b).

Females began to spawn within 80 min of their emergence from shelter holes, the average time until the onset of spawning being 28.1 min (± 1.6 SE, $n = 90$). In 44 out of 90 cases (48.9%), no males visited and courted the females before spawning. Females that had been courted less frequently on the previous day tended to begin spawning later in the morning (Fig. 3), the time before spawning being negatively correlated with the frequency of dips received on MPS ($r_s = -0.31$, $p < 0.01$, $n = 72$) and EPS ($r_s = -0.24$, $p < 0.05$, $n = 79$) and caudal displays on MPS ($r_s = -0.29$, $p < 0.05$, $n = 72$). The correlation was not significant for caudal displays on EPS ($r_s = -0.18$, $p > 0.05$, $n = 79$).

When a female was absent from her territory for spawning, other fishes, including conspecifics, often intruded into her territory. The number of intruders (per 5 min) increased significantly when a female began to spawn later in the morning ($r_s = 0.39$, $p < 0.05$, $n = 30$ spawnings).

The males that succeeded in spawning with a female had performed dips more frequently than other males on MPS, EPS and MS (Table 1). The spawning males had also performed caudal displays

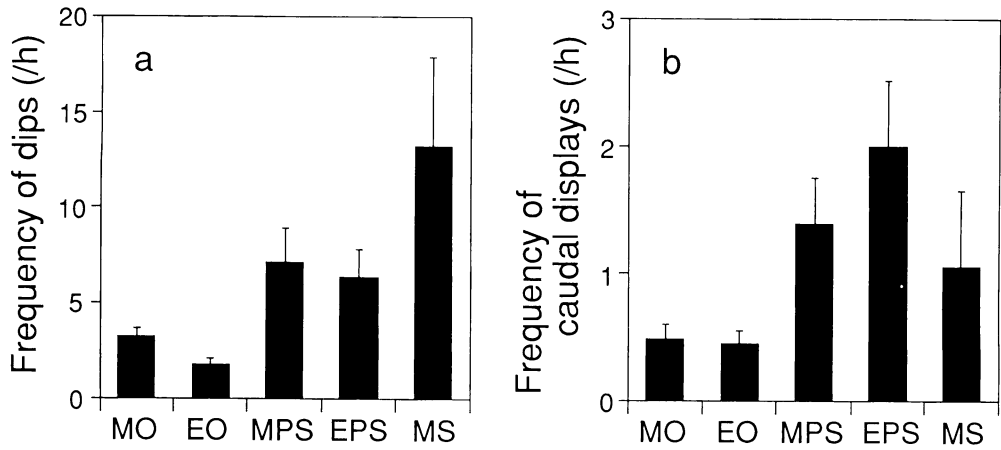


Fig. 2. Average frequencies (/h) of the two courtship displays, (a) dips and (b) caudal displays, by males in a female territory in each period ($n=8$ female territories). Vertical bar on each column indicates SE. Abbreviations as in Figure 1.

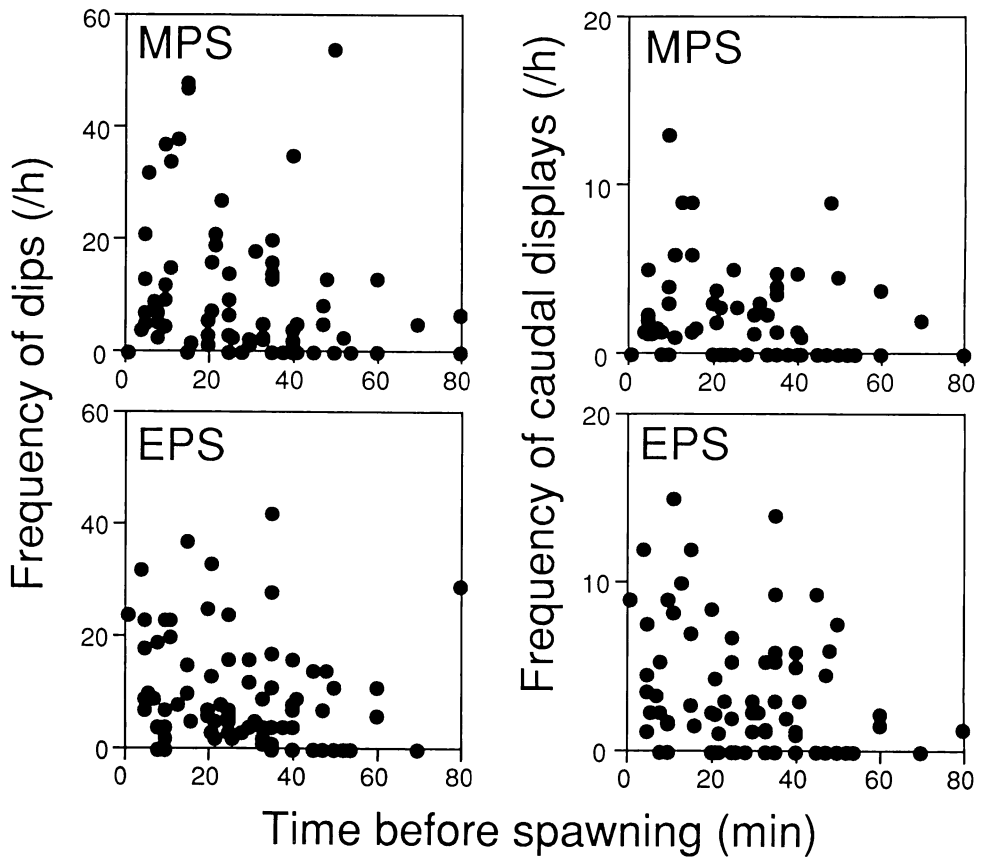


Fig. 3. Relationships between time before spawning by a female and frequency (/h) of dips (left) and caudal displays (right) in the female's territory on the morning (MPS: top) and evening (EPS: bottom) of the previous day.

more frequently on MPS and EPS, than the non-spawning males (Table 1). The frequencies of displays performed by the spawning males differed significantly among the five periods for both dips (Friedman test; $\chi^2=16.7$, $df=4$, $p<0.01$, $n=8$) and caudal displays (Friedman test; $\chi^2=12.4$, $df=4$, $p<0.05$, $n=8$). The spawning males performed

dips most frequently on MS. Although the difference was not significant between MS and MPS or EPS (Wilcoxon signed-ranks test, $p>0.05$ for both combinations), the frequency was significantly higher on MPS, EPS and MS than on MO and EO (Wilcoxon signed-ranks test, $p<0.05$ for each combination). The frequency of caudal displays by the spawning males was higher on the day prior to spawning, significant differences being found between EPS and MS, MO and EO, and between MPS and both MO and EO (Wilcoxon signed-ranks test, $p<0.05$ for each combination). Similar tendencies were found in the non-spawning males, but no significant differences occurred among the five periods for either dips (Friedman test; $\chi^2=0.9$, $df=4$, $p>0.05$, $n=8$) or caudal displays (Friedman test; $\chi^2=7.6$, $df=4$, $p>0.05$, $n=8$).

Females tended to choose the male (spawning male) that had performed the greatest or second-greatest frequency of courtships on the previous day, the former beginning spawning before receiving male courtship displays on MS (Table 2). By contrast, other females which began spawning after receiving courtship displays on MS, did so with mates that had been less often ranked 1st or 2nd in courtship frequency on the previous day, though the difference was significant only for dips on EPS (χ^2 test, $p<0.05$). No significant differences in the percentage of being ranked 1st or 2nd occurred between MS and EPS or MPS (χ^2 test, $p>0.05$; Table 2).

Table 1. Comparison of the frequency (/h) of courtship displays between spawning and non-spawning males in each period

Period*	Spawning males $\bar{x} \pm SE$	Non-spawning males $\bar{x} \pm SE$	Difference p
Dips			
MO	0.55 \pm 0.14	0.41 \pm 0.10	0.34
EO	0.34 \pm 0.08	0.34 \pm 0.08	1.00
MPS	2.73 \pm 0.62	0.64 \pm 0.23	0.02
EPS	2.20 \pm 0.60	0.50 \pm 0.13	0.02
MS	6.02 \pm 2.31	1.11 \pm 0.72	0.03
Caudal displays			
MO	0.10 \pm 0.04	0.06 \pm 0.05	0.32
EO	0.09 \pm 0.02	0.08 \pm 0.03	0.65
MPS	0.46 \pm 0.15	0.16 \pm 0.05	0.04
EPS	0.65 \pm 0.17	0.23 \pm 0.10	0.02
MS	0.37 \pm 0.14	0.17 \pm 0.08	0.22

* See text and Figure 1 for explanation of each period. Statistical analysis was conducted by Wilcoxon signed-ranks test ($n=8$ female territories).

Table 2. Ranking of the spawning male among the 8 males observed, relative to courtship frequency in a female territory in each period

Period*	Type of courtship	Ranking of the spawning male			
		1st		1st or 2nd	
		%	(n)	%	(n)
When females began spawning before male courtships on MS					
MPS	Dips	55.6	(15/27)	88.9	(24/27)
	Caudal displays	60.0	(12/20)	95.0	(19/20)
EPS	Dips	62.5	(20/32)	93.8	(30/32)
	Caudal displays	52.0	(13/25)	92.0	(23/25)
When females began spawning after male courtships on MS					
MPS	Dips	43.3	(13/30)	76.7	(23/30)
	Caudal displays	50.0	(8/16)	75.0	(12/16)
EPS	Dips	33.3	(12/36)	61.1	(22/36)
	Caudal displays	44.0	(11/25)	76.0	(19/25)
MS	Dips	51.4	(19/37)	70.3	(26/37)
	Caudal displays	26.9	(7/26)	53.8	(14/26)

* See text and Figure 1 for explanation of each period.

Discussion

Female *Stegastes nigricans* were visited by a greater number of males and courted by caudal displays most frequently on the day prior to spawning, but received dips most frequently on the spawning morning. The spawning male chosen by a female was that which had performed dips and caudal displays in her territory more frequently than the other males on the morning and evening of the previous day. In addition, the spawning males performed dips more frequently than the other males on the spawning morning. However, male courtship at this time may not always be necessary for female choice, since the females often (49%) began spawning before males visited them to court. This suggests that females assessed males mainly by the frequency of the courtship displays received on the day prior to spawning. In fact, when females began spawning before male courtships, they tended to choose the male that had performed the greatest or second-greatest frequency of courtship displays on the previous day. In another damselfish, *Chrysiptera cyanea*, females also assess their mates on the day prior to spawning, males courting more frequently at that time rather than on the spawning day (Gronell, 1989).

Why do female *S. nigricans* choose males on the basis of courtship frequency on the day prior to spawning, rather than that on other days? Knapp and Kovach (1991) revealed that female *Stegastes partitus* used the frequency of male courtship displays to choose males of high parental quality, owing to the eggs under the care of low-courting males being more frequently eaten by the males themselves due to their low energy reserves. Because *S. nigricans* also shows paternal care and females choose mates mainly on the basis of frequency of courtship displays (Karino, 1995), they may in addition, be assessing the condition of said male and the likelihood of their eggs' survival under his care. Since male condition, such as degree of energy reserves, changes temporally, especially in fishes with paternal care (Unger, 1983; Marconato et al., 1993; Sabat, 1994), females should assess males using the most recent information on the males' traits that reflects their immediate condition (Zahavi, 1975; Zuk et al., 1990), such as courtship frequency (Bischoff et al., 1985; Kennedy et al., 1987). Male courtship immediately before spawning may provide the most recent information in *S. nigricans*, but females may lack the time to assess every males' courtship, since spawning

as early as possible reduces the risk of deprivation of their food resource (algae) by other diurnal herbivores during their absence from their territories, as has been suggested for other herbivorous and territorial damselfishes (Kohda, 1988). It was observed that when females began spawning later in the morning, a greater number of fishes intruded into their territory during the former's absence. Clearly, the optimum situation for female *S. nigricans* is the choosing of mates based on the male courtship frequencies received on the day prior to spawning.

In some cases, however, females used the frequency of courtships received on the spawning morning to assess their mates. Such females, having been courted less frequently by males on the previous day, began spawning later in the morning, owing to the need to acquire further information for mate assessment. Consequently, non-mated males necessarily performed courtship displays toward those females on the spawning morning. Assessment at that time seemed to be mainly by the frequency of dips, since although the frequency of caudal displays by subsequently spawning males tended to be higher than by non-spawning males, the difference was not significant.

According to the timing of female choice, males, especially the spawning males, performed courtship displays much more frequently on the day prior to spawning, and dips on the spawning morning, than on other days. This suggests that males understood the females' condition, concentrating their courting effort at the most effective time for female choice. Gronell (1989) suggested that the frequent displays by male *C. cyanea* was a response to the female's "soliciting" behavior, during her visit to the male territory on the day prior to spawning. In *S. nigricans*, such female behavior was not observed, males instead visiting females' territories for the purpose of courting. At present, it is unknown how males assess female condition on the day prior to the spawning, although the swollen abdomen in the latter would provide a visual clue on the morning of spawning.

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クロソラスズメダイの雌による配偶者選択のタイミングとそれに対する雄の効率的な求愛ディスプレイ

狩野賢司

クロソラスズメダイの雌が配偶者を選択するタイミングと雄の求愛ディスプレイの頻度変化を沖縄のサンゴ礁で調査した。本種は雌雄ともに縄張りを持ち、それらが集まってコロニーを

形成する。雌は早朝に雄の縄張りで産卵し、雄が孵化まで卵の保護を行う。雌が産卵する朝だけでなくその前日の早朝と夕刻にも、多くの雄がその雌の縄張りを訪れ、頻繁に求愛ディスプレイを行った。雌は産卵当日の朝に雄からディスプレイを受ける前に産卵を始めることが多く、これらの雌は産卵前日より多くのディスプレイを行った雄と産卵していた。これらの結果から、本種の雌は主に産卵前日の求愛ディスプレイ頻度によって配偶者となる雄を選択していることが示唆された。一方、産卵前日にあまり求愛を受けなかった雌は、産卵開始時刻を遅らせて雄か

らディスプレイを受ける傾向があり、これに対応して、雄は産卵前日ばかりでなく産卵が行なわれる朝にも頻繁に求愛していると考えられた。

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