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POPULATION DENSITY AND THE ECONOMICS OF TERRITORIAL DEFENSE IN A CORAL REEF FISH¹

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Abstract. We propose that in some species, local population density can strongly affect the economic defendability of a mating territory. This is so because the numbers of females and potentially interfering males determine allocations of time and energy to reproduction and defense. At low densities, allocations to defense should be small and territorial mating success should initially rise with local density, reflecting the supply of females. If defense takes priority over mating, higher population densities can create a situation in which the time or energy devoted to defense against other males detracts from allocations to reproduction. Thus a point is reached where territorial mating success declines with increasing density, as a function of the number of nonterritorial males.

We investigated these hypotheses by recording changes in the daily mating success of territorial males of the bluehead wrasse (*Thalassoma bifasciatum*) following experimental manipulations of local population size and composition. On large reefs, where mating population densities are already high, territorial mating success varied inversely with changes in overall population density and with changes in nonterritorial male numbers only; changes in female numbers had little effect. Thus at higher densities the demands of defense appear to be more important in determining mating success than the supply of available mates. Territorial mating success varied directly with population density changes only on the smallest experimental reef, where there were few nonterritorial males. The reduction of mating success at higher densities was correlated with a decrease in both the time spent in courtship and the efficiency of courtship itself. The effect of population density should be particularly important in species with short breeding periods and where the male contributes relatively little time or energy to each mating.

Key words: *Caribbean; coral reefs; fishes; mating success; population density; territoriality; Thalassoma; time-energy allocations; wrasses.*

INTRODUCTION

In this paper we investigate how changes in the population density surrounding a mating territory affect reproductive success of a resident territorial male. Although the numbers of available mates and potential intruders are clearly important factors in determining the economic defendability of a territory (see Brown 1964, 1975), most studies in the past have concentrated on the qualities of the territorial defender or the distribution of the resource being defended. Certainly if a male is old or large enough to control access to a resource which is critical to reproduction, his reproductive success could be limited by the number of females the resource can support. This is a common argument in much of the past work on territoriality (e.g., Willson and Pianka 1963, Brown 1964, 1969, Verner 1964, Verner and Willson 1966, Orians 1969, Schoener 1971, Altmann et al. 1977, Bradbury and Vehrencamp 1977).

By this reasoning, the mating success of a territorial male could be quite high if he is defending only a mating site and contributes no paternal care to the young, because the resource is essentially nondepletable. However, there often can be constraints to territorial

mating success which lie in the time or energy budgets of the resident male rather than in the space or energy content of the territory itself. We suggest that the time and energy allocations of territorial males depend in large part on the composition and density of the surrounding population, and we offer a set of simple hypotheses relating population density to territorial mating success. We then test these hypotheses through experimental manipulations of density in local populations of the bluehead wrasse, *Thalassoma bifasciatum*, a common coral reef fish of the western Atlantic Ocean.

POPULATION DENSITY AND MATING TERRITORIALITY

The effect that a local population has on the economic defendability of a territory can be complex, because both females and interfering males are involved. The critical question is how time and energy devoted to interactions with females and other males relate to mating success. For simplicity, consider a species where only the mating site is defended and where the territorial male has sufficient energy to maintain himself through the mating period. An increase in the number of females can raise the benefits derived from territoriality as long as the male has time available for increased mating activity. An increase in social inter-

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ference from other males could result in higher territorial costs because defense can detract from time otherwise available for mating. Three situations emerge:

1) Low population density. When population densities around a territory are low enough, a territorial male can have sufficient time for successful defense and for mating with all available females. In this case, increased time spent in male-male interactions does not decrease the total time spent in mating. If the time required for each mating is short relative to the entire mating period, territorial mating success should initially rise with increases in local population density, reflecting an increase in the supply of females.

2) Higher population densities. An increasing number of interfering males means that the territorial male must spend a greater amount of time in defense. If this activity takes precedence over the courtship of females (which it should if interfering males can disrupt or participate in a mating), a male's mating success should decline when many interfering males are present. In other words, time spent in male-male interactions places a limit on time available for mating activities. In this situation, territorial mating success should decline with increasing local population density, independent of the number of available females. Note that territories at this stage remain economically defendable in the sense that the reproductive success of a territory holder is higher than that of a nonterritorial male.

3) Economic undefendability. Territories can become too costly to maintain in areas where high densities of interfering males reduce territorial mating success to levels below that of males with other mating behaviors. The defending male may abandon the site entirely and move his territory to a less crowded area, or he may adopt nonterritorial behavior.

In summary, we suggest that territorial mating success should vary directly with local population density up to a certain point (a function of the supply of females), and then decline thereafter due to limitations imposed by interfering males. At very high local densities, territoriality should be abandoned.

The above arguments could be cast in terms of energy budgets as well. Whether a male is actually limited by time or by energy appears to depend upon the length of time during which females are available for mating, and upon availability of food supplies outside the mating period. If females are available over an extended length of time, males may not be able to gather and store enough energy reserves to maintain themselves over the entire mating period, and may thus be truly energy limited (e.g., Campanella and Wolf 1974). On the other hand, if males can maintain a territory over the entire mating period, their limitations may lie solely in time. In either case, time limitations may always be present in a proximal sense, because a male usually cannot court and defend at the same time.

The bluehead wrasse offers an excellent opportunity to investigate the relationship between population density and territorial mating success because (1) local populations are isolated and alterations of their characteristics can be easily made, (2) large males maintain territories in fixed locations, (3) females have an alternative to territorial mating, and (4) spawning occurs daily within a limited time period (see Warner et al. 1975). Most importantly, the species occurs over a broad range of mating population densities. The spawning site becomes increasingly more crowded on larger reefs, apparently because the locations used for mating do not increase in size proportionately with reef area (Warner and Hoffman 1980).

We expected that the mating success of a territorial male should vary inversely with changes in population size on larger reefs, where the effect of interfering males should be the strongest. In contrast, on the smallest reefs, territorial males have a better chance of controlling nonterritorial males. In this case, it should be the supply of females that is critical and mating success should increase directly with population size.

For this study, we focus on the short-term effects of experimental changes in local population size on the mating success of a particular territorial male. Elsewhere we discuss how the interaction of population density and territoriality can shape the evolution of mating systems and sexual life histories in this species (Warner and Hoffman 1980).

NATURAL HISTORY

The bluehead wrasse, *Thalassoma bifasciatum*, is one of the most conspicuous members of the western Atlantic coral reef community. Large aggregations can be found in shallow water at the up-current ends of most reefs, where individuals feed primarily on plankton. Major aspects of reproductive behavior in this species are described elsewhere (Reinboth 1973, Warner et al. 1975, Robertson and Hoffman 1977, Warner and Robertson 1978), and we repeat here only the pertinent details.

T. bifasciatum occurs in two color phases. Initial color phase individuals can be either males or females. The much less common terminal phase fishes are males, and they tend to be the largest individuals in any local population (Warner and Robertson 1978). Terminal phase males are the result of a permanent color change which the largest initial phase individuals undergo. If the largest initial phase individual is a female, she undergoes sex as well as color change as she enters the terminal phase. Changes in sex and coloration are under social control (Warner et al. 1975).

After a planktonic larval stage of unknown duration, individuals settle onto a reef and appear to remain there for their entire lives. The absence of adult immigration or emigration may be due to the lack of suitable refuge sites and high numbers of predators on the

sand and grass flats surrounding the reefs (Randall 1967, Hobson 1968, 1975). Experimentally reduced populations are replaced strictly by juvenile recruitment. When we changed population sizes through transplants (see below), population levels remained at the altered level for at least 6 wk (our longest observation period). We have never seen marked individuals from one reef appear on any other reefs. In other words, individuals will not leave a reef on which they were placed, even under crowded conditions. This makes adult transplant experiments feasible, without the complications of fish movements on and off reefs. It also means that all adult interactions take place within the same closed group.

Periods of sexual activity occur once a day for an average of 114 min ($N = 125$ spawning periods). During our study, the spawning period began as early as 1115, and as late as 1415. Most of the mating occurs on the down-current edges and projections of the reef. In the spawning area, large terminal phase males defend temporary territories of ≈ 10 m². They defend these areas vigorously against both initial and terminal phase males through direct, aggressive chases and lateral displays. Most aggression is directed toward initial phase males (91% of 39,153 aggressive acts observed). Terminal phase males return to and defend the same area over many weeks, and mate totally within their territories. On larger reefs, initial phase males also gather at the mating site and engage in spawning activities. They are nonaggressive and do not defend territories.

During most of the spawning period, a female remains at the up-current end of the reef and continues to feed on plankton. When an individual female is ready to spawn, she moves down-current to the mating site, spawns, and immediately returns to the feeding school. These down-current sites are probably favored because there is a greater chance that the pelagic eggs released there will be swept off the reef and away from reef-based planktivores (Randall and Randall 1963). Nearly all females spawn once a day (Warner et al. 1975, and see below).

Spawning itself consists of gamete release with external fertilization. Eggs are pelagic and there is no parental care. There are two main forms of mating behavior, pair-spawning and group-spawning (Warner et al. 1975, Robertson and Hoffman 1977). A pair-spawn consists of a female and a terminal phase male. If the terminal phase male is successful in courtship activity (described below), the female will rush toward the surface with him and both will release gametes at the apex of the rise. The female quickly leaves and the terminal phase male resumes courtship and territorial defense. An important aspect of this behavior is that the male will break off courtship and engage in aggression if he detects any initial phase males in the vicinity of the spawning site.

Group-spawning consists of a single female mating

with more than one male. A group of initial phase males will pursue a female for as long as 5 min and she eventually may spawn with as many as 100 males. Often, groups of initial phase males move into a terminal phase male's territory and begin to chase a female that is waiting to pair-spawn.

Pair-spawning can also suffer various forms of direct interference by initial phase and smaller terminal phase males. The males may rush into the territory and join a pair just as they are spawning, or unobtrusively follow a female into a territory and induce a pair-spawning as she is being courted by the territorial male. Because of this, large males aggressively exclude other males from their territories.

METHODS

We gathered data on reproductive behavior from 21 August to 31 October 1976, and from 1 March to 15 December 1977. The experiments were conducted between 1 October and 28 November 1977. All observations were made in the San Blas Islands, Republica de Panamá, near the island of Porvenir (Ogden and Buckman 1973, Robertson and Hoffman 1977).

Our experiments altered initial phase population density or composition on individual reefs. Because territorial males do not change the location of their territories over the course of weeks, we could measure the time budget and mating success of a given male for a series of days before and after a manipulation.

Possible manipulations include raising or lowering the size of the initial phase population as a whole (keeping sex ratio constant), or changing only the numbers of males or females. On all but the smallest reef, converse experiments were run at the same time on neighboring reefs of similar size. For example, if population levels were raised on one reef, they were lowered on a nearby, similar reef on the same day. This served to control for large-scale factors (e.g., changes in plankton supply, predation, or visibility) that could conceivably cause changes in mating success over many reefs. Our hypothesis about the effects of density was rejected unless the mating success of territorial males on the two reefs both changed, but in opposite directions.

Population size, sex ratio, and manipulations performed are given in Table 1. For efficiency, we often performed successive alterations on a particular reef. On all reefs, we would census the adult population at least five times before and after any manipulation. Censuses were taken in the morning, when nearly the whole population would be feeding in the water column at the up-current end of the reef. The observer would quickly swim in a grid pattern over the entire reef, recording the numbers of fishes and their color phases. The average coefficient of variation for all census series was 7.1%.

Initial phase sex ratio for a reef was determined by capturing at least 100 individuals by means of a lift net

TABLE 1. Initial population characteristics and manipulations performed on the San Blas study reefs. Values in parentheses are the number of successive alterations of the stated type performed on a particular reef.

Reef	Population size	Proportion of initial phase that is male	Manipulations		
			Overall initial phase population	Initial phase males only	Initial phase females only
A	304	0.24	Decreased(3)	Increased(1)	
B	217	0.16	Increased(2)	Decreased(1)	
C	583	0.42	Increased(1)	Decreased(1)	
D	250	0.40			Increased(1)
E	889	0.26			Decreased(1)
F	46	0.09	Decreased(1)	Increased(1)	

baited with crushed sea urchins (*Diadema antillarum*). The fishes were kept in a holding net at the surface, sexed by inspection of the genital papilla, and then returned to the reef. The accuracy of our sex identifications, verified by dissection of 175 individuals, was 100%.

For the population manipulations, initial phase individuals were captured by means of a lift net and transported to other reefs. Transport time was always <5 min. In population augmentation experiments, the sex ratio of the added individuals was adjusted to conform to our previous estimate of the actual sex ratio on the experimental reef. These adjustments were necessary because sex ratio varies from reef to reef (Table 1; Warner et al. 1975, Warner and Hoffman 1980). Single-sex alterations were accomplished in similar fashion, except, of course, the sex ratio on the experimental reef was altered as a result of the manipulation. For all experiments, excess captured individuals were placed on designated large reefs that were not used in this study for any other purpose.

Initial phase males and females appeared unaffected by capture or transplantation. Within 30 min, the individuals were feeding normally. Males and females marked by fin-clipping (20 of each on two different reefs) were seen mating the day after being transplanted. Our censuses revealed no changes in the number of terminal phase males nor any detectable losses of individuals over the course of the investigation, indicating that our manipulations did not result in increased adult mortality.

Each experiment was focused on a single territorial male in the same locality. For this study, we observed the largest territorial male on each manipulated reef. These males were followed for the entire spawning period, which began with the initiation of territorial defense and ended when courtship ceased and females were no longer in the mating area. We always waited at least 30 min after the last courtship to ensure that no further spawning took place, and our observations throughout the day indicated that mating occurs only within the designated spawning period.

We recorded 5 d of reproductive activity immediately prior to a manipulation, followed by 5 d of post-

manipulation observations. Data were collected on small waterproof tape recorders and slates while snorkeling on the surface. We alternated 15-min intervals of recording event frequency data on a slate with 5-min intervals where the activity was continuously recorded on tape. Frequency and duration estimates were made for the following behaviors:

- 1) Aggression (given or received): aggressive acts consisted of an active chase when directed at initial phase males or wandering terminal phase males; in interactions between adjacent territory owners, a chase was often preceded by a series of lateral displays, with the fins held stiffly erect. The time spent in aggression includes only lateral displays and direct chases. Each individual chase was recorded as a separate event.
- 2) Courtship: this is identified by rapid vibrations of the terminal phase male's pectoral fins. Each time courtship was initiated, it was scored as a separate event. Thus a single female might be courted several times.
- 3) Spawning: the numbers of pair-spawns (mutual upward rushes of the male and female) and interference spawns (a pair-spawn joined by one or more other males) were recorded, as was the number of interfering males.

Daily mating success was estimated as the total number of spawnings in which a male participated, each discounted by the total number of males participating. Thus a spawning in which a territorial male was joined by a single interfering male was considered worth half of a pair-spawn.

For the most part, our analyses consist of simple comparisons of territorial mating success before and after a population manipulation. In broader comparisons, where data from several experiments were combined, all changes in variable values were expressed as ratios: the mean value of a particular parameter before a manipulation divided by the mean value afterward. For example, a mating success ratio with a value <1 indicates that mating success increased after a particular manipulation. Changes in population sizes for each sex were expressed in a similar fashion.

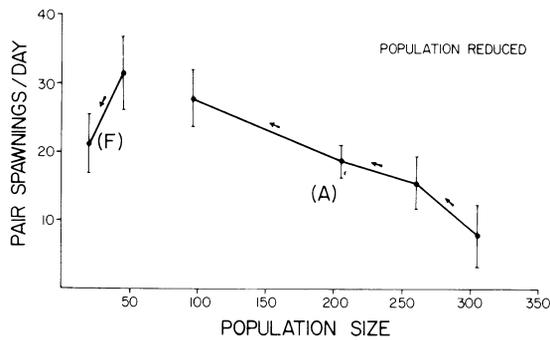


FIG. 1. Changes in a territorial male's daily mating success associated with reductions in initial phase population size. Sampling extended for 5 d in all cases. Brackets are 95% confidence intervals of the mean. Reef names are in parentheses.

RESULTS

Numerical alterations of entire populations

In all of the contrasting pairs of experiments involving alterations of the size of the entire initial phase population, mating success of observed territorial males changed in opposite directions on the two reefs. This indicates that the observed changes were not due to large-scale temporal fluctuations.

In addition, no manipulation resulted in a significant change in either (1) the proportion of total spawnings that were interfered with by nonterritorial males or (2) the average number of males participating in an interference spawning. Thus reported changes in mating success were due to changes in the actual number of spawnings completed by the terminal phase male.

When population size was experimentally reduced, mating success declined on the reef with the smallest population (Reef F, Table 1), but increased on a reef (A) with a much larger population size (Fig. 1). Three successive reductions in population size on Reef A, from a beginning population of 304 to an ending population of 97 initial phase individuals, resulted in significantly increased mating success of the observed terminal phase male (Kruskal-Wallis test, $P < .005$). Note that since initial phase sex ratio on this particular reef was 24% male, the increase in mating success occurred even though the actual number of females on the reef was reduced from 231 to 74.

The reduction of mating success with a decrease in population size on the smallest reef (F) was not surprising, because the original population size of initial phase males was only four. On even smaller reefs ($n < 20$), the prediction becomes trivial, since initial phase males are absent (Warner and Hoffman 1980).

The converse experiments of increasing population size on larger reefs had a negative effect on territorial male mating success (Reefs B and C, Fig. 2). Two successive population increases on a single reef (B,

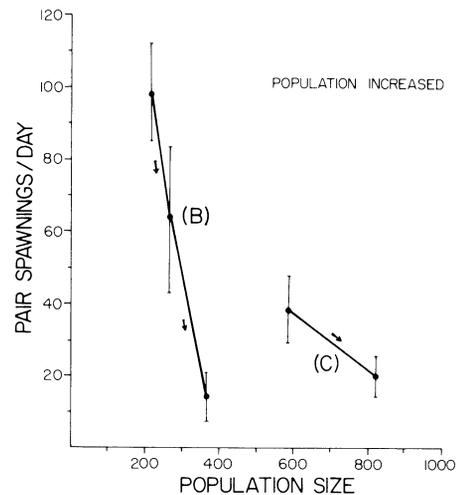


FIG. 2. Changes in a territorial male's daily mating success associated with increases in initial phase population size. Format as in Fig. 1.

Table 1), from 217 to 265 to 362, resulted in drastic, significant reductions in the mating success of the observed terminal phase male (Kruskal-Wallis test, $P < .003$). This occurred even though five times more females than males were added to the reef.

On reefs even larger than A, B, or F, the mating territories are located up-current from the most favored mating sites, apparently as a reaction to the extremely high initial phase male densities at the down-current end of the reef (Warner and Hoffman 1980). However, a separate population augmentation (+40%) on one of these larger reefs (Reef C, Table 1) had an effect similar to that seen before: the mating success of the observed territorial male was reduced to approximately half of its former level (Fig. 2).

For all but the smallest reef, the predicted negative relationship between changes in population density and territorial male mating success was significant (Sign test, $P < .05$).

Numerical alterations of single sexes

The above results indicate that, on all but the smallest reef, the number of interfering males strongly affects the economic defendability of territories. Single-sex alterations further substantiate this idea. Changes in the number of initial phase males on three larger reefs (A, B, and C) had a strong effect on territorial male mating success in the predicted directions (Fig. 3).

We added 20 males to a small reef (F) in order to test further the hypothesis that territorial male success is not affected by the number of initial phase males in small populations. This increased the resident initial phase male population tenfold. The mating success of the territorial male was not lowered by this manipulation (Fig. 3). In fact, the mean level rose to a value

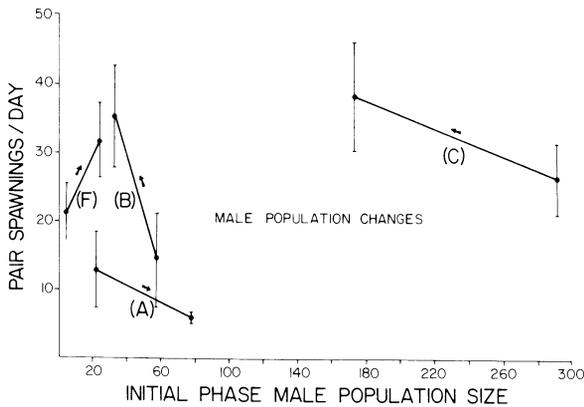


FIG. 3. Changes in a territorial male's daily mating success associated with alterations in initial phase male population size. Format as in Fig. 1.

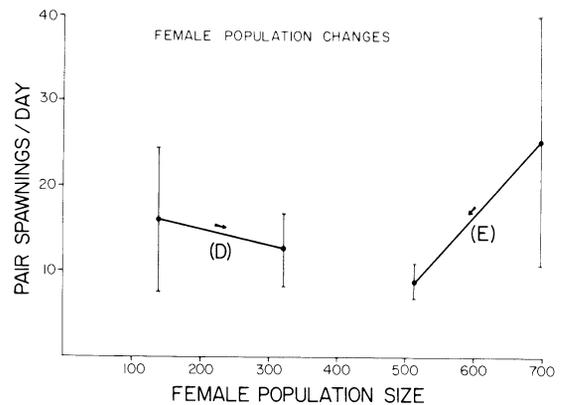


FIG. 4. Changes in a territorial male's daily mating success associated with alterations in female population size. Format as in Fig. 1.

higher than the number of females on the reef! The terminal male in this case retained complete control of the spawning site, but females apparently became more cautious in their mating activity. They would often initially spawn with the terminal male without releasing eggs, and then spawn again, with egg release, immediately thereafter. Since visibility conditions often precluded determination of whether there were eggs present in any particular spawning, we always counted all spawning rushes as actual matings. Although false spawning was noted on other reefs, it was never seen with as much regularity as on this small reef after the experimental addition of males.

Alteration of female numbers on two larger reefs (D and E) gave more equivocal results than those from the male manipulations. In this case, territorial male mating success declined both where female numbers were increased and where females were removed (Fig. 4). This suggests that some larger scale variable, rather than female numbers, was affecting mating success. The effect of females should not be totally discounted, however, because the decline in mating success on the reef where females were removed was significant (Mann-Whitney U test, $P = .05$).

By combining the results from all large reef manipulations in a multiple regression analysis, it is possible to test further the relative effect of changes in number of nonterritorial males vs. changes in number of females on territorial mating success in larger populations. The results clearly indicate the overriding importance of initial phase male numbers (Table 2). Changes in male numbers accounted for nearly all of the explainable variation in mating success of territorial males.

Behavioral mechanisms

In what manner do interfering males reduce territorial male mating success on larger reefs? We can explore this question through an analysis of the cor-

relation matrix of changes in activity parameters measured before and after the experiments (Table 3). Two major factors appear to contribute to changes in mating success when the density of interfering males is altered. First, the time spent in defense increases with the density of interfering males. The time spent in courtship is negatively correlated with time spent in defense, and mating success, in turn, declines when less time is spent in courtship.

Second, interfering males affect the efficiency of courtship as well. As the density of initial phase males increases, the average duration of aggressive bouts declines; this means that each interfering male is chased for a shorter distance. The closer proximity of initial phase males appears to lower greatly the effectiveness of each courtship bout in eliciting a mating. In other words, the duration of aggressive events is significantly correlated with matings per courtship event, and this, of course, is a strong factor in determining overall mating success. Reduced efficiency of courtship could result from increased reluctance of the female to mate when potentially interfering males are nearby, from the terminal phase male breaking off courtship more often to attack other males, or both. Since the courtship duration does not drop signifi-

TABLE 2. Effects of alterations of the numbers of initial phase males and females on changes in territorial male mating success.

	df	Sum of squares	F value	P	r^2
Model	3	3.59	5.37	.031	.70
Male alterations	1	3.34	15.01	.006	
Female alterations	1	0.01	0.08	.779	
Interaction	1	0.22	1.01	.348	
Error	7	1.56			

TABLE 3. Correlation coefficient matrix of changes in the number of initial phase males, changes in mating success and other activities of territorial males, and the efficiency of courtship. Probability values are given in parentheses.

	Male numbers	Mating success	Time in aggression	Aggressive bout duration	Time in courtship	Courtship bout duration	Matings per courtship bout
Male numbers	1.00	-.81 (.003)	.70 (.016)	-.55 (.079)	-.45 (.167)	-.33 (.320)	-.48 (.134)
Mating success		1.00	-.50 (.119)	.55 (.078)	.68 (.025)	.49 (.124)	.68 (.022)
Time in aggression			1.00	-.18 (.605)	-.56 (.076)	-.50 (.123)	-.10 (.766)
Aggressive bout duration				1.00	-.09 (.784)	-.11 (.756)	.69 (.019)
Time in courtship					1.00	.88 (.001)	.14 (.675)
Courtship bout duration						1.00	.24 (.475)
Matings per courtship bout							1.00

cantly when initial phase males are added, female reluctance may be the more important factor.

DISCUSSION

A hypothesis has real value when its generality can be translated into specific, falsifiable predictions. With *Thalassoma*, we were aided by the fact that the mating population densities in this species occur over a broad range of values which depend on local population size and area of the mating site. Thus we could make qualitative predictions about changes in territorial mating success under widely different conditions of density.

The results for *Thalassoma* appear to be consistent with these predictions. In most cases, the daily mating success of a territorial male varies inversely with changes in local population density. Because the numbers of both interfering males and available females changed when density was altered, the demands of defense appear to be a more critical determinant of mating success than does the supply of potential mates. When faced with increased numbers of initial phase males, territorial males increase time spent in defense, decrease time spent in courtship, and suffer a lower mating efficiency while courting. The only exception to this pattern is also consistent with the hypothesis: on the smallest reef, where few initial phase males were present, territorial mating success varied directly with population density.

These are short-term results from rather drastic alterations of population density. Over longer periods, one would expect responses to changes in mating success on the part of the territorial male. In *Thalassoma*, terminal phase males on larger reefs do not establish territories in down-current localities where there are high densities of initial phase males, even though most females mate in these localities (Warner and Hoffman

1980). We suspect that territories are simply economically undefendable in these areas.

Several other authors have suggested that higher levels of defensive activity can lead to increasing constraints on the mating activities of a defending male (Estes 1969, Bartholomew 1970, Campanella and Wolf 1974, Geist 1974, LeBoeuf 1974, Constanz 1975). However, these constraints are not always reflected in the mating success of the territorial individual. At low population levels, increasing density can result in higher mating success (e.g., Campanella and Wolf 1974, LeBoeuf 1974; Emlen and Oring 1977 cite evidence for this occurring to a dominant female in a polyandrous species). Even as this is occurring, the relative mating success of the territorial individual can decline. That is, as population density increases, the proportion of available females mated by the territorial male declines, but at a rate slower than the increase in the supply of those females (Campanella and Wolf 1974, LeBoeuf 1974, suggested in Bartholomew 1970). These conditions also lead to an increase in the overall success of subordinate males (LeBoeuf 1974, Emlen 1976, Howard 1978).

Eventually, population densities should reach a point where further increases will lower the absolute mating success of a territorial male, as was shown here for *Thalassoma*. Geist (1974) suggests that this would be true for some ungulates, as do Campanella and Wolf (1974) for dragonflies, but data are generally lacking. A most illuminating series of results are those of LeBoeuf (1974) for elephant seals: for most years, when population density increased, the mating success of the dominant male increased, but his share of the total females available declined. At the highest densities in one location (Point Harem, 1972 and 1973), the absolute mating success declined as well. In both

of these years, population numbers of Point Harem increased $\approx 20\%$ over the previous year, but the absolute mating success of the dominant male declined by $\approx 20\%$.

We have suggested that if defense must take priority over reproduction, then reproductive success must decline if there is not enough time and/or energy for both sorts of activities. This has been termed "aggressive neglect," and can apply to both intra- and interspecific defense (Hutchinson and MacArthur 1959, Ripley 1961). It is important to remember that the loss due to aggressive neglect does not necessarily lower relative fitness to maladaptive levels. Although low mating success may be associated with a territory in a high-density population, it may still be higher than that of a nonterritorial male. Conversely, territoriality can still be adaptive in low-density populations, up until a point is reached where it may be more profitable to seek mates actively than to remain in one place and attempt to attract them.

Although constraints in time and energy can potentially be critical factors in determining the mating success associated with territoriality, in many circumstances they may play a minor role. This should be true in species where the breeding period is long or where there is no alternative to territorial mating, especially if each female exacts a relatively large time and energy commitment from the male. Because the breeding periods of the bluehead wrasse are short and frequent, the effect of population density on male mating success is immediately apparent. It may be much less so in long-term seasonal breeders where time waste carries a smaller penalty in loss of fitness (see Parker 1974).

Even if an organism fits criteria in which one might expect short-term time or energy constraints to be important, a specific prediction regarding the direction of change in territorial mating success with changes in local density requires some idea of (1) the present time and energy budgets of territorial males and (2) the priorities of the potential defender to activities which place further demands on time and energy. These priorities can depend on the risks associated with different activities such as courtship (see Robertson and Hoffman 1977), and on the physical aspects of mating itself. When fertilization is external, mating may never be completely safe from interference, and mating success can depend on keeping potential interferers away from the mating site. Intruders cannot be ignored, and territorial defense should take precedence over mating. With internal fertilization, mating can be inviolate beyond a certain point in time, and territorial defense may be secondary to courtship and other behaviors influencing female choice of mates.

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