

**Activity budget of the princess parrotfish (*Scarus taeniopterus*): a comparison between daylight and sunset periods**

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## **Abstract**

Most animals are active either during the day, night, or twilight, and transition periods between these times exhibit interesting behavior. Actions may be related to avoiding predators, seeking shelter, defending territory, feeding, or other interests. Herbivorous fishes on coral reefs, such as parrotfishes, forage constantly throughout daylight periods due to inefficient feeding and reliance on light. At sunset, parrotfishes seek cover under which to rest at night, to conserve energy and avoid predation. To do so, parrotfish decrease feeding and increasing migration and aggression to do so. This study compared how initial phase (IP) and terminal phase (TP) princess parrotfish (*Scarus taeniopterus*) allocate time between daylight and sunset periods, specifically regarding time spent feeding and being aggressive. Observations were performed using SCUBA at Yellow Sub dive site on Bonaire, Dutch Caribbean. Individuals of *S. taeniopterus* were followed for 1 min (to allow for acclimatization), followed by 5 min of behavioral observation. Percent time spent on each behavior was calculated and averaged across each category (e.g. IP, daylight), and mean percent time spent feeding and being aggressive were tested using a two-way analysis of variance (ANOVA), with phase and time of day as factors. Both IP and TP fish had a higher mean percent time feeding and a lower mean percent time being aggressive in the morning than at sunset, and time of day and phase were both significant factors affecting variation in both behaviors. The results of this study give insight into the adaptations parrotfish have developed to increase survival.

## **Introduction**

Transition periods between day and night show a marked difference in behavior of many animals, such as cattle, plankton, salmon, and tropical reef fishes (Gonyou and Stricklin 1984; Enright 1977; Fraser et al. 1993; Hobson 1972). Most animals, terrestrial and marine, are diurnal, nocturnal, or crepuscular: active during one part of the day, and inactive the rest of the time. Adaptations for one light level tend to reduce ability in another (Fraser et al. 1993), resulting in a difference in abundance of visible species between day and night in a habitat. The period between daylight and darkness is transitional, when diurnal animals find cover for the evening, and nocturnal ones emerge to hunt. During transitions, animals may be searching for prey, avoiding predators, seeking shelter, defending territory, feeding, migrating, or behaving in any number of unique ways (Helfman 2011). Animals may also display more unique behavior, such as the daily vertical migration of plankton that occurs across many species and locations (Enright 1977).

Herbivorous fishes on coral reefs are most abundant and active during the daylight hours, because of reliance on vision for foraging (Lewis 1986). One of the most abundant groups of herbivorous fishes is the parrotfishes, family Scaridae (Ogden and Buckman 1973). Parrotfish use fused, beak-like jaws to scrape algae turf from dead coral (Guidetti and Boero 2002), consequently ingesting calcium carbonate, which is used to grind plant matter in their pharyngeal mill (Randall 1967). Inefficiency of feeding and low nutrient content of algae means parrotfish must consume large quantities during the day to satisfy energy needs. Parrotfish must spend much of the day feeding; *Sparisoma amplum* may take 50 or 60 bites per minute during active periods (Bonaldo et al. 2006), and adults of *Scarus vetula* take 16,000-25,000 bites per day (Bruggemann et al. 1996).

At night when low light levels make foraging difficult for parrotfish, resting conserves energy and reduces oxygen consumption (Curran 1992). At dusk, parrotfish settle on the soft bottom, usually under partial cover, and stay quiet through the night, sometimes secreting mucus bubbles for protection from nocturnal predation (Hobson 1965). The function of the cocoons is not fully understood. Individuals may form envelopes only when injured or under stress (Hobson 1965). A cocoon may mask an individual's scent, reducing effective predation by morays (Winn and Bardach 1959), since moray eels are nocturnally active and use smell to locate prey (Bardach et al. 1959).

During the transition period between daylight and darkness, there is a marked change in behavior of many fish on the reef, including parrotfish. Transition behaviors are usually manifested as a decrease in feeding accompanied by an increase in migration and aggression (Hobson 1972), to search for and subsequently protect nighttime resting locations (Hobson 1965). Low-light conditions are favorable for large predators, so diurnal fishes, such as parrotfish, must roam cautiously before settling down for the night (Hobson 1973). Aggression is necessary especially for terminal phase (TP) males, which defend their territories to protect their initial phase (IP) female mates from other males who may intrude during their sunset migrations (Streelman et al. 2002).

This study aims to determine how the princess parrotfish (*Scarus taeniopterus*) allocates time for different behaviors during the day versus at sunset. The purpose is to determine whether time of day significantly affects time allocated to feeding versus aggressive behaviors by testing the following hypotheses:

H<sub>1</sub>: The mean percent time *S. taeniopterus* spends foraging will be higher during daylight hours than at sunset for both developmental phases.

H<sub>2</sub>: The mean percent time *S. taeniopterus* spends being aggressive will be lower during daylight hours than at sunset for both developmental phases.

Studying behavior can give insight into the adaptations a species has acquired to increase fitness and aid survival. Behavior shows how a species interacts with its environment, including other species (Hobson 1972). Studying behavior reveals adaptations for coexistence. A change in behavior reflects changing conditions, such as increased possibility of predation, which may not be apparent to the observer.

## **Materials and Methods**

### Study organism

*S. taeniopterus* is one of the parrotfish species that is known to produce a cocoon at night (Curran 1992). Individuals of this species have also been known to show interesting behavior at sunset, such as tailstands, when an individual assumes a head-up position in the water column as daylight fades, a behavior which is not fully understood, but is thought to enlarge visual fields to detect predators and territory intruders (Dubin and Baker 1982). The range of *S. taeniopterus* is throughout the Caribbean, South Florida, Bahamas, and Bermuda, and is common around the island of Bonaire, Dutch Caribbean (Fig 1). All observations were performed at Yellow Sub dive site (12°09'36.47"N, 68°16'55.16"W), on the west coast of the island from September through November, 2012. Bonaire has a tropical climate, with a fringing reef close to shore. Parrotfish are very abundant at Yellow Sub, and the site is easily accessible by shore. The site is popular with divers, so fish are largely not disturbed by their presence. The visibility is very good

underwater, so observations are possible without getting very close to the parrotfish and there is a minimal effect on behavior.

Both IP and TP stages of *S. taeniopterus* were included in the study. Juveniles were excluded from the study since there may be a difference in behavior from adults. *S. taeniopterus* has a similar body shape, size, and markings to *S. iserti* (striped parrotfish), and were differentiated by markings along the top and bottom of the tails of both phases, which are absent in *S. iserti*.

### Behavioral Observations

All behavior was observed using SCUBA. The observation portion of each dive was approximately 40 min, at depths between 11 and 14 m, which has the highest parrotfish density at Yellow Sub according to Adler (2009). Daytime dives took place in the morning between 09:00 and 12:00 h. Hobson (1972) documented cover-seeking behavior that started 15 min before sunset and ended 45 min after sunset. However, during preliminary observations, it became apparent that behavioral observations without lights were not possible more than about 20 min after sunset, and fish are disturbed by artificial lights (Hobson 1965). Therefore, sunset behavioral observations began 20 min before sunset, and continued until 20 min after sunset. Sunset times were determined by a table produced online by the United States Naval Observatory (USNO) Astronomical Applications Department.

Parrotfish are small enough to allow observers to follow them closely in the field (Ogden and Buckman 1973). Once an *S. taeniopterus* individual was selected, it was followed for 1 min (to allow for acclimatization), then 5 min while recording behavioral data. The observer

remained at a distance of no closer than 2-3 m, above and behind the fish when possible, to avoid disturbing behavior, as suggested by Dubin and Baker (1982). Developmental phase was recorded (IP or TP), and equal numbers of each phase were followed at each time of day. Behavior was categorized as feeding, defecating, swimming, stationary, aggression, and other behavior. Aggression was subdivided into aggressor or offender, and whether the interaction was with another *S. taeniopterus*, another parrotfish, or a non-parrotfish.

Swimming occurs between most other activities as a transition behavior that is non-specific, and the underlying purpose is not clear. Therefore, swimming was considered a separate behavior, recorded by subtracting cumulative time spent on other behavior from total observation time for each individual. All other behaviors were timed using a watch with seconds. One continuous feeding period was defined as the amount of time an individual spent hovering at a single location. If the individual moved to another location, it was considered a new feeding period, and the interim was counted as swimming. Aggression was defined as apparent defense of territory, mostly as direct chasing. Fin flaring was not counted as aggression even though it is an aggressive display, because an individual could be doing another behavior such as feeding simultaneously.

Other general notes about behavior were also recorded. If an individual was lost or traveled too far out of the proposed depth range, its behavior was included in the analysis to avoid bias. If an individual approached an observer, the observer remained as still as possible to avoid disturbing behavior.

Data analysis

For each fish followed, percent time spent on each behavior was calculated, and then averaged over all fish. Mean percent time spent in feeding and aggressive activity were each compared between daylight and sunset periods for each developmental phase using a two-way analysis of variance (ANOVA). Using the statistical program StatView, percents were arcsine transformed so their distribution was approximately normal, and then tested. An alpha level of  $\alpha=0.05$  was used for significance.

## **Results**

Data were collected over a total of 10 daylight dives and 12 sunset dives. For each pair of variables (phase and time of day; e.g. IP, daylight), 31 fish were followed, for a total of 124 fish (Fig 2).

Both IP and TP fish had a higher mean percent time feeding in the morning than at sunset (Fig 3). An ANOVA test on feeding (Table 1) found time of day to be a significant factor explaining variation in percent time feeding ( $p<0.0001$ ). Phase was also a significant factor, although not as strong ( $p=0.04$ ). There was a significant interaction between phase and time of day affecting feeding ( $p=0.002$ ).

Both IP and TP fish had a lower mean percent time being aggressive in the morning than at sunset (Fig 4). An ANOVA test on aggression (Table 2) found phase to be a significant factor explaining variation in percent time being aggressive ( $p<0.0001$ ), as well as time of day ( $p=0.005$ ). There was a significant interaction between phase and time of day affecting aggression ( $p=0.01$ ).

## Discussion

Both developmental phases of *S. taeniopterus* had a higher mean percent time feeding during daylight than at sunset, supporting the hypothesis that on average, *S. taeniopterus* feeds more during daylight compared to sunset periods. Time of day was a more significant factor affecting feeding than developmental phase, showing that variation in feeding is explained most by time of day. Previous studies have had similar findings that during the sunset transition period, behavioral changes include decreased feeding for many reef fish (Hobson 1972). A small amount of feeding by some TP fish was observed at sunset, but no feeding by IP fish was observed. This may be due to the timing of observations, as TP males stop feeding later than IP females. TP fish are bigger, require more food to survive, and are less vulnerable to predation, so feeding for longer after the sun starts setting and risking predation has more benefits than costs. When feeding, IP fish seemed to have longer continuous periods of taking bites, hovering near one head of coral, while TP fish would take a few bites before swimming to another location to feed or to chase away another *S. taeniopterus*. Some *S. taeniopterus* were observed to join feeding schools comprised mostly of blue tang, but also including Spanish hogfish, various parrotfish, sergeant major, trumpetfish, schoolmaster, and trunkfish. This group foraging behavior has been previously documented, as some algal mats are well defended by damselfish, so forming a school means individual biting rates increase because individuals suffer attacks less frequently than they would alone (Foster 1985).

The mean percent time spent being aggressive was lower during daylight than at sunset for both developmental phases, as hypothesized. This study supports previous findings that among the changes during the sunset transition period are increased aggression (Hobson 1972).

Aggression was mostly directed at other *S. taeniopterus*. TP males were more aggressive than IP females at both times of day, as expected, because they must defend their territories and mates from other males (Streelman et al. 2002). Aggression is increased at sunset to address the increased migration of other fish into territories (Hobson 1972), but phase was a more significant factor affecting aggression than time of day. Aggression seemed to become more pronounced as time went on during sunset periods, but this study did not examine changes in behavior over time within the sunset period. There also seemed to be more fin flaring during sunset than daylight periods, but this behavior was not studied.

Time of day and developmental phase each separately affected the behavior of *S. taeniopterus* significantly. There was also a significant interaction between time of day and phase, meaning much of the variation in the results for feeding and aggression is due to the combined effect of both factors. Although differences in percent time swimming were not statistically tested, means were higher at sunset than daylight times for both phases. During sunset periods, some *S. taeniopterus* were observed performing tailstands, a head-up position in the water column during sunset periods thought to aid detection of predators and territory intruders (Dubin and Baker 1982). Some individuals also were observed swimming under coral heads and hovering stationary there for short periods of time, as though trying out resting locations, but were not observed to return to any of them later, contrasting with previous studies showing strong affinity of some fishes to specific resting locations (Hobson 1972). Some *S. taeniopterus* were observed to swim under a coral head and stay there for the rest of the observation period, explaining the high mean percent time spent stationary during sunset periods.

This study was limited in time and space. Future studies should take place over a longer period of time, to include seasonal changes such as spawning behavior. Studies should also

incorporate more locations, as due to the territoriality of parrotfish and small size of the study location, it is likely some *S. taeniopterus* were observed more than once. Future work could follow one individual over several entire sunset periods to examine the level of affinity of individuals to certain locations. Through studying the behavior of *S. taeniopterus*, inferences can be drawn about the adaptations it has acquired to increase fitness and survival. Halting feeding in favor of increased aggression and migration during sunset periods allows individuals to protect suitable nighttime resting locations and avoid predation. Such adaptations are just one example of how coexistence is achieved among cohabiting organisms, the keystone of ecological success.

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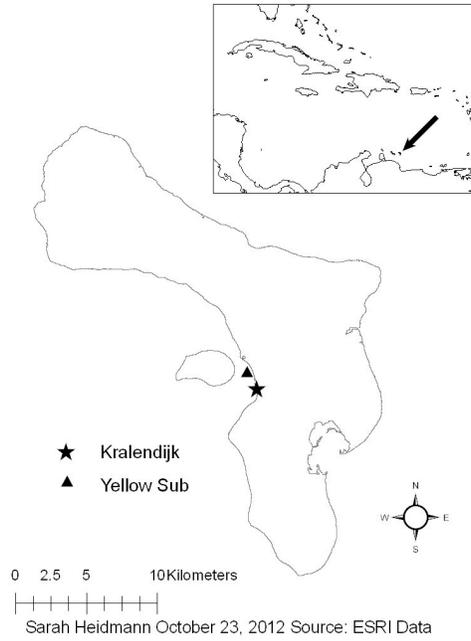


Fig 1. Map of Bonaire, Dutch Caribbean in the context of the Caribbean Sea, insert above. Kralendijk, the capital, is marked with a star. The study site, Yellow Sub, is marked with a triangle.

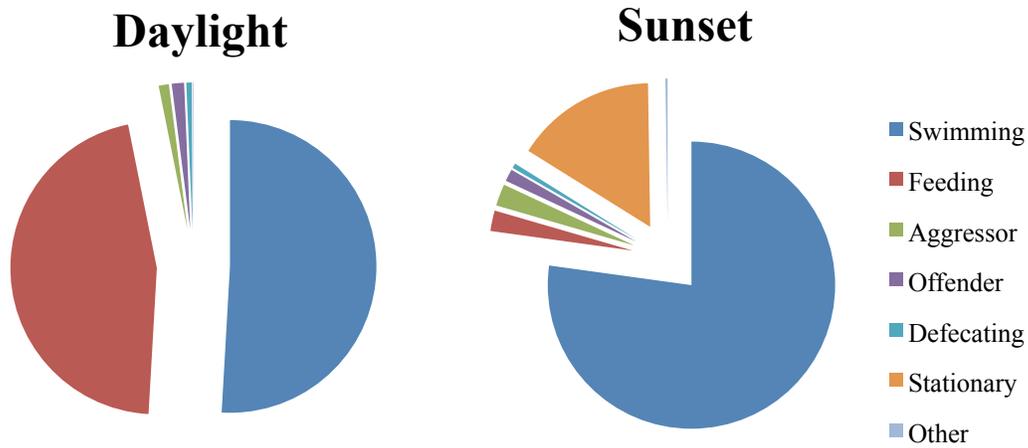


Fig 2. Comparison of mean percent time spent in various behaviors of initial phase and terminal phase *Scarus taeniopterus* during daylight (0900-1200 h) and sunset (20 min before and after sunset), n=62 (total number of fish=124). Behaviors were categorized as swimming (dark blue), feeding (red), aggressor (green), offender (purple), defecating (light blue), stationary (orange), and other (periwinkle).

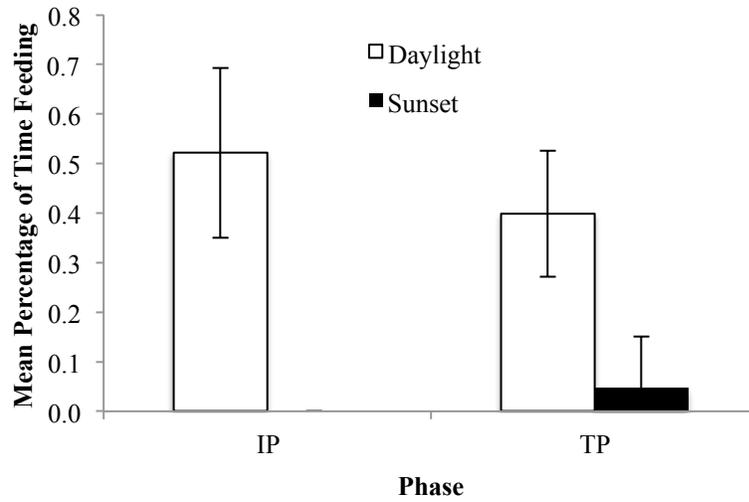


Fig 3. Comparison of mean percent time feeding ( $\pm$ SD) between initial phase (IP) and terminal phase (TP) *Scarus taeniopterus* at daylight and sunset (n=31). White bars represent daylight periods, and black bars represent sunset periods.

Table 1. Two-way analysis of variance (ANOVA) table for percent time feeding (arcsine transformed) of *Scarus taeniopterus*. Factors tested each had two levels, developmental phase (IP or TP) and time of day (day or sunset)

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Phase	1	0.082	0.082	4.161	0.0436
Time of Day	1	6.718	6.718	339.335	<0.0001
Phase*Time of Day	1	0.301	0.301	15.227	0.0002
Residual	120	2.376	0.02		

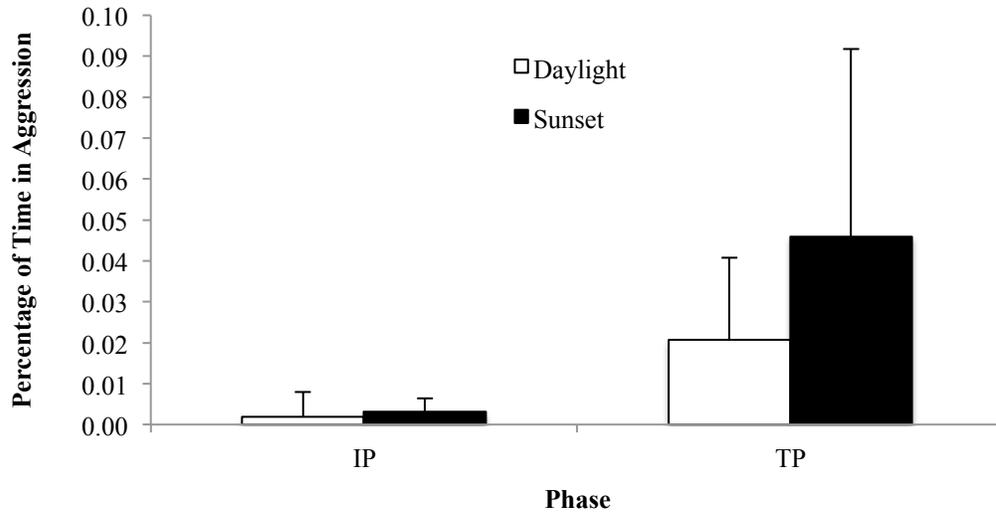


Fig 4. Comparison of mean percent time spent being aggressive ( $\pm$ SD) between initial phase (IP) and terminal phase (TP) *Scarus taeniopterus* at daylight and sunset (n=31). White bars represent daylight periods, and black bars represent sunset periods.

Table 2. Two-way analysis of variance (ANOVA) table for percent time spent being aggressive (arcsine transformed) of *Scarus taeniopterus*. Factors tested each had two levels, developmental phase (IP or TP) and time of day (day or sunset)

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Phase	1	0.029	0.029	44.527	<0.0001
Time of Day	1	0.006	0.006	8.362	0.0046
Phase*Time of Day	1	0.004	0.004	6.731	0.0107
Residual	120	0.079	0.001		