Locomotor compensation in the sea: body size affects escape gait in parrotfish

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There has been surprisingly little attention to adaptive variation in the locomotor speed and gaits used in antipredator behaviour. We investigated the relationship between body size and the use of two alternative gaits by three species of parrotfishes (princess, *Scarus taeniopterus*; queen, *Scarus vetula*; stoplight, *Sparisoma viride*) escaping an approaching snorkeller in their natural fringing reef habitat in Barbados. As body size increased from about 7 to 58 cm, the proportion of fish using an energetically more costly but relatively faster escape (body and caudal fin swimming) rather than a less costly and relatively slower escape (paired fin swimming) decreased from 100% to 0%. In contrast, the study confirmed previous research showing that larger fish fled at greater distances from the snorkellers, behaviour which would have increased safety but incurred higher opportunity costs. We conclude that small fish require a more expensive gait to attain an adequate escape speed. Thus, the gait used for escaping shows a compensatory relationship with body size because small individuals with lower swimming capacity use a higher proportion of that capacity. On the other hand, flight initiation distance shows cospecialization with body size because larger fish with higher swimming capacity further reduce their risk by fleeing sooner.

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Avoiding predation involves a sequence of interactions between potential prey and potential predators in which the behaviour of the potential prey changes according to the context (Lima & Dill 1990). Animals often demonstrate adaptive plasticity in the threshold at which they initiate these defensive responses or in the intensity with which they perform them, with variation related to the current state of the individual and the environmental context (Lima & Dill 1990). Although the majority of studies of antipredator behaviour focus on only one or a few closely related components of the sequence, there is growing interest in how the response thresholds and response intensity for different components relate to each other and to other predation-reducing traits such as morphological defences (Endler 1995; DeWitt et al. 1999; Sih & Bell 2008; Rodriguez-Prieto et al. 2008).

Locomotor decisions such as speed and gait have been investigated much less frequently than other components of antipredator behaviour such as vigilance, flight initiation distance (FID, the distance from an approaching threat at which an animal starts to flee) and hiding time (Irschick 2000). Gaits such as walking versus

galloping in mammals and hopping versus flying in birds are distinct, alternative patterns of locomotion characteristic of a limited range of speeds (Alexander 2003). As such, identification of gaits can provide insight into the relative speed an animal uses to flee. Fleeing from a predator at the greatest speed possible minimizes the time taken to reach a refuge or safe distance from the predator. However, moving more rapidly also requires a higher rate of energy expenditure (Alexander 2003) and a longer recovery period if anaerobic metabolism is used (e.g. Lee et al. 2003). Nonenergetic costs associated with higher speeds, such as increased risk of injury and impaired detection of predators, conspecifics and obstacles (Kramer & McLaughlin 2001), are also likely. Thus, there is a fundamental trade-off between the costs and the benefits of escape speed. Animals should therefore optimize rather than maximize their escape speeds (Domenici & Blake 1997; Domenici 2010).

For taxa in which individuals develop through a wide range of body sizes while living independently of parental care, the trade-off between the benefits and costs of high escape speeds may change with size (Clark 1994; Sogard 1997; Reinhardt 2002; Gotanda et al. 2009). Larger animals can, in general, move faster than smaller ones of similar form (Alexander 2003). For example, in fishes, maximum swimming speed increases with body size (Videler 1993). If some minimal speed is necessary to avoid a predator, smaller individuals

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need to use a greater proportion of their capacity when escaping. This is the locomotor compensation hypothesis (Irschick 2000; Irschick et al. 2005), which is a particular case of the more general concept of trait compensation. Trait compensation occurs when individuals with a trait that makes them more vulnerable to predators than they would be with an alternative expression of that trait (e.g. smaller body size or reduced defensive spines) express higher levels of a different antipredator trait that makes them less vulnerable (e.g. stronger behavioural avoidance: DeWitt et al. 1999). The opposite of trait compensation is trait cospecialization, a 'positive correlation between the degree of prey defence shown for two types of antipredator traits' (DeWitt et al. 1999). For example, if larger fish accept less risk than smaller fish do, or if they perceive a particular threat as more dangerous, they may escape at speeds that are higher relative to their capacity, resulting in cospecialization between the size-related increase in maximum speed and the increase in the proportion of their capacity used (DeWitt et al. 1999).

Gaits offer an opportunity to examine escape locomotion in nature because each of the alternative gaits within the locomotor repertoire of a species is used over a limited range of speeds and because it is much easier to identify gaits than to measure absolute speeds in the field. Some fish species can swim using two distinct gaits, flapping paired fins (often the pectorals) while holding the body rigid (PF locomotion), or undulating the body and caudal fin to create thrust (BCF locomotion) (Webb 1998). PF locomotion is considered to provide greater manoeuvrability but lower speeds, while BCF provides the greater power output needed for higher speeds and acceleration (Webb 1998; Korsmeyer et al. 2002). Laboratory studies using controlled speeds show that many fish species that are capable of PF use this gait only at lower speeds, switching to BCF at higher speeds (Korsmeyer et al. 2002; Cannas et al. 2006; Svendsen et al. 2010). There have been few studies of the use of alternative gaits of fish in the field and none that have examined the use of gaits in escape.

The primary goal of the present study was to investigate whether body size influences escape gait in parrotfishes. The compensation hypothesis predicts that smaller fish, having lower maximum capacity, would be more likely than larger fish to use BCF locomotion when escaping. The cospecialization hypothesis predicts that larger fish with greater capacity would be more likely than smaller fish to use BCF locomotion. Our specific objectives were to answer the following three questions. (1) Do parrotfish use PF or BCF or both gaits to escape an approaching threat? (2) If parrotfish use both gaits, does the probability of using the BCF gait decrease or increase with body size? We also checked to see whether species or distance to a refuge explained or modulated any effect of body size. (3) How do size and the use of alternative escape gaits relate to other stages of escape behaviour, specifically FID and whether the fish flee into a hole on the reef or swim away?

METHODS

Study Site and Species

Our study took place at depths of about 3–6 m in the spur and groove zones of two adjacent fringing reefs, North and South Bellairs Reefs (13°11′30″N; 59°38′30″W) in the Barbados Marine Reserve adjacent to the Bellairs Research Institute on the west coast of Barbados, West Indies. At this location, Gotanda et al. (2009) recently showed that FID of parrotfishes strongly increased with size and that it was higher outside the reserve. We studied three common species of parrotfish: princess, *Scarus taeniopterus*; queen, *Scarus vetula*; stoplight, *Sparisoma viride*. Princess parrotfish reach a total length of about 35 cm, while queen and stoplight parrotfish

reach about 60 cm. These diurnal species are strongly associated with solid substrates and spend much of the day moving over the reef within a home range, grazing microscopic algae from hard substrates (Bruggemann et al. 1994). They are protogynous hermaphrodites in which juveniles, 'initial phase' adults (both males and females), and larger 'terminal phase' males can be distinguished by colour pattern (Robertson & Warner 1978; Humann & DeLoach 2002). In Barbados, adult parrotfish are likely to encounter natural potential predators only rarely. There are no predatory birds or marine mammals, and fish large enough to capture adult parrotfishes are rare (D. L. Kramer & K. Turgeon, unpublished observations). However, juvenile parrotfish are at risk from many smaller predatory fishes. Genetic evidence indicates that stoplight parrotfish have relatively open populations (Geertjes et al. 2004), presumably through dispersal of their planktonic eggs and larvae, so natural selection for antipredator behaviour may continue to affect populations where such predators are currently or historically rare. Parrotfish do have larger predators in other Caribbean locations (Ogden & Buckman 1973; Newman et al. 2010). Parrotfish in Barbados are a target of spearfishers, but spearfishing is illegal and rare within the Barbados Marine Reserve (K. Turgeon, unpublished observations). On the other hand, parrotfish within the reserve are frequently exposed to (presumably) benign contact with recreational snorkellers and SCUBA divers (K. Turgeon, unpublished observations). After settling from the plankton, parrotfishes do not move frequently among reefs (Chapman & Kramer 2000), so individuals found within the reserve would not be likely to have experienced spearfishing outside the reserve.

Data Collection

To examine escape gait, FID and refuge type, we used an approaching free-diving snorkeller as a threat stimulus. Use of a human stimulus is common in studies of predator avoidance in terrestrial birds, mammals and lizards (Irschick 2000; Frid & Dill 2002), but rarer in fishes (Grant & Noakes 1987; Gotanda et al. 2009). Even when habituated to nonlethal encounters with humans, animals show responses similar to those shown to predators, although thresholds may change (Frid & Dill 2002; Cooper 2008). An individual subject was selected according to the criteria that it was not in a group and that it was foraging, stationary or moving slowly but not engaged in courtship or other interactions with other conspecifics. We recorded three independent variables (species, size and distance to the reef) and three response variables (gait, FID and refuge type). We identified the species, life history stage and size (total length, cm) of the subject. Species and life history stages were determined following Humann & DeLoach (2002). Before data collection, all observers practised estimating the length of objects underwater using premeasured sections of PVC pipe and stationary objects on the reef until they reached a precision of ±1 cm. This technique provides estimates within 3% of actual lengths (Jennings et al. 1996; Harvey et al. 2002). Furthermore, it yields a very high correlation (∼0.99) between estimated and actual lengths (Polunin & Roberts 1993), all that was required for the present study. Once an individual subject had been identified, a snorkeller (D. J. Sanders) with an outstretched arm swam at a constant, rapid speed directly towards the parrotfish, perpendicular to the fish's direction of movement and at an angle of about 45° from the surface. Three observers meanwhile remained relatively motionless at the surface and farther from the subject than the stimulus snorkeller. Starting distances were approximately 2–4 m but were not recorded for each trial. Some variation in starting distance was necessary because of changes in visibility and the need to be closer to identify species and estimate size of small individuals. A separate set of tests following the main study indicated no effect of starting distance (see

Supplementary Material). When the parrotfish began to flee, defined as cessation of previous foraging or slow swimming and swimming more rapidly away from the approaching snorkeller, the snorkeller dropped markers to indicate the location of his outstretched hand and of the fish at the time it started to flee. Two surface observers (K. L. M. Lewtas & L. H. McDonnell) recorded whether the fleeing fish used PF (synchronous pectoral fin movements with the body held rigid) or BCF (body and tail undulating laterally). In response to a predator strike or startling stimulus, fish often initiate escape by a rapid movement known as a 'C-start' during which the body curves first in one direction then in the other within about 30 ms (Domenici & Blake 1997). We did not consider C-starts as BCF, but recorded the gait with which the fish continued its locomotion because our questions related to gaits used during the fleeing bout. If fish subsequently changed gaits, we considered only the first one used. We categorized refuge types used as a 'hole' if the fish entered an enclosed space on the reef, or 'swim' if the fish did not enter shelter in the reef but moved away towards deeper water or around reef structure. A third observer (B. M. Miller) placed a marker to indicate the location of a hole used as a refuge. Initially, swimming towards deep water and swimming around reef structure were distinguished in the data set. However, preliminary analyses (one-way ANOVA) found no significant differences in body size, distance to reef, FID or gait in the fish showing these two swimming responses, so they were combined to facilitate the interpretation. We measured FID (horizontal distance between the snorkeller's outstretched arm and the fish at the time the fish began to flee) and distance to reef (horizontal distance to nearest continuous solid substrate) to the nearest 1 cm. Although the nearest part of the reef did not necessarily provide a potential refuge for all subjects, refuge holes were always on the reef, and this measure allowed us to have a comparable measurement whether a fish hid or swam away. All four observers generally agreed on the response; ambiguous trials were not included in the data set. To reduce the risk of repeating observations on the same individual, we never sampled two individuals of the same species and life history stage within 50 m (Gotanda et al. 2009). In total, we obtained data from 95 individuals: 33 princess (14–33 cm), 32 queen (8–50 cm) and 30 stoplight (7–58 cm) parrotfish. The procedures were approved by the McGill University Animal Care Committee (Protocol No. 5039).

Data Analysis

We used generalized linear models (GLMs) to test the effect of four predictors (body size, species, distance to reef, and the interaction between body size and distance to reef) on each of three response variables (gait: proportion of fish using BCF; FID; refuge type: proportion of fish fleeing to a shelter). GLM uses the maximum likelihood method to build models and to estimate and test hypotheses about effects. For each response variable, we built models that included all three predictors and the body size*reef distance interaction as well as all possible subsets. All models included a constant. The plausibility of each model from the subset of all possible models was assessed by the AICc approach as described below. For gait and refuge type, we used a binomial error structure and a logit link function in the GLM. For FID, we used a Gaussian error structure and an identity link function. FID and distance to reef were log transformed and z standardized prior to analysis. Body size was also z standardized. Species were included as a treatment contrast with princess parrotfish as the contrast group. We tested for multicollinearity among the predictors by examining tolerance values. These range from 0 to 1, with 1 indicating no collinearity. Tolerance value is the inverse of the variance inflation factor and a measure of the amount of variation unique to each predictor (Neter et al. 1985; Tabachnick & Fidell 2001). For all three predictors for each response

variable, tolerance values were greater than 0.73. To examine how gait was related to other stages of escape behaviour, we also used GLMs to examine the effect of FID and refuge type on the proportion of fish using BCF. Because gait was associated with both body size and FID, we also examined their relative strength as predictors by including FID, body size and their interaction in GLMs predicting the proportion of fish using BCF. For these two models, we used a binomial error structure and a logit link function.
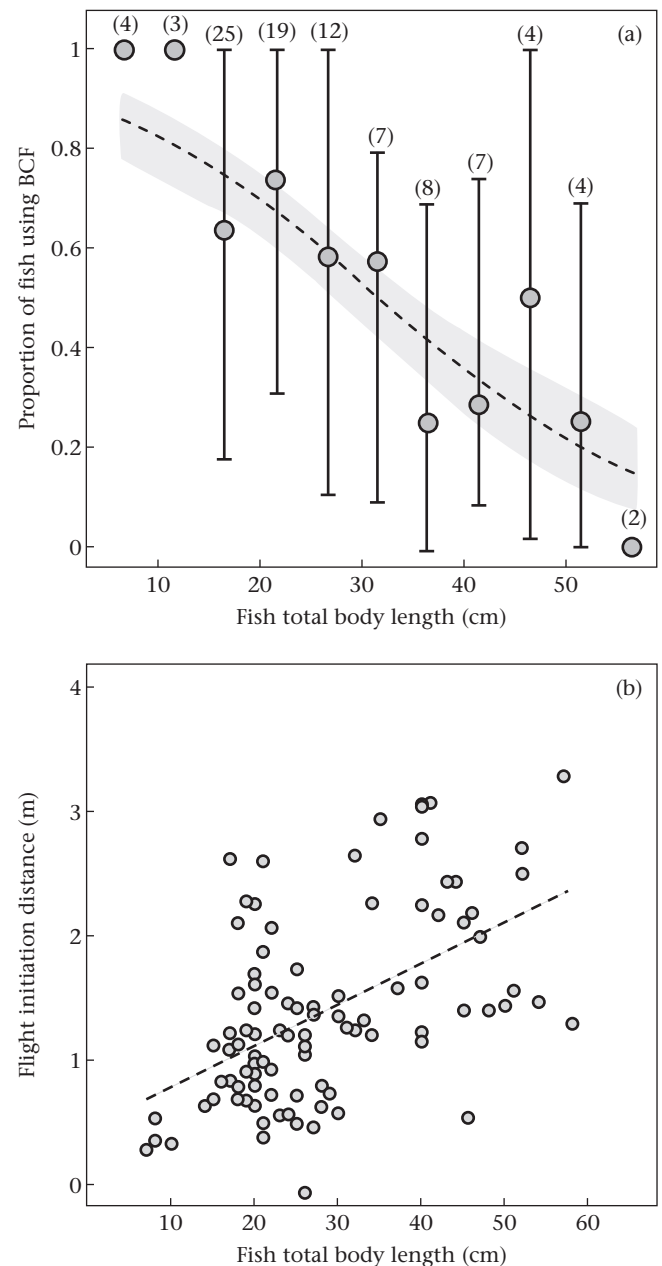
Figure 1. Relationship between body size (total length, cm) of 95 parrotfish (three species combined) and two measures of escape from an approaching snorkeller: (a) proportion using the body and caudal fin gait (BCF) to escape and (b) flight initiation distance (m). In (a), each data point is based on a bin of 5 cm in body size, starting at 5 cm (e.g. 5–9 cm, 10–14 cm) with the number of observations per bin indicated in parentheses. Error bars on each data point represent ±1 SE, calculated as $\sqrt{(p(1-p)/n)}$, where p is the probability of using BCF, back-calculated from the logit. The dashed line represents the best fit model prediction from original data (not bins) from a GLM using a binomial error and a logit link function. Shaded areas represent ±1 SE from the model fit predictions. In (b), the dashed line represents the best fit model prediction using a Gaussian error and identity link function.

To select the best subset among the candidate models, we used the Akaike's Information Criterion modified for small sample sizes (AICc; Burnham & Anderson 2002). As a general rule of thumb, the confidence subset of candidate models includes all models for which the model-normalized Akaike weight (w_{im}) is within 10% of the maximum weight (Burnham & Anderson 2002). For each response variable, the w_{im} value of the model with the maximum weight was less than 0.9, indicating that alternative candidate models within 10% of the maximum also had substantial support. In this situation, Burnham & Anderson (Anderson et al. 2001; Burnham & Anderson 2002) suggest model averaging to provide unconditional model variances and improve the parameter estimates for each predictor. To determine the reliability of the predictor estimates from model averaging, we calculated their weighted unconditional standard errors and confidence intervals (95% CI). When the 95% CI of a predictor does not include 0, we can conclude that there is support for an effect on the response variable. To assess the relative importance of the predictors, we compared their parameter-normalized Akaike weights (w_{ip}). To calculate w_{ip}, the Akaike weights calculated for each model (w_{im}) that contains the parameter of interest are summed. Higher weights indicate greater importance (maximum 1.0). For each model retained in the best subset for each response variable, we computed the percentage of the deviance explained. This measure expresses the fit of the model, weighted by the effective number of degrees of freedom (i.e. taking into account the number of predictors and the number of observations) used to build the model (Guisan et al. 1999; Engler et al. 2004).

RESULTS

Body size influenced escape gait and FID. Distance to reef influenced FID and refuge type. However, species did not affect any of the components of predator avoidance. Parrotfish ($N = 95$) used both PF (42%) and BCF (58%) gaits to avoid the approaching snorkeller. Among the smallest fish tested (7–16 cm), 100% used BCF. In contrast, none of the largest fish (55–58 cm) used BCF, all fleeing by means of PF locomotion. At intermediate sizes, some fish showed each gait, with a clear, decreasing trend towards less BCF with increasing size (Fig. 1a). Model selection based on AICc scores of the candidate models provided substantial support for an effect of body size, but no strong support for an effect of species or distance to reef on the proportion of fish using BCF (Table 1). The best model of the subset included only body size and was three times more likely than the second-best model, which included body size and distance to reef. With model averaging, body size was the only parameter whose 95% CI did not include 0, and its w_{ip} value was maximal. Body size explained 11.5% of the deviance,

and the presence of additional predictors in the model did not improve the percentage of the deviance explained.

As in Gotanda et al.'s (2009) study, FID increased with size (Fig. 1b). Above 30 cm, however, there appeared to be little change in average FID with increasing size. Model selection based on AICc scores of candidate models showed substantial support for an effect of body size and distance to reef and weak support for an effect of species (Table 2). The model including body size and distance to reef was at least 2.4 times more likely than the two other models, which included species and the interaction between body size and distance to reef, to explain variation in FID. Model averaging revealed that the 95% CI for body size and distance to reef did not include 0 and that they had maximal w_{ip} values. Body size had a larger effect on FID than distance to reef did, as indicated by its higher coefficient, but effects of both predictors were equally well supported by the analysis. As distance to reef increased, FID also increased, on average, even though not all fish used refuges. We also compared FID in the present study with that obtained by Gotanda et al. (2009), even though our methods differed (Gotanda et al. used SCUBA diving, which allowed a horizontal approach, whereas we used snorkelling, which necessitated an approach at an angle from the surface), because both studies involved the same species at the same location. The data distributions broadly overlapped. There was no evidence for a difference between the studies in the horizontally measured FID or its relationship to body size, as indicated by very low support for a main effect of the study (GLM: estimate of the study coefficient $\pm$ SE $= 0.250 \pm 0.175$; 95% CI $= -0.093, 0.594$; $t_{1,122} = -1.431$, $N = 125$) or the interaction between study and body size (GLM: estimate of the interaction coefficient $\pm$ SE $= -0.240 \pm 0.168$; 95% CI $= -0.569, 0.089$; $t_{1,121} = -1.427$, $N = 125$).

When approached by the snorkeller, 30 fish sought refuge in a hole, while the other 65 swam away (31 remaining close to reef structure and 34 swimming towards open water). There was no support for an effect of body size or species on refuge type, but there was support for an effect of distance to reef (Table 3). Distance to reef was the only parameter whose 95% CI did not include 0, and it had maximal w_{ip}. Fish closer to the reef were more likely to use a hole. Although smaller fish were found closer to the reef, on average (GLM: deviance explained $= 9.11\%$; estimate of the body size coefficient $\pm$ SE $= 0.302 \pm 0.100$; 95% CI $= 0.108, 0.496$; $t_{1,91} = -1.431$, $N = 95$), distance to reef was a better predictor of whether the fish would use a hole or swim away than was either body size or the body size*distance to reef interaction (Table 3).

Escape gait was negatively associated with FID, but not clearly related to refuge type, and the relationship to FID was primarily due to the association of both with body size. Because both escape gait

Table 1
Predictors and interaction terms of the five GLMs whose normalized Akaike weights were within 10% of the best model explaining variation in the escape gait (probability of using body and caudal fin locomotion) of 95 parrotfish of three species

Predictors	Model rank					β	SE	95% CI	w_{ip}
	1	2	3	4	5				
Constant	●	●	●	●	●	−0.293	0.273	−0.242, 0.827	1.00
Body size	●	●	●	●	●	**−0.882**	**0.258**	**−1.387, −0.377**	**1.00**
Distance to reef		●		●	●	0.001	0.075	−0.146, 0.147	0.31
Species: Princess vs Queen			●		●	0.146	0.169	−0.186, 0.478	0.21
Species: Princess vs Stoplight			●		●	−0.003	0.128	−0.254, 0.248	0.21
Size*distance to reef				●		0.012	0.021	−0.030, 0.050	0.07
No. of parameters (K)	3	4	5	5	6				
AICc	120.72	122.90	123.13	124.70	125.36				
ΔAICc	0.00	2.18	2.41	3.98	4.65				
w_{im}	0.535	0.180	0.160	0.073	0.053				
% Deviance explained	11.5	11.5	13.0	11.8	13.1				

Variables included in models are indicated with filled circles (●). Number of parameters (K) used in each model, AICc, ΔAICc (AIC of model$_i$ − AIC of best model), model w_{im} (normalized Akaike weights) and percentage of deviance explained are shown below each model. Model-averaged estimates of parameters (β), unconditional standard errors (SE), 95% confidence intervals (CI) and the parameter-normalized Akaike weight (w_{ip}) are shown for each predictor. Bold font indicates that the 95% CI of a predictor did not include 0.

Table 2
Predictors and interaction terms of the three GLMs whose normalized Akaike weights were within 10% of the best model explaining variation in flight initiation distance (FID) of 95 parrotfish of three species

Predictors	Model rank			β	SE	95% CI	w_{ip}
	1	2	3				
Constant	●	●	●	0.002	0.095	−0.183, 0.188	1.00
Body size	●	●	●	**0.385**	**0.093**	**0.204, 0.567**	**1.00**
Distance to reef	●	●	●	**0.286**	**0.093**	**0.103, 0.467**	**1.00**
Species: Princess vs Queen		●		0.009	0.020	−0.031, 0.049	0.09
Species: Princess vs Stoplight		●		−0.003	0.020	−0.042, 0.037	0.09
Size*distance to reef			●	−0.015	0.025	−0.064, 0.033	0.27
No. of parameters (K)	4	6	5				
AICc	244.20	245.93	248.26				
ΔAICc	0.00	1.73	4.06				
w_{im}	0.644	0.271	0.085				
% Deviance explained	29.2	29.6	29.6				

Variables included in models are indicated with filled circles (●). Number of parameters (K) used in each model, AICc, ΔAICc (AIC of model$_i$ − AIC of best model), model w_{im} (normalized Akaike weights) and percentage of deviance explained are shown below each model. Model-averaged estimates of parameters (β), unconditional standard errors (SE), 95% confidence intervals (CI) and the parameter-normalized Akaike weight (w_{ip}) are shown for each predictor. Bold font indicates that the 95% CI of a predictor did not include 0.

and FID were related to body size, it is not surprising that they were related to each other. Model selection based on AICc scores of candidate models to predict gait indicated substantial support for FID and lower support for refuge type. The 95% CI for FID did not include 0 but that for refuge type did (Table 4). FID was 2.4 times more likely than refuge type to explain gait, based on the w_{ip} values. However, FID explained less of the deviance in escape gait (8.4%, Table 4) than body size did (11.5%, Table 1). When both body size and FID were included as potential predictors of escape gait, only body size was strongly supported. After model averaging, the 95% CI of body size did not include 0 but that for FID did (Table 5). Body size was 1.3 times more likely than FID to explain gait, and models that included FID did not explain any more of the deviance than models without it. We attempted an analysis of residuals to examine whether BCF gait was more likely when FID was small for the body size and distance to refuge of an individual fish, but our sample size was too small to obtain a clear conclusion from this approach.

DISCUSSION

Which Gaits Do Parrotfish Use to Escape?

Parrotfish used both BCF and PF locomotion to flee from an approaching snorkeller. Fulton (2007) showed that many species capable of both PF and BCF swimming use BCF relatively infrequently in the field, but he did not report the context in which each

was used. In five parrotfish species observed by Videler (1993, pp. 219–220), territorial males used PF for nearly all their locomotion, with only 3–5% of total time using BCF, primarily in the context of mating and agonistic behaviour.

In our study, many fish avoided the approaching snorkeller using only PF locomotion, providing evidence that fish use less than their maximal speed in response to a threat in natural circumstances and thus indicating that they modulate their escape according to contexts, as suggested by Domenici & Blake (1997) and Domenici (2010).

How Do Gait Use and Escape Speed Vary with Body Size?

Body size explained some of the variation in gait selection, but there was no apparent effect of distance to reef or of species. Smaller individuals were more likely to use BCF locomotion than larger individuals. The effect size was very large with a transition from 100% BCF to 100% PF over the size range tested. Laboratory studies in which swimming speed is controlled by water velocity in a flume show that individual parrotfish switch from PF to BCF locomotion as increasing flow velocity necessitates swimming at higher speed (Korsmeyer et al. 2002). This strongly suggests that fish that used BCF were escaping at higher speeds relative to their body size than fish that used the PF gait. Higher speed should reduce predation risk by decreasing the time to reach cover or a safe distance from a threat. It is likely that the fish that used BCF

Table 3
Predictors and interaction terms of the four GLMs whose normalized Akaike weights were within 10% of the best model explaining the proportion of 95 parrotfish of three species that used a hole as a refuge rather than swimming away

Predictors	Model rank				β	SE	95%CI	w_{ip}
	1	2	3	4				
Constant	●	●	●	●	**−0.891**	**0.263**	**−1.407, −0.375**	**1.00**
Body size		●		●	−0.015	0.076	−0.164, 0.135	0.29
Distance to reef	●	●	●	●	**−0.972**	**0.269**	**−1.499, −0.444**	**1.00**
Species: Princess vs Queen			●		−0.009	0.046	−0.100, 0.081	0.08
Species: Princess vs Stoplight			●		−0.026	0.055	−0.133, 0.082	0.08
Size*distance to reef				●	−0.001	0.018	−0.035, 0.034	0.07
No. of parameters (K)	3	4	5	5				
AICc	108.23	110.37	112.37	112.60				
ΔAICc	0.00	0.34	0.13	0.11				
w_{im}	0.632	0.217	0.080	0.071				
% Deviance explained	13.9	14.0	14.2	14.0				

Variables included in models are indicated with filled circles (●). Number of parameters (K) used in each model, AICc, ΔAICc (AIC of model$_i$ − AIC of best model), the model w_{im} (normalized Akaike weights) and percentage of deviance explained are shown below each model. Model-averaged estimates of parameters (β), unconditional standard errors (SE), 95% confidence intervals (CI) and the parameter-normalized Akaike weight (w_{ip}) are shown for each predictor. Bold font indicates that the 95% CI of a predictor did not include 0.

Table 4
Predictors and interaction terms of the three GLM models explaining the proportion of 95 parrotfish using body and caudal fin gait (BCF) in relation to flight initiation distance (FID) and refuge type

Predictors	Model rank			β	SE	95% CI	w_{ip}
	1	2	3				
Constant	●	●	●	0.350	0.258	−0.152, 0.860	1.00
FID	●	●	●	**−0.754**	**0.284**	**−1.311, −0.197**	**1.00**
Refuge type		●	●	−0.044	0.235	−0.506, 0.417	0.42
FID*refuge type		●		−0.072	0.169	−0.404, 0.260	0.23
No. of parameters (K)	3	5	4				
AICc	124.69	126.55	126.83				
ΔAICc	0.00	1.86	2.14				
w_{im}	0.574	0.226	0.197				
% Deviance explained	8.4	8.7	8.5				

Variables included in models are indicated with filled circles (●). Number of parameters (K) used in each model, AICc, ΔAICc (AIC of model$_i$ − AIC of best model), model w_{im} (normalized Akaike weights) and percentage of deviance explained are shown below each model. Model-averaged estimates of parameters (β), unconditional standard errors (SE), 95% confidence intervals (CI) and the parameter-normalized Akaike weight (w_{ip}) are shown for each predictor. Bold font indicates that the 95% CI of a predictor did not include 0.

also had a higher energetic cost of escaping than those that used PF. In general, metabolic rate increases with relative swimming speed in fishes (Videler 1993) and higher costs of swimming when BCF is used at higher speeds have been documented in parrotfish (Korsmeyer et al. 2002) as well as in other species (Cannas et al. 2006) that switch from PF to BCF. Furthermore, the transition between PF and BCF is considered an important 'breakpoint', representing equivalent effort in fish of different sizes (Drucker 1996; Mussi et al. 2002), so the use of BCF by smaller fish indicates greater effort. Thus, for an individual of a given size, the use of BCF instead of PF is likely to provide both higher benefits and higher costs.

To the best of our knowledge, only three previous studies, all on terrestrial organisms, have examined how intrinsic and environmental factors influence escape gaits, and only two have considered size as a possible factor. Dangles et al. (2007) studied the response of wood crickets *Nemobius sylvestris*, released in typical habitat, to a piston imitating the approach of a predatory wolf spider. Juveniles were more likely than adults (which were about 1.6 times longer than juveniles) to escape by jumping rather than running or walking. Rodriguez-Prieto et al. (2008) recorded whether blackbirds (*Turdus merula*) flew or ran from approaching humans in urban parks. In this case, juveniles were more likely to fly than adults were. The probability of flying also increased as FID decreased and as the number of people in the area increased. de Barros et al. (2010) found that juvenile tegu lizards (*Tupinambis merianae*) in the laboratory were more likely to run from a threat, whereas adults (about twice as long as juveniles) were more likely to walk away or use aggression. Thus, all previous studies indicate that, as in parrotfishes, younger individuals are more likely to use the more expensive but faster and presumably more effective escape gaits. However, compared to the 100% decrease in BCF with an 8.3-fold size increase in the present study, the changes in the percentage of individuals using the faster gait were considerably less in the previous studies (crickets: decrease of 22%, from 96% to 74% jumping, Dangles et al. 2007; blackbirds: decrease of 20%, from 67% to 47% flying, Rodriguez-Prieto et al. 2008; lizards: decrease of about 67%, from 85% to 18% running, estimated from Figure 2d, e in de Barros et al. 2010).

Other studies have examined escape speeds without directly considering gaits. In fishes, acceleration and the maximum speed after a given time during the fraction of a second involved in a C-start escape tend to be size independent (Domenici 2001). In studies measuring escape speed over a more prolonged period, speed has not been related to size in fishes, although other factors can affect it (Domenici 2010). However, juvenile lizards fled at higher speeds than adults did, relative to their body size and to their maximum speed (Irschick 2000; Husak & Fox 2006). In other taxa, fleeing speed can vary with substrate and incline (Blumstein et al. 2004), distance to a refuge (Bonenfant & Kramer 1996), and states of hunger and rest (Stankowich 2009). These studies suggest that maximum capacity is only one factor influencing escape speeds. Indeed, despite the strong effect size in our study, body size only explained about 11% of the deviance in gait, indicating a potential role for other, unmeasured, variables. There is considerable scope for incorporating speed and gait into the developing discipline of escape theory (e.g. Cooper & Frederick 2007; Cooper 2009) that now focuses primarily on FID and hiding time.

Table 5
Predictors and interaction terms of the three GLMs explaining the proportion of 95 parrotfish using body and caudal fin gait (BCF) in relation to flight initiation distance (FID) and body size

Predictors	Model rank			β	SE	95% CI	w_{ip}
	1	2	3				
Constant	●	●	●	0.376	0.258	−0.130, 0.883	1.00
FID	●	●		−0.475	0.275	−1.014, 0.063	0.76
Body size	●	●	●	**−0.717**	**0.310**	**−1.322, −0.111**	**1.00**
FID*body size	●			−0.027	0.127	−0.278, 0.222	0.39
No. of parameters (K)	5	4	3				
AICc	119.735	119.794	120.717				
ΔAICc	0.000	0.059	0.982				
w_{im}	0.375	0.364	0.229				
% Deviance explained	11.5	13.9	13.9				

Variables included in models are indicated with filled circles (●). Number of parameters (K) used in each model, AICc, ΔAICc (AIC of model$_i$ − AIC of best model), model w_{im} (normalized Akaike weights) and percentage of deviance explained are shown below each model. Model-averaged estimates of parameters (β), unconditional standard errors (SE), 95% confidence intervals (CI) and the parameter-normalized Akaike weight (w_{ip}) are shown for each predictor. Bold font indicates that the 95% CI of a predictor did not include 0.

How Does Gait Relate to Other Components of Escape?

FID increased with body size, confirming the pattern found by Gotanda et al. (2009) and some, though not all, previous studies (reviewed in Gotanda et al. 2009). Indeed, the data did not differ quantitatively from the data that Gotanda et al. (2009) collected earlier at the same location, even though the present study used a snorkeller approaching from the surface as the stimulus, while Gotanda et al. (2009) used a SCUBA diver approaching at the same level. Higher FID is likely to reduce risk by maintaining a greater distance from a threat, but to increase costs because other activities such as foraging will be interrupted sooner and more often. Separate analyses confirmed that fish with shorter FID were more likely to use BCF locomotion, but that this relationship was likely because both were related to body size (or some other well-correlated variable) rather than that they were related to each other. However, it would be reasonable to expect a direct relationship independent of body size. A fish that responds to a threat when it is more distant may not need to swim away as quickly. Conversely, when a threat is responded to at less than the normal FID, perhaps because of insufficient vigilance or the presence of a valuable resource, one might expect a faster flight in compensation. Indeed, some previous studies have found inverse relationships between escape gait or speed and FID even when controlling for size or age (Semeniuk & Dill 2005; Rodriguez-Prieto et al. 2008).

As in Gotanda et al. (2009), distance to the reef had a positive effect on FID in the present study. This relationship is predicted by antipredator theory because fish that used holes as refuges found them only on the reef, and an animal closer to a refuge needs less time to gain safety, so it does not need to terminate other fitness-increasing activities such as foraging as early (Ydenberg & Dill 1986; Cooper & Frederick 2007). Even though two-thirds of the fish did not use holes but swam away over the reef or into deep water without using a refuge, removing the fish that had sought refuge on the reef greatly weakened the relationship (K. Turgeon, unpublished analyses), suggesting that the overall effect was primarily related to hole use, as assumed by the theory, rather than some other effect of proximity to the reef.

In contrast to FID, refuge type (hole versus swim) was not related to escape gait or body size. Although smaller fish were, on average, closer to the reef, and fish closer to the reef were more likely to shelter in a hole, there was little evidence of a relationship between size and refuge type once distance to the reef was taken into account. Our finding that small fish did not use holes more than large fish did was surprising because the lower maximum swimming speed of small fish should favour refuge use over speed to avoid a pursuing predator. Also, an earlier study showed that juvenile stoplight parrotfish up to the size of the smallest individuals used in the present study consistently hid in coral when approached by a predatory fish model (Wolf 1985).

In summary, of the three measured components of escape, gait and FID showed opposite relationships with body size, with smaller fish using the higher cost–lower risk gait and larger fish using the higher cost–lower risk FID, while refuge type was unrelated to size. Therefore, in relation to the size-related increase in swimming capacity, escape gait is an example of compensation, while FID is an example of cospecialization, and refuge type showed no relationship.

Conclusions

Although accurately measuring the speed of animals as they accelerate and change directions in their natural habitat is challenging, more attention to locomotor capacity and to the costs and benefits of variation in speed would greatly add to our understanding of escape tactics and variation in predation risk. Because they provide good correlates of relative speed and are readily identified in the field, gaits may be a useful tool to increase our understanding of the use of locomotion in escape. Using gaits, this study has provided the second example, to the best of our knowledge, of locomotor compensation during escape in an organism other than a lizard and the first example to involve swimming. In addition, it illustrates the occurrence of both compensation and cospecialization among the components of escape to the same threat. The framework provided by the concepts of compensation and cospecialization will be a useful tool for further investigation of the relationship among the components of escape and especially their relationship to body size.

Supplementary Material

Supplementary material for this article is available, in the online version, at doi:10.1016/j.anbehav.2011.08.005.

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