

Behavioural measures determine survivorship within the hierarchy of whole-organism phenotypic traits

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Abstract

1. Mortality through predation is often selective, particularly at life-history bottlenecks. While many studies have looked at the importance for survival of specific prey characteristics in isolation, few have looked at a broad array of attributes and how they relate to survival in a realistic context.
2. Our study measures 18 morphological, performance and behavioural traits of a juvenile damselfish that have been hypothesized as important for prey survival, and examines how they relate to survival in the field immediately after settlement. These attributes included size, relative false eye-spot size, fast-start escape response kinematics, thigmotaxis, laterality, and space use and activity in the field.
3. Using conditional inference trees, we identify the most important drivers out of a reduced suite of 13 characters. Fast-start response latency, boldness, feeding rates and two measures of activity were found to significantly contribute to survival. Morphological variables and most laboratory measures of performance appeared to contribute little to survival.
4. Results suggest selection works on a suite of characters associated with boldness. Bold and active fish are those that will be best able to learn using public information, but because of the relative naiveté of newly metamorphosed fishes, speed to react to a strike from an unknown predator is of critical importance.
5. Findings substantiate the ecomorphological paradigm by suggesting that selection on behaviour modifies the correlations of morphological and performance variables with survival probabilities, since behaviour modifies performance capabilities by making them specific to context.

KEYWORDS

body condition, boldness, coral reef fish, fast-start escape response, lateralization performance, mortality, phenotypic selection, predator selectivity

1 | INTRODUCTION

Darwinian selection focuses on the performance of individuals within an environmental context, and biologists have often studied selection within a conceptual framework known as the “ecomorphological paradigm,” originally conceived by Arnold (1983). This framework integrates multiple levels of biological organization and how they may influence survival/fitness. In its simplest conceptualization, morphology

is linked to fitness through performance. Subsequent refinements by Garland and others have modified the paradigm to view behaviour as a filter intervening between performance capabilities and selection (e.g. Garland & Losos, 1994; Orr & Garland, 2017; Storz, Bridgman, Kelly, & Garland, 2015).

The addition of factors that drive the context specificity of morphology, biochemistry, behaviour and performance (Storz et al., 2015) means that these targets of selection can rapidly turn into a complex

network of interrelationships (Lailvaux & Husak, 2014; Orr & Garland, 2017). Together they can have indirect and direct effects that may combine to have simple or emergent influences on fitness and survival (Orr & Garland, 2017). Within this paradigm, organisms use behaviours to choose among a range of possibilities to make performance appropriate to context. Survival is the result of the compound effects of morphology, performance and behaviour (plus other external factors; Lailvaux & Husak, 2014) and is, therefore, an emergent property of these traits acting together. Additionally, the hierarchical structure of these traits inherently means that the ability to predict the emergent property (survival; Korn, 2005) will be greatest in the higher order traits (e.g. behaviour) and least in lowest order traits (e.g. morphology).

For organisms with complex life cycles (Wilbur, 1980), such as fishes, amphibians and many invertebrates, the juvenile life stage represents a critical bottleneck as individuals transition from a life form suited to their larval life to one suited to the juvenile environment (Pechenik, 2006). Here, mortality is not only high, but typically selective (Johnson, Grorud-Colvert, Sponaugle, & Semmens, 2014). A review of selection on performance traits across taxa suggests that selection tends to be directional on performance traits and favours high rather than low performance (Irschick, Meyers, Husak, & Le Galliard, 2008). This is of crucial importance because such short-term but intense selection has the capacity to carryover and be amplified through to the longer lasting life stages (Gagliano, McCormick, & Meekan, 2007). These later life stages often have the key life-history roles of growth and reproduction (Wilbur, 1980). Hence, selective mortality that occurs within these bottlenecks plays an important role in influencing the distribution of phenotypes within the reproductive population, and if the targeted traits of selection have genetic basis, the genotypes within the next generation (e.g. Jensen, 2013; Pini, Planes, Rochel, Lecchini, & Fauvelot, 2011; Planes & Romans, 2004; Vigliola et al., 2007).

The phenotypic traits that are advantageous to surviving a predatory encounter can be divided into morphological, performance and behavioural traits, which may have independent and interactive consequences for fitness (Garland & Losos, 1994; Langerhans & Reznick, 2010). For organisms with complex life cycles, important traits linked to fitness include large relative size (Perez & Munch, 2010), large locomotory structures (Langerhans, 2009), distracting pigmentation (Lönstedt, McCormick, & Chivers, 2013; Stevens, 2005), high growth rates (Hoey & McCormick, 2004), turning bias (i.e. lateralization, Chivers et al., 2016), efficient escape responses when threatened (Dugatkin & Godin, 1992; McCormick & Allan, 2017a), and being more active or bolder in the face of risk (Fuiman, Meekan, & McCormick, 2010; May, Page, & Fleming, 2016; McCormick & Meekan, 2010). While latency to respond to a predator strike has been found to be important, and though it makes intuitive sense that higher performance in escape kinematics should be important to survival, few studies have expressly examined the mechanics of escape performance related to survival under a direct predation threat (Katzir & Camhi, 1993; Langerhans, 2009; Walker, Ghalambor, Griset, McKenney, & Reznick, 2005).

Studies often use experiments to determine the importance of one trait (Garland & Losos, 1994; Irschick et al., 2008). This is often due to the complex logistics of undertaking multifactorial manipulative experiments. Laboratory tests also usually only examine survival against one species of predator of a particular size. Although these studies can be useful to generate variables of potential importance, the inevitable covariance of phenotypic attributes makes it difficult to conclude the role that one factor plays in affecting survival. This problem is magnified by the use of laboratory tests, as with constant conditions and control comes many artefacts, such as a modified sensory regime (e.g. Rogers, Hawkins, Popper, Fay, & Gray, 2016), that make interpreting dynamics in the wild problematic (e.g. White, McCormick, & Meekan, 2013). Arnold (1983) noted that laboratory studies are useful for determining the effects of morphological variation on maximum performance, while measures of fitness are best undertaken under natural field conditions. It is only by using a combination of laboratory and field studies that the relative importance the hierarchy of traits that influence fitness and survival can be determined within the ecomorphological paradigm (Orr & Garland, 2017).

Coral reef fishes are ideal model organisms with which to study the drivers of selection and survival, as marine organisms often enter the juvenile life stage in vast numbers and exhibit a type III mortality schedule (Caley, 1998), where most mortality occurs in the early life stages. Moreover, recent studies have shown strong links between performance capabilities (e.g. escape responses under predation risk) and behaviour (e.g. McCormick & Allan, 2017a; Ramasamy, Allan, & McCormick, 2015; Ramasamy et al., 2017), suggesting a hierarchical link to survival. The present study explores the extent to which commonly used morphological, performance and behavioural measures predict survival in the field for fish at metamorphosis. By focusing on the juvenile phase, the present study examines the importance of selection on morphological, performance and behavioural traits without the potentially confounding influence of other types of selection that may be contrary to selection on performance, such as sexual selection (Johnson & Hixon, 2011). The hierarchical framework linking morphology, performance and behaviour to survival (Garland & Losos, 1994; Orr & Garland, 2017) means that the ability to predict the emergent property of survival should be greatest in the higher order traits, such as behaviour. Thus, we predicted that morphological variables would not be as important at this critical transition because of the limited variability in size range (Kerrigan, 1996; McCormick & Molony, 1993); that escape responses would be important due to high predation pressure; and that behavioural measures within the field would be good predictors of survival, due to their relevance to the environmental context of predation pressure (Domenici, 2010). We use conditional inference trees to identify the most important drivers out of a reduced suite of 13 characters. These models are particularly useful in this circumstance as they can fit complex nonlinear relationships and automatically handle interaction effects between predictors (Elith, Leathwick, & Hastie, 2008).

2 | MATERIALS AND METHODS

2.1 | Study species

Newly metamorphosed white-tailed damselfish, *Pomacentrus chrysurus* (Pomacentridae), were collected using light traps (Meekan, Wilson, Halford, & Retzel, 2001) in the waters off Lizard Island (14°40'S, 145°28'E) in the northern Great Barrier Reef, Australia, during October to November 2016. This species is a common component of the benthic fish fauna of Indo-Pacific reefs and adults inhabit algal-covered rubble areas of lagoons and inshore reefs. *Pomacentrus chrysurus* naturally settle on patch reef environments near the continuous reef. In this habitat, juveniles are exposed to a diverse range of predators that use a variety of feeding modes from ambush (lizardfish *Synodus dermatogenys* and the small cod *Cephalopholis microprius*) to pursuit (dottybacks *Pseudochromis fuscus* and wrasse *Thalassoma lunare*). These predators can be observed to capitalize on juveniles that venture too far from shelter (McCormick, 2012).

2.2 | Protocol summary

Each of the 120 fish used in the study was put through a broad array of performance tests, measured and then placed on habitat patches in the shallow lagoon (a habitat to which they naturally settle), where their behaviour and survival was assessed. Fast-start (kinematic) variables could not be obtained for all individuals, so this reduced the overall number of individuals used in the comparison to 111 ($n_{\text{survived}} = 59$, $n_{\text{died}} = 52$). For all variables chosen, previous research has either found that they are the focus of selective mortality, or responsive to the magnitude of risk (Table 1). The key to achieving such a potentially stressful series of tests on small juvenile fish was to minimize their stress at every step in the process. Indeed, at each step, a certain minimum level of habituation was necessary before data were collected. For instance, the startle stimulus was dropped to obtain a fast-start response (below), when fish were active in the central third of the arena (indicating habituation). In the field trials, all fish were observed to feed, suggesting again that they had habituated to the new conditions. Physiological studies have found that juvenile coral reef fishes recover very quickly from stressful situations (e.g. exhaustion from the assessment of maximum aerobic capacity, Rummer et al., 2014).

Once collected with light traps, juveniles were sorted to species and left in 30-L flow-through seawater aquaria to recover from the stress of capture. On the day of assessment, fish were measured and assayed for a number of phenotypic variables, details of which are given below: (1) body size and weight; (2) lateral body area; (3) relative size of the false eye spot—an indication of risk history; (d) routine swimming—as a measure of activity and an indicator of exploratory behaviour, sometimes used as indices of laboratory assessed boldness; (e) thigmotaxis—that is, “wall-hugging” as an indication of anxiety/assurance in a novel environment; (f) fast-start kinematics—the startle response necessary to evade predator attacks under a repeatable stimulus; (g) space use in the field; (h) behaviour in the field; and (i) survival over 3 days in the field.

The sequence of assessments and measurements were as follows. Fish were left for 2 days to recover from the stress of capture in the light traps, during which time they were fed *Artemia* nauplii twice a day. They were transferred individually from 35-L holding tanks into individual 1-L aquaria held in a flow-through water bath to maintain water temperature (27–28°C) and to habituate to isolation. Twenty to 40 min later, they were carefully transferred to the fast-start arena where they were left for 5 min to habituate. Fish were then filmed at 30 fps for 2 min for the assessment of routine swimming, after which a repeatable drop stimulus elicited a fast start. Fish were then placed into a 1-L labelled aquaria of aerated water and left for 20 min prior to being transferred to a lateralization chamber with a fine-mesh hand net, where they were left for a further 3 min to habituate to the apparatus. After they had been assessed for laterality, they were placed into individually labelled 1 L aquaria (in a water bath) and left for 20–40 min prior to being weighed (quickly but carefully blotted) in a known weight of water and placed into labelled 1 L clip-seal plastic bag of aerated seawater and photographed laterally against a 1 cm grid. Fish within the 1 L bags were then stored in a 60 L flow-through plastic aquarium under shade cloth to minimize stress for c. 2 hr, and taken out to the shallow field site just off the research station. Divers on SCUBA then released the fish individually onto numbered patch reefs ($n = 1$ fish per reef) made of dead coral (their natural recruitment habitat), and a small cage allowed the fish to habituate to the new habitat without threat of predation. Most fish started feeding within 30 s of transfer, suggesting that they rapidly habituated to their new habitat. The cage was removed 40–60 min later, and their behaviour and space use were assessed. The patches were surveyed three times per day for next 3 days to quantify survival as evidenced by the presence/absence of the focal fish.

2.3 | Laboratory measures of morphology and performance

2.3.1 | Morphology

Morphology was quantified from the lateral photographs of fish against a 1-cm grid using the image-analysis package Image-J (imagej.nih.gov/ij/). The morphological variables measured were standard length, eye area, ocellus area and lateral body area (Figure S1).

2.3.2 | Routine swimming, thigmotaxis and fast-start protocol

Routine swimming, thigmotaxis and fast starts were examined in a transparent circular acrylic arena (diameter 200 mm; height 70 mm), within a large opaque-sided plastic tank (585 × 420 × 330 mm; 60 L) with a transparent Perspex bottom to allow responses to be filmed from below using the fish's silhouette (Figure S2). The water level was maintained at 60 mm to reduce movements in the vertical plane, and the water in the arena was emptied and refilled with fresh seawater after every fourth trial to maintain water quality and temperature. The arena was illuminated by an LED light strip wrapped around the

TABLE 1 Phenotypic variables measured for each juvenile white-tailed damselfish to examine their relationship with survival on habitat patches in the field. Descriptive statistics for the 111 fish used are given together with their coefficient of variation (CV). The variables used in the final analyses are denoted by an asterisk after their name. Variable with superscript (1) were standardized by distance from stimulus, while those with (2) were standardized by standard length for analysis. Skewness of the overall distribution of the raw variables are given as are references that postulate the importance of the variables to fitness

Variable type	Variable	M	SD	Min, Max	CV	Skew	References
Morphological	Weight (g) ²	0.47	0.028	0.39, 0.55	5.91	0.19	Holmes and McCormick (2010)
	Standard length (SL, cm)*	1.27	0.065	1.07, 1.42	5.13	0.07	McCormick and Hoey (2004)
	Ocellus/eye area*	0.69	0.136	0.38, 1.02	19.66	0.06	Lönstedt et al. (2013)
	Lateral body area	0.21	0.024	0.14, 0.27	11.52	0.36	Kern et al. (2016)
Kinematic	Response latency (s)* ¹	0.015	0.007	0.005, 0.036	45.13	1.05	Katzir and Camhi (1993)
	Response distance (m)* ¹	0.020	0.003	0.01, 0.027	14.00	-0.33	Allan et al. (2015)
	Response speed (m/s)* ¹	0.67	0.10	0.41, 0.94	14.76	-0.46	Fuiman et al. (2010)
	Maximum response speed (m/s)* ¹	0.96	0.15	0.59, 1.45	15.88	0.43	Allan et al. (2015)
Routine swimming	Distance (m)*	1.32	0.88	0.001, 5.05	66.68	1.12	Fuiman et al. (2010)
	Average speed (m/s)	0.011	0.007	0.0008, 0.042	66.40	1.13	Fuiman, Rose, Cowan, and Smith (2006)
Thigmotaxis	Innermost area (s)*	30.11	24.05	0, 114	79.86	0.98	Johansen, Allan, Rummer, and Esbaugh (2017)
	Outermost area (s)	89.83	24.03	6,120	26.75	-0.98	
Lateralization	Absolute laterality	26.17	21.82	0, 100	83.37	0.82	Ferrari et al. (2015)
	Relative laterality*	0.17	34.15	-100, 80	20491	0.05	Bisazza et al. (1998)
Behaviour/ space use	Bite rate*	30.68	31.97	0, 196	104.19	1.94	McCormick (2009)
	Total distance moved (cm)*	14.71	13.20	0, 60	89.75	1.63	Lönstedt et al. (2012)
	Maximum distance ventured (Max DV, cm)*	3.38	3.62	0, 14	107.13		McCormick (2012)
	Boldness (0–3 index)*	1.33	0.90	0.1, 3	67.94		McCormick and Meekan (2010)

outside of the holding tank with light penetrating with even illumination through the white plastic sides.

At the end of the 5-min habituation period, routine activity (used to determine routine swimming and thigmotaxis) was recorded as a silhouette from below, at 30 fps for 2 min. A fast start was then stimulated by the release of a conical weight with a tapered end into the testing arena and recorded at 480 fps (Casio EX-ZR1000). Fish were only startled when they moved to the middle portion of the tank, allowing an individual to move an equal distance in any direction and standardizing for fish position relative to the stimulus. The weight was released from an electromagnet and was governed by a piece of fishing line that was long enough such that the tapered tip of the weight only just touched the surface of the water. To avoid a premature escape response associated with visual stimulation occurring, the test tube was released from above into a 550-mm piece of 48.5 mm diameter PVC pipe with the bottom edge at a distance of 10 mm above the water level. To ensure a standardized protocol, fast-start variables were only measured when fish performed a C-start (commencement of fast-start that results in the individual forming a C-shape, Domenici & Blake, 1997). Trials were conducted between 8.00 and 14.00 hr.

Routine swimming was analysed from the 2-min, 30-fps video sequences and measured by tracking the distance (metres) covered by the fish every second, resulting in 120 data points. From this distance measure, average speed was also calculated (m/s).

To quantify thigmotaxis, the location of an individual was marked every second and assessed for the proportion of time spent swimming near the wall of the arena (i.e. within 2.5 body length of the wall; defined as “anxious”) or further into the centre of the arena (defined as “assure”).

Kinematic variables associated with the fast-start response were analysed using Image-J, with a manual tracking plug-in. The centre of mass (CoM) of each fish was tracked for the duration of the response. The following kinematic variables were measured:

1. Response latency (s) was measured as the time interval between the stimulus onset and the first detectable movement leading to the escape of the animal.
2. Response distance (m) is a measure of the total distance covered by the fish during the first two flips of the tail (the first two axial bends, i.e., stages 1 and 2 defined based on Domenici and Blake, 1997),

which is the period considered crucial for avoiding ambush predator attacks (Webb, 1976).

3. Response speed (m/s) was measured as the distance covered within a fixed time (25 ms). This fixed duration was based on the average duration (22.8 ms) of stages 1 and 2 (as defined above).
4. Maximum response speed (m/s) was measured as the maximum speed achieved at any time during stage 1 and stage 2.

2.3.3 | Lateralization test

Laterality of each fish was determined using a detour test (Bisazza, Facchin, Pignatti, & Vallortigara, 1998). The apparatus consisted of a cream-coloured PVC tank (600 mm length × 300 mm width × 154 mm height), with a runway in the middle (250 mm length × 30 mm width × 120 mm height) and grey PVC barriers (120 mm length × 120 mm height) positioned perpendicular to the orientation of the runway at both ends (30 mm ahead of the runway). Water in the lateralization arena was 60 mm deep and was changed every five trials to avoid changes in water temperature and dissolved oxygen levels in the arena. Water temperature in the arena was 27–28°C. At the start of each trial, a single fish was introduced into the middle of the runway and left for 2 min to habituate. During each trial, fish were gently manoeuvred to the starting point of the runway. The fish then swam along the runway until it faced the barrier. Fish then made a decision to turn left or right around the barrier. To account for any possible asymmetry in the setup, tests were carried out alternately on the two ends of the runway (Bisazza et al., 1998). To avoid fish taking “a familiar route,” the fish entered the runway from a different side from which they exited. Turning was scored by direct observation. The criterion used for scoring was the first turning direction taken by the fish when exiting from the runway. Ten consecutive tests were conducted for each fish. Absolute laterality was used to quantify the level of turning bias according to the formula (Bisazza et al., 1998): absolute value of $\{[(\text{number of right turn} - \text{number of left turn}) / (\text{total number of trials})] \times 100\}$. This yields a score between zero (no side preference) and 100 (absolute side preference). Relative lateralization of each fish was computed using the formula $\{[(\text{number of right turns} - \text{number of left turns}) / (\text{number of right turns} + \text{number of left turns})] \times 100\}$ (Domenici, Blagburn, & Bacon, 2011).

2.4 | Behavioural measures and survival in the field

2.4.1 | Space use and boldness in field

Individual fish were placed onto uniquely numbered habitat patches (25 × 20 × 20 cm) constructed of dead bushy coral (*Pocillopora damicornis*), located on sand 3 m from the edge of a shallow reef and 4 m apart. All resident fishes and mobile invertebrates were removed from the patch reefs using a hand net prior to the introduction of the focal fish. A small cage (30 × 30 × 30 cm cage; 12-mm square mesh) was placed over the patch for 30–60 min to prevent any loss of fish from the patches during the habituation

period. Our previous studies have shown that individually tagged recruit-sized damselfishes do not move between patches and that any loss from these patch reefs is due to predation (McCormick, 2009; McCormick & Meekan, 2007). For instance, in one study, 20 elastomer-tagged (Hoey & McCormick, 2004) newly settled damselfish were placed on each of 15 patch reefs 8 m apart, and the difference in the colour of the tags between adjacent reefs allowed movement to be quantified. This study found only 3 of the 300 fish had moved to the adjacent patch reefs over a 3-day period (Hoey & McCormick, 2004), suggesting that movement does not represent a significant bias for the present study. In the present study, fish usually started feeding within 30 s of release, indicating that despite the stresses associated with their previous performance assessments, they readily habituated to their new surroundings and were minimally stressed.

After the habituation period, the cage was slowly removed and fish were assessed for their feeding rates (strikes per minute), space use and boldness over a 3-min period following the protocol of McCormick (2009). Briefly, the behaviour of each fish was assessed by a scuba diver positioned ~1.5 m away from the patch. A magnifying glass (4×) aided the assessment of bite rates and space use over the 3-min focal animal sampling period for each fish. Four aspects of activity and behaviour were assessed: (1) bite rate; (2) total distance moved (cm); (3) maximum distance ventured from the habitat patch (cm); and (4) boldness (recorded as a continuous variable on a scale from 0 to 3, where 0 was hiding in hole and seldom emerging; 1 was retreating to a hole when scared and taking more than 5 s to re-emerge, weakly or tentatively striking at food; 2 was shying to shelter when scared but quickly emerging, purposeful strikes at food; and 3 was not hiding when scared, exploring around the coral patch, and striking aggressively at food). This measure of boldness has been found to be repeatable between observers, consistent in the short term for newly settled damselfish and related to survival in the field (McCormick & Meekan, 2010; White, Meekan, & McCormick, 2015). Total distance moved and maximum distance ventured were estimated by keeping track of where the fish travelled and from knowing the measured dimensions of the patch reef. Behavioural assessments were made between 14:30 and 16:30.

2.4.2 | Survival

Habitat patches were censused for the presence or absence of the white-tail damselfish recruits 72 hr after they had been placed onto the reefs. Fish were not tagged to minimize handling stress, so the absence of a fish on the labelled patch reef was equated to mortality, presumably due primarily to predation.

2.5 | Statistical analyses

Phenotypic variables (independents) were screened for their power to predict survival (dependent) using a chi-square statistic and *p* value for each independent variable. When independent variables were similar measures of the same phenotype (e.g. for routine

swimming, distance travelled in 2 min, and average speed), the variable with the best characteristics regarding predictive power and normality was chosen for inclusion in further analyses. This left 13 variables within the analyses (Table 1). Pearson's correlations were used to provide a simple quantification of the associations both within and between the different types of variables (morphological, performance [kinematic, routine swimming, thigmotaxis, lateralization] and behavioural).

Four classification models were used to relate the remaining 13 phenotypic variables (independents) to whether fish survived for 72 hr on habitat patches (dependent). These four models were then compared and allowed to "vote" (through a process known as bagging) for a final solution. Using ensembles of models typically outperforms individual models (Breiman, 2001). An examination of scatterplots of independent variables found that linearity was the most parsimonious relationship between all variables. Significant linear relationships were evident between distance to stimulus and all kinematic fast-start variables, so residuals of these relationships were used for further analysis to remove the effect of variable distance.

The four classification techniques were used: general classification and regression trees (C&RT, Breiman, Friedman, Olshen, & Stone, 1984), chi-squared automatic interaction detector (Exhaustive CHAID; Kass, 1980), stochastic gradient boosting trees (Friedman, 2002), and random forest (Breiman, 2001). The performance of models were compared by examining their performance in lift and gains charts. All models identified the same top five independent variables that explained the most discriminatory power with respect to survival; however, the boosted regression model performed slightly better than the others when models were compared.

A boosted regression tree classification consists of a collection or ensemble of simple models to give improved prediction. Such machine learning approaches tend to be less sensitive to the effects of variable collinearity than other classification approaches (Dormann et al., 2013). They have no need for prior data transformation or elimination of outliers, can fit complex nonlinear relationships, and can automatically handle interaction effects between predictors (Elith et al., 2008). The relative importance in predictive power among independent variables was computed using a modification of the approach of Breiman et al. (1984). Statistics were undertaken using the Data Mining package in Statistica version 13.2 (Dell Inc., 2016).

3 | RESULTS

Forty-six per cent of fish died after 72 hr on the patch reefs. Pearson's correlations found that there were significant associations both within and between the morphological, performance and behavioural variables (Table S1). There were no correlations of any variables with standard length, possibly due to the low variability of this variable, with the exception of lateral body area (Table S1). There were moderately strong associations among kinematic variables, but also strong negative relationships between response latency and in situ behavioural variables ($r = -.46$ to $-.58$; Table S1). Lastly, there were strong

positive associations among all in situ behavioural variables ($r = .50$ to $.82$; Table S1). Response latency and boldness both had five significant correlations with other variables (Table S1).

All four analytical models chose the same five variables as being most important in predicting the survival of white-tail damselfish on habitat patches over 72 hr. All four models also ranked response latency as the most important variable. The boosted regression tree analysis performed marginally better and found that latency in the fast-start response was the most important variable, followed by boldness and bite rate while on the habitat patch (Figure 1). Maximum distance ventured away from the patch and total distance moved within the 3-min behavioural assessment contributed equally to predicting survival. The morphological variables (SL, lateral area, ocellus/eye area), routine swimming, thigmotaxis (use of inner zone of the arena), and all but one of the kinematic fast-start variables (i.e. latency) had no significant power to predict whether a fish would survive 72 hr on a habitat patch (Figure 1). The overall accuracy of the four models in allocating a subsample of observations to one or other survival category was very similar and between 77% and 78%.

Lateralization was not significantly associated with survival. Overall the relative lateralization scores of the assessed group was significantly non-normal (Shapiro-Wilk $W = 0.97$, $p = .003$), with a slight right skew (skewness 0.048). While there were slight differences in the degree of skewness (survived 0.02 vs died 0.0), there was no significant difference in the distribution (Kolmogorov-Smirnov test, $p < .1$; Figure S3).

Univariate plots of the five key predictor variables show how the variables relate to whether fish survived in the field (Figure 2). Fish that survived 72 hr on the habitat patches where those that had a fast (i.e. short) response latency in a fast-start test (Figure 2a), were substantially bolder when placed on a reef (Figure 2b), had a higher bite rate (Figure 2c), were more active (Figure 2d), and ventured further from the reef (Figure 2e).

4 | DISCUSSION

This is the first study to relate survival in the field to such a broad array of morphological, performance and behavioural characteristics measured on each focal individual. All 18 measures used in this study have been previously hypothesized to be associated with performance in the face of risk; however, seldom are the relationships with survival tested in a field setting. The present study found that morphological traits and most of the laboratory measures of performance capacity did not relate to survival in the field. However, behavioural measures of activity, space use and boldness strongly predicted survival over the period when the juveniles were most vulnerable (e.g. Almany & Webster, 2006). These findings are in keeping with the predictions of the ecomorphology paradigm, which suggests that behavioural traits are likely to have the strongest effects on survival because they represent a higher order trait (Arnold, 1983; Garland & Losos, 1994; Orr & Garland, 2017). The high variability in many of these behavioural traits at settlement (Fuiman et al., 2010; this study) gives scope for

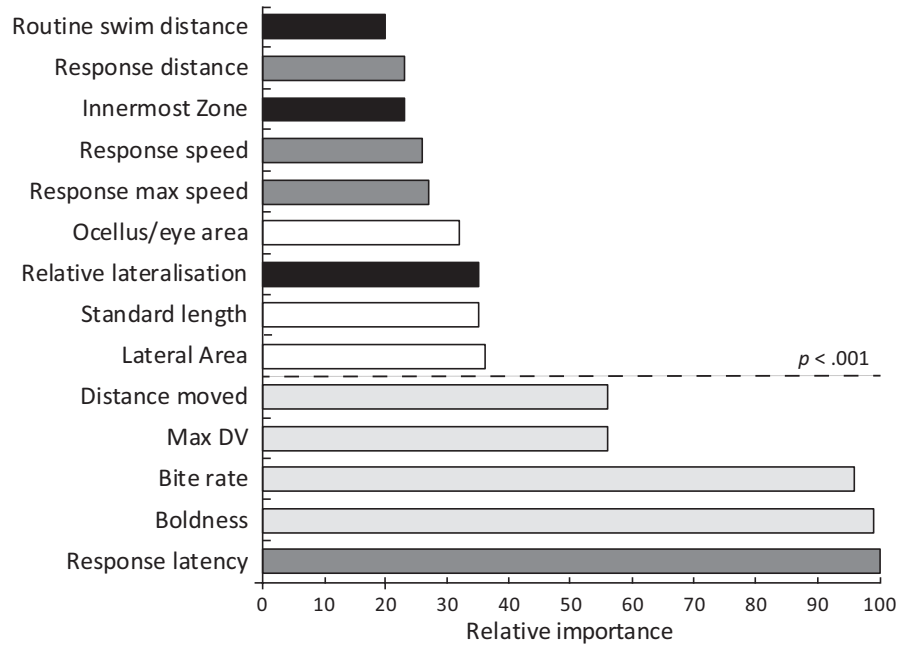


FIGURE 1 Relative importance of phenotypic variables of juvenile white-tail damselfish to predict survival over 72 hr on habitat patches in the field, as determined by a random forest categorical analysis. $n = 111$ fish

selection, and it is the selection during this mortality window that will affect the distribution of performance traits in later life stages.

Survivors were those individuals that displayed characteristics associated with being daring, and reactive to either the approach or strike of a predator—high boldness and a fast reaction once startled. The finding that these variables, which are closely associated with anti-predator responses, best define survivors highlights the vulnerability of this early life stage to predation. Research suggests that, while larvae bring some information with them about predators that is relevant after metamorphosis (e.g. Agrawal, Laforsch, & Tollrian, 1999; Vail & McCormick, 2011), most information about local relevant predators has to be rapidly learnt (Lönngstedt, McCormick, Meekan, Ferrari, & Chivers, 2012). Moreover, recent experiments suggest for a congeneric of the same life stage that there is a link between the propensity to explore and the speed at which individuals learn (White, McCormick, & Meekan, 2018). Our findings can be interpreted as two parts of this process; bold and active fishes are those that will be best able to learn using public information (e.g. Manassa & McCormick, 2013; Mathis, Chivers, & Smith, 1996), but because they are relatively naive, reaction time to a unknown predator that has been allowed to approach close enough to initiate a strike is of critical importance.

Latency to respond when startled was found to be the variable that best predicted survival in the field. Those fish that were the fastest to respond when startled survived. Fuiman et al. (2010) studying juveniles of a congeneric to our study species, the Ward's damselfish (*Pomacentrus wardi*), found latency to respond was unimportant to survival in the field, but the swimming speed once they had initiated their escape was important. Katzir and Camhi (1993) exposed predator-naive freshwater mollies (*Poecilia sphenops*) to aerial predation from a single pied king-fisher (*Ceryle rudis*) in the laboratory, and the survivors of the 15 trials were found to have shorter escape latencies. A number of studies that have looked at escape kinematics

under a predator threat have not measured latency, despite its key role as the initiation of the escape sequence, because of the nature of the experimental setup precluding unconfounded latency estimates (Johnson, Burt, & DeWitt, 2008; Walker et al., 2005). Recent studies have shown that fast-start latency is strongly influenced by available information on current risk (Bohórquez-Herrera, Kawano, & Domenici, 2013; Domenici, 2010; McCormick & Allan, 2016; Ramasamy et al., 2015, 2017), suggesting that those fishes that are best able to gauge risk respond more quickly to a predation threat.

Those fish that possess the most up-to-date information concerning the motivation of predators nearby will be those individuals that are most active and searching for food. Our findings showed that fish that were the boldest, most active and had the highest bite rates also had the highest survival. Boldness has been previously found to be associated with survival in situ for a congeneric, the Ward's damselfish (*P. wardi*, McCormick & Meekan, 2010). A broader examination of the literature shows that while the bold-shy axis is often correlated with survival, whether a shy or bold personality type is advantageous to survival is context and taxon specific. For instance, shy individuals that have low exploratory behaviour were found to survive better among trapped brushtail possums (May et al., 2016). Captive-bred foxes who were bold died more often than expected by 6 months after release (Bremner-Harrison, Prodohl, & Elwood, 2004). Dugatkin (1992) also found that guppies (*Poecilia reticulata*) who displayed a propensity to examine predators died faster in a separate survival trial, suggesting that boldness came at a cost. In direct contrast, Godin and Davis (1995) found that bold guppies which inspected a predatory cichlid (*Aequidens pulcher*) were less likely to be attacked compared with those that did not inspect. Similar survival advantages to inspection have been found for many taxa including gazelles (*Gazella thomsonii*; FitzGibbon, 1994) and the European minnow (*Phoxinus phoxinus*; Magurran, 1990) among others. Those studies that find a survival

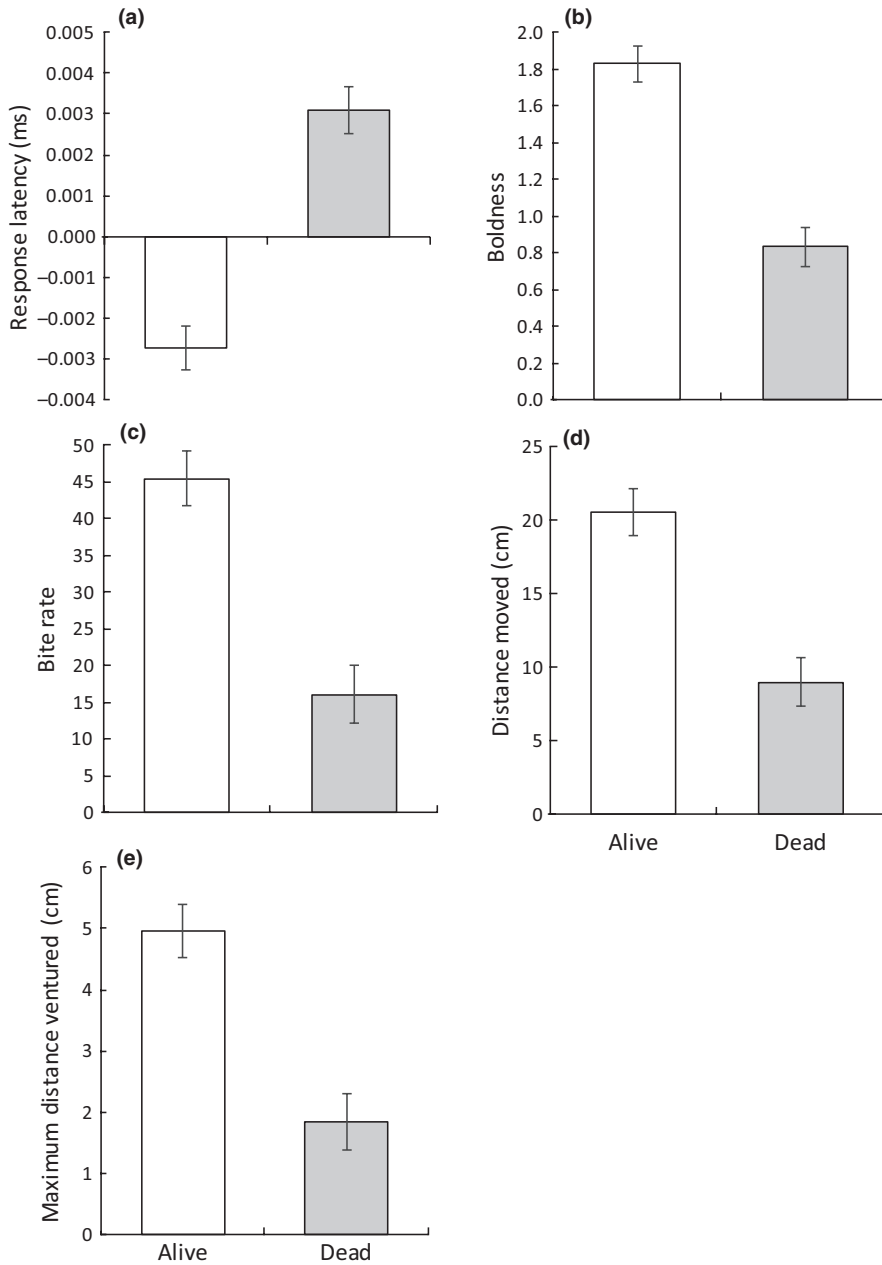


FIGURE 2 Comparison of the variables that significantly discriminated between those white-tailed damselfish juveniles that survived on habitat patches and those that died. (a) Response latency (residualized), (b) boldness, (c) bite rate (bites/3 min), (d) total distance moved, (e) maximum distance ventured from shelter. Mean \pm SE displayed for $n_{\text{survived}} = 59$, $n_{\text{died}} = 52$

advantage to such bold behaviour argue that the survival advantage comes from the cost to the predator of chasing an aware prey and the lower probability of capture (Godin, 1997). Clearly, given the widespread occurrence of predator inspection, it is hypothesized to be adaptive and one of the benefits of superior information acquisition by bold individuals (Dugatkin & Godin, 1992).

Latency of the fast-start response had much stronger correlations with field behavioural variables than fast-start kinematic variables. This may be because latency to respond to a startle can be under a degree of behavioural control (Domenici, 2010; Marras, Killen, Claireaux, Domenici, & McKenzie, 2011). Ramasamy et al. (2015) found that forewarning a spiny chromis (*Acanthochromis polyacanthus*) to a known predator by a visual or olfactory cue reduced the response latency to a startle stimulus by one-third. Such behavioural control of escape response kinematics has previously been

thought to fall within the economic model proposed by Ydenberg and Dill (1986) and Lima and Dill (1990). This theory states that there is a cost to escaping and so individuals weigh up the level of threat against this cost to determine when to best react. Clearly, there are behavioural decisions being made concerning when to react to a strike and it will be those individuals best informed about the identity, proximity and motivation of predators that will have the best chance of survival. Our data suggest that it is the bolder fish, who explore their environment to a greater extent than shy fish that will be better able to assess their high state of predator threat (remember ~50% fish die in 3 days) and consequently will be better able to optimize their fast-start response. This represents an example of how performance capabilities can be modified by behavioural decisions to become relevant to context (Domenici, 2010; Garland & Losos, 1994).

Our study found a surprising lack of relationships between performance variables and fish length. Size is the most universal predictor of the outcome of behavioural interactions and status within social systems in vertebrates (Werner & Gilliam, 1984). Dominant individuals are often those that get the best access to more or higher quality food, and this acts as a positive feedback through growth such that dominant individuals maintain their position. Size is usually positively associated with physical performance over the whole size range of an animal (e.g. Losos, 1990; Wilson & Franklin, 2000). However, at a particular developmental age, such as a developmental boundary like metamorphosis in amphibians and fishes, there are often poor correlations between performance and size (e.g. Holmes & McCormick, 2009; McCormick & Molony, 1993). In the present study, the newly metamorphosed fishes collected prior to settlement had a very low size range, with a coefficient of variation of only 5%. It is likely that this low variance prevented the detection of any positive associations between performance and size, if it existed. At this life stage, size may have been more important had fish been placed in social groups, because smaller individuals tend to get pushed into riskier parts of the habitat and suffer higher mortality in damselfish (McCormick, 2009), so once again, the result is likely to be context dependent. In the case of the white-tailed damselfish used in the present study, fish at settlement are highly territorial and aggressive to one another so tend to be solitary in their distribution, so the single individuals used on our patch reefs are the most ecologically relevant context within which to study this species at settlement.

It was also surprising that laterality had no influence on survival. A number of studies have found that fish exposed to high risk for 4 days developed a risk-adverse phenotype (Brown, Gardner, & Braithwaite, 2004; Chivers et al., 2016; Ferrari et al., 2015), which used space more conservatively, were lateralized and in one instance survived better in laboratory mesocosms (Ferrari et al., 2015). Despite the good range and normal distribution in relative lateralization found in the present study, there was no suggestion that mortality was biased by the levels of lateralization displayed by individuals. Recently, Chivers et al. (2016) experimentally demonstrated that whether juvenile fusiliers (*Caesio teres*) were strongly lateralized could be manipulated by the imposition of a temporal pattern in the magnitude of risk, suggesting that lateralization was very malleable to context. These recent findings emphasize that while lateralization can be beneficial to survival, the high cost of lateralization means that fish adapt their level of lateralization to suit current circumstances. This suggests that although lateralization measured in the laboratory could be pertinent to survival in a laboratory mesocosm, the same fish within a field context may not necessarily display the same level of lateralization, so no relationship between a laboratory assessment of lateralization and field survival would be evident.

The present paper is one of the only studies to explore the relative influence of morphological, performance and behavioural traits on survival in a natural field context. Findings suggest that, under the constraints of the experimental field conditions, ecological selection is promoting a bold phenotype. This phenotype represents a

variety of correlated behavioural traits, together with their emergent functional properties and performance traits. Such a grouping of associated traits under selection is expected (Irschick et al., 2008) and appears to be common (e.g. Ferrari et al., 2015; Kern, Robinson, Gass, Godwin, & Langerhans, 2016). Our analysis emphasized the importance of behaviour to survival, which is likely to function through two mechanisms: first, it is how an organism uses space that influences its vulnerability to selective predators (e.g. Holmes & McCormick, 2009, 2010); second, behaviour alters the relationships between morphological variables and performance by modifying the performance response to best fit the context, in keeping with the ecomorphological paradigm (Arnold, 1983; Orr & Garland, 2017). While latency was found to be important to predicting survival, it is interesting that it was perhaps one of the most behaviourally mediated of the kinematic variables and known to be influenced by behavioural inputs (Domenici, 2010). Most analyses assume that predators simply eat vulnerable prey, meaning that the attributes of the prey determine survival. Studies of predators find they are highly selective feeders (e.g. Gallon, Thompson, & Middlemas, 2017; Holmes & McCormick, 2010) and often idiosyncratic in their choices of prey attributes (Bolnick et al., 2002; Toscano, Gownaris, Heerhartz, & Monaco, 2016). Future studies will benefit from including predator choice into the survival equation, and inevitably these choices may be context specific which may also affect the balance of morphological, performance and behavioural variables that affect prey survival.

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AUTHORS' CONTRIBUTIONS

M.I.M. and B.J.M.A. conceived and undertook the laboratory and field study; E.F. analysed the videos and images; M.I.M. statistically analysed and wrote the first draft; B.J.M.A. and E.F. substantially contributed to the final manuscript.

DATA ARCHIVE

Data are archived at Tropical Data Hub <https://doi.org/10.4225/28/59c47d4b3a5f2> (McCormick & Allan 2017b).

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