



Who wins in the battle for space? The importance of priority, behavioural history and size



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The pulsed nature of new individuals entering into existing communities means that prior residents can greatly influence the establishment and persistence of later-arriving individuals. The unique set of interactions experienced by an individual can also affect how it behaves and its likelihood of winning future encounters. In the present study, we used field experiments to investigate the circumstances under which residency (resident or intruder), behavioural history (prior dominance or subordination) and body size determined the direction and strength of intraspecific interactions. We paired recently metamorphosed individuals of a coral reef damselfish, *Pomacentrus amboinensis*, with different suites of these traits to observe how each behaved in a competitive interaction. Our results show the importance of priority and size advantages, and suggest that prior behavioural history has the least influence on the outcome of future confrontations. Prior history was only important when combatants were of similar size, with previously subordinate residents losing against similarly sized previously dominant intruders. Aggression affected space use on a habitat patch and was itself affected by the relative size difference between combatants. Aggressive residents were larger than their competitors, occupied higher areas of the patch and chased intruders to lower areas of the patch and further away from the patch. Space use was not affected by behavioural history. These results demonstrate the importance of priority effects in structuring fish communities, and how an individual's physical and behavioural characteristics interact to predict community dynamics. This has important implications for predicting fish community structure under certain environmental or ecological scenarios.

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Identifying the factors that affect the outcomes of competitive interactions is important in understanding community dynamics and predicting the composition of organisms (Denno, McClure, & Ott, 1995; Schoener, 1983). Many communities of organisms experience strong competition for space, food and other resources (Connell, 1983). Young-of-the-year are most affected by resource limitation because even small changes in key resources can significantly reduce growth and survival (McCormick & Molony, 1992; Newman, 1998). In this way, competitive interactions can influence the numbers of individuals surviving to the next life stage and their distribution patterns, ultimately determining the structure of communities (Jones & McCormick, 2002; Wilbur, 1980). Repeated periods of colonization are common in many populations, with many new juveniles arriving in pulses during a recruitment season (Blaustein & Margalit, 1996; Lawler & Morin, 1993; Milicich & Doherty, 1994), or because individuals migrate to a new habitat as

resources or resource requirements change (Werner & Gilliam, 1984). As these individuals move into an area they bring with them a unique set of interaction experiences that will affect how they behave in future encounters with competitors (Frost, Winrow-Giffen, Ashley, & Sneddon, 2007).

The intensity of interactions and the likelihood of winning are often related to size differences, because size correlates naturally with strength, aggression (Buston & Cant, 2006; Sauer & Slade, 1987; Semlitsch, Scott, & Pechmann, 1988) and ultimately survival (Haramis, Nichols, Pollock, & Hines, 1986; Perez-Dominguez & Munch, 2010). Since many animal communities are size or age structured (Alatalo & Moreno, 1987; Werner & Gilliam, 1984) individuals need to compete against larger, smaller or similarly sized opponents. For example, in *Paragobiodon xanthosomus* (Gobiidae) communities, body size determines social rank, and subordinates are faced with a 'cooperation by regulation of body size' or 'punishment by eviction' dilemma as they await inheritance of dominant status (Wong, Buston, Munday, & Jones, 2007). Under these circumstances the larger individuals in a particular habitat are usually the more dominant individuals, which have a superiority and strength advantage over others. But size is not always the

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principal determinant of success. A history of winning or losing can significantly affect future success because previous experience can influence the outcome of interactions (Beaugrand, Payette, & Goulet, 1996; Dugatkin & Druen, 2004). However, the overall effect of history depends on the other circumstances present, such as familiarity with the immediate environment and the identity of the competitor (Geange & Stier, 2009). Individuals may enter a habitat patch at different times, and those that arrive first ('prior residents') gain a competitive advantage (Tupper & Boutilier, 1995). These priority effects, where prior residents affect the establishment and persistence of individuals arriving later ('intruders'), have been shown to influence survival (positively or negatively) in a range of organisms, including insects (Palmer, Young, & Stanton, 2002; Shorrocks & Bingley, 1994), amphibians (Alford & Wilbur, 1985), plants (Kardol, Souza, & Classen, 2013), fungi (Kennedy, Peay, & Bruns, 2009) and fishes (Almany, 2004; Beaugrand et al., 1996). The importance of priority effects has been demonstrated in several studies, such that a reversal in order of arrival can reverse individuals' competitive advantage and ultimately the outcome of competitive interactions (Blaustein & Margalit, 1996; Geange & Stier, 2009; Sandell & Smith, 1991). Prior residents benefit from information gained during their prior establishment, such as knowledge of the local habitat (Geange & Stier, 2009), or may benefit through the exploitation and subsequent depletion of a limited resource (Amarasekare, 2002). While some studies have found that prior residency (Chellappa, Yamamoto, & Huntingford, 1999; Switzer, 2004) or a prior history of winning (Beaugrand et al., 1996) is more important in paired encounters than the size difference between individuals, other studies have shown size to be of primary importance (Beaugrand et al., 1996; Evans & Shehadi-Moacdieh, 1988; McCormick & Weaver, 2012; Munday, Jones, & Caley, 2001). Comparing the relative contributions of these contest asymmetries gives insight into the deterministic factors driving local community structures.

Coral reef fish communities are an ideal model system with which to explore the relative importance of size, behavioural history and priority effects in influencing community development. Marine fishes typically have complex life cycles (McCormick, Makey, & Dufour, 2002), and adult populations are replenished episodically by pulses of larvae that metamorphose and settle into juvenile habitats (Milicich & Doherty, 1994). Fish that settle first in an extended recruitment season that involves multiple pulses of recruits will face a distinctly different social environment than those that settle at the end of the season. For these and other animals that have pulsed entry of offspring into nursery areas, prior residency and behavioural history may play a crucial role in structuring local communities. The present study aimed to investigate the role and relative importance of residency, behavioural history and size in determining the direction, strength and outcome of intraspecific interactions between juvenile damselfish. To achieve this goal we used a field experiment that involved a factorial manipulation of prior residency, size and behavioural history (i.e. a history of winning or losing interactions) in paired interactions of the ambon damselfish, *Pomacentrus amboinensis*.

METHODS

Study Site and Species

Pomacentrus amboinensis is a common damselfish, found in high densities on shallow coral reefs in the Indo-Pacific. At the study location the reproductive season extends from October to February. Pulses of newly metamorphosed fish settle into adult habitat (McCormick & Meekan, 2007) after a larval period of 15–23 days (Kerrigan, 1996), with greatest abundances occurring around the

new moon (Milicich & Doherty, 1994). Fish are aggressive at settlement and intra- and interspecific interactions greatly affect their distribution and survival in the hours and days following settlement (McCormick, 2009, 2012; McCormick & Weaver, 2012). *Pomacentrus amboinensis* is a protogynous hermaphrodite (Jones, 1987) and matures at 1–2 years old (~45 mm standard length) at Lizard Island, Great Barrier Reef, depending on whether they settled at the start or end of the summer recruitment period (McCormick, n.d.).

This study was undertaken at Lizard Island (14°38'S, 145°28'E) on the northern Great Barrier Reef, Australia, during November and December 2012. Small patch reefs were constructed from *Pocillopora damicornis* in 3.5 m of water depth, on sand and at least 50 m away from the nearest natural reef. All patches were 3 m apart and of similar size (approximately 0.3 cubic metres) and structure (pyramidal in shape, consisting of two heads of healthy *P. damicornis* collected from a nearby reef). A terracotta paving stone was placed underneath each patch reef to prevent the coral from sinking and being smothered by sand.

Collection and Tagging of Study Species

Approximately 320 settlement-stage *P. amboinensis* were caught in light traps (Meekan, Wilson, Halford, & Retzel, 2001) moored overnight at the back-reef of Lizard Island. Traps were protected from predators as they were located high in the water column away from reefs. Fish that were caught in the light traps may have been captured for up to 8 h before being collected at first light. Immediately after collection they were transported by boat in a 60-litre nally bin (up to approximately 300 fish per nally bin) to the laboratory, which took approximately 20 min for the fish collected first. To minimize stress and mortality (estimated to be less than 3%), a lid was placed on the nally bin to provide low light conditions, and the sea water was aerated. In the laboratory they were transferred to 25-litre flow-through aquaria systems where they were held under natural light conditions and fed twice daily ad libitum with newly hatched *Artemia* sp. nauplii. Water temperature was kept constant throughout this process as it was maintained at the existing ocean temperature. Holding time varied depending on the size of individuals required for the experiment; some individuals were held for up to 6 weeks to gain a size advantage, while others were used a minimum of 48 h after collection. Because individuals were collected from light traps, all were naïve to the field environment and had never experienced reef-based predators (White, McCormick, & Meekan, 2013).

One day prior to transplantation of fish to patch reefs, individuals were placed one at a time in a clip-seal bag with enough sea water to cover them, and measured for standard length ($SL \pm 0.1$ mm) using callipers, then tagged with a subcutaneous fluorescent elastomer tattoo using a 27-gauge hypodermic needle. Different tag colours were used to differentiate between individuals that would become residents and intruders. This tagging technique is commonly used on this species and has been shown not to affect growth or survival of newly settled *P. amboinensis* individuals (Hoey & McCormick, 2006).

This research was approved by the James Cook University Ethics Committee under application A1720 and was undertaken with a permit from the Great Barrier Reef Marine Park Authority. At the conclusion of the study all fish were captured using hand nets and released onto a nearby natural reef.

Experimental Protocol

To determine the importance and hierarchy of priority, behavioural history and size in *P. amboinensis*, we used eight treatments,

each consisting of a pair of individuals with different attributes. To establish the effects of size, we split the eight pairs into two size groups: four pairs were similar in size (differed by <1 mm SL; mean difference in size \pm SE = 0.22 ± 0.02 mm; mean size \pm SE = 14.13 ± 0.05 mm), and four pairs had a substantial size difference (mean difference in size \pm SE = 2 ± 0.05 mm; difference range 1.5–3.7 mm). Previous studies on *P. amboinensis* have shown that these small size differences account for the outcome of competitive interactions (McCormick, 2009). Once size groups were established we manipulated the priority (resident or intruder) and behavioural history (previously dominant or previously subordinate) traits (see Appendix Fig. A1). Thus we had four pairs in each of the two size groups as follows: a dominant resident versus a dominant intruder, a dominant resident versus a subordinate intruder, a subordinate resident versus a subordinate intruder, and a subordinate resident versus a dominant intruder. Each pair was then replicated 15–16 times. For pairs with a size difference, the resident was always larger than the intruder. Pairs where the intruder was larger than the resident were excluded from this study because in natural systems (and particularly from a recruitment perspective), it is more likely that residents will be larger than intruders since late arrivals are younger and hence usually smaller.

Individuals were paired according to size, and those that were to become residents were held in individual clip-seal bags filled with aerated sea water for transport to patches. The individuals that would become intruders remained in aquaria. The residents were manipulated on caged patch reefs to give them a dominant or subordinate history, by pairing them with another individual (which would not be used in the eventual paired interactions) and was either larger or smaller in size by more than 2 mm, and left in this social situation for 30 min (see Appendix Fig. A1, for a pictorial representation of these manipulations). Once dominant/subordinate status was established on a patch (confirmed by observers monitoring the interaction), the residents (now with a prior recent history of winning or losing) were moved onto new patch reefs vacant of any fish, and left for 3 h. Competitive interactions have been shown to be most intense within the first few hours after settlement (Almany, 2003). During the period of resident acclimation, the fish that were to become intruders were transported to patch reefs and underwent the same procedures as residents to manipulate behavioural history (dominant or subordinate). They were then added to the patch reefs with the residents (one pair per patch) and given a 30 min acclimation period under a cage (see Appendix Fig. A1).

Behavioural observations (adapted from McCormick, 2009) were then recorded during a 3 min period for each individual. These included (1) percentage of time spent 0, 2, 5, 10 cm away from the patch, (2) percentage of time spent at different heights within the patch (top, middle or bottom), (3) displays and chases towards and avoidance of the other individual. To determine who 'won' the interaction, we used an adjusted form of the 'aggression index' developed by McCormick (2009), which was the number of displays plus chases, minus avoidances, where a positive value was a 'win' and a negative value was a 'lose'. Previous studies have shown that a 3 min observation is sufficient to quantify the behaviour of these juvenile fish because there is a high degree of individual behavioural consistency through time (McCormick & Meekan, 2010). Our pilot study indicated that dominance status was quickly established, and dominance rankings determined 30 min after release onto a reef were the same those determined 4 h after release (see Appendix Table A1). To minimize disturbance and to reduce the effect of the presence of a scuba diver, the diver was situated at least 1.5 m away from the patch reef during all observations and used a magnifying glass (2 \times magnification) to assist in watching behaviours.

Statistical Analysis

A binary logistic regression was conducted to examine the probability of winning an interaction (aggression index as the independent variable) as a function of size, residency, behavioural history (dependent variables) and their interactions. We tested the effects of residency status, behavioural history (dominant/subordinate history) and size difference with two-factor ANOVAs, followed by Tukey HSD post hoc tests, on the aggression index, the relative difference in height on the patch and the relative difference in distance ventured from the patch. The latter two variables are weighted means and they refer to the difference in relative height/distance moved between both individuals in each pair. The two size groups tested (size-matched and size difference) were further grouped into three categories to differentiate between individuals that had a size difference, of being either larger or smaller than their combatant: 'smaller than' (-4 to -1.1 mm SL), 'similar in size' (-1 to 1 mm SL) and 'larger than' (1.1 to 4 mm SL). Residual analysis was used to examine the assumptions of normality and homogeneity of variance.

RESULTS

Probability of Winning

The majority of encounters were won by residents (which were either larger than or similar in size to the intruder), and when the resident was larger it won a greater percentage of the encounters (Table 1). A logistic regression revealed that if residents were the same size as intruders, they had a reduced chance of winning compared to when the resident was larger than the intruder, leading to a significant interaction between size and residency (size difference*residency: $P = 0.03$; Tables 1, 2). Also, when a previously subordinate resident was paired against a similarly sized previously dominant intruder, the intruder marginally won the majority of encounters, emphasizing the importance of a dominant status gained from a previous encounter (size difference*behavioural history: $P = 0.03$; Table 2). Yet, if this pair had a size difference (i.e. when the resident was larger), then the resident won nearly all the encounters, highlighting the overwhelming importance of a size advantage (Tables 1, 2). While the significant interactions indicate the nuances that affect who wins the interactions, the magnitude of the test statistic strongly indicates that size is the most influential factor driving the model (Table 2, Fig. 1).

The logistic regression curves illustrate that the probability of winning an encounter partly depended on the size difference between competitors: residents with a greater size advantage had a

Table 1
Outcome for resident *Pomacentrus amboinensis* of winning or losing an encounter at a settlement site

Resident	Intruder	Size	Outcome for resident	
			Win (%)	Lose (%)
Dominant	Dominant	R=I	67	33
		R>I	73	27
Dominant	Subordinate	R=I	53	47
		R>I	73	27
Subordinate	Subordinate	R=I	56	44
		R>I	75	25
Subordinate	Dominant	R=I	47	53
		R>I	93	7

Residents and intruders had similar or different behavioural experience (recent history of being dominant or subordinate) and the resident was either larger than the intruder or of a similar size (R: resident; I: intruder).

Table 2
Logistic regression model examining the contribution of each predictor variable (and their interactions) to the probability of winning a paired encounter

Source	df	Chi-square	P
Size difference	1, 242	84.71	<0.001*
Residency	1, 241	6.33	0.011*
Behavioural history	1, 240	0.70	0.401
Size difference × residency	1, 239	4.47	0.035*
Size difference × behavioural history	1, 238	4.68	0.031*

The interactions between residency and behavioural history and between all three predictors were removed from the model since they did not significantly contribute to the outcome.

* $P < 0.05$.

greater chance of winning, as did intruders that were closer in size to the resident (Fig. 1). For previously dominant residents, the curve started above 0.5, indicating that they initially began with a high chance of winning (greater than 50%) compared to the previously subordinate residents. Therefore, any size advantage given to a previously dominant resident only increased its chance of winning slightly, as illustrated by the gentle slope of the curve (Fig. 1a). Previously subordinate residents, however, had a dramatically increased chance of winning with only a small size advantage, highlighted by the steepness of the curve (Fig. 1b). For an intruder to have an equal chance of winning against a resident (regardless of behavioural history), it needed to have a greater size advantage. For previously subordinate intruders (bent curve) to have an equal chance of winning against dominant intruders (straighter curve), they needed to be closer in size to their competitor (Fig. 1). Previously dominant residents that were size-matched to their competitor had a higher chance of winning than previously subordinate residents (approximately 60% and 50%, respectively), with a similar pattern shown for dominant and subordinate intruders (approximately 40% and 25%, respectively; Fig. 1).

Aggression

Residents were more aggressive than intruders when they were larger than or similar in size to the intruder, but aggression between residents and intruders was not as intense when they were similarly sized (residency: $F_{1,243} = 7.301$, $P = 0.007$; size difference: $F_{2,243} = 8.195$, $P < 0.001$; Fig. 2). The highest level of aggression was witnessed between a previously subordinate resident paired against a smaller, previously subordinate intruder, during which the resident chased the intruder 20 times throughout the 3 min observation period. Level of aggression was not affected by behavioural history ($F_{2,243} = 0.548$, $P = 0.579$), but larger, previously dominant and subordinate fish were more aggressive than individuals that were similar in size to their competitor, which were again more aggressive than individuals that were smaller than their competitor ($F_{2,243} = 34.242$, $P < 0.001$; Fig. 2).

Habitat Use

Size and residency affected the vertical positioning of individuals on a patch (size difference: $F_{2,243} = 6.334$, $P = 0.002$; residency: $F_{1,243} = 6.984$, $P = 0.009$; Fig. 3). Residents that were larger than intruders were higher on the patch than residents that were similar in size to intruders. Size-matched pairs were not separated by as much vertical distance on the patch as pairs where the resident had a size advantage, in which case the intruder generally stayed lower on the patch than the resident. Relative difference in height on the patch was not affected by behavioural history, but was affected by size differences between previously dominant and subordinate fish (behavioural history: $F_{1,243} = 0.222$, $P = 0.638$; size difference: $F_{2,243} = 28.785$, $P < 0.001$). Individuals with a size advantage occupied the higher parts of a patch compared to their smaller competitors, and similarly sized individuals were located closer in height to one another on the patch

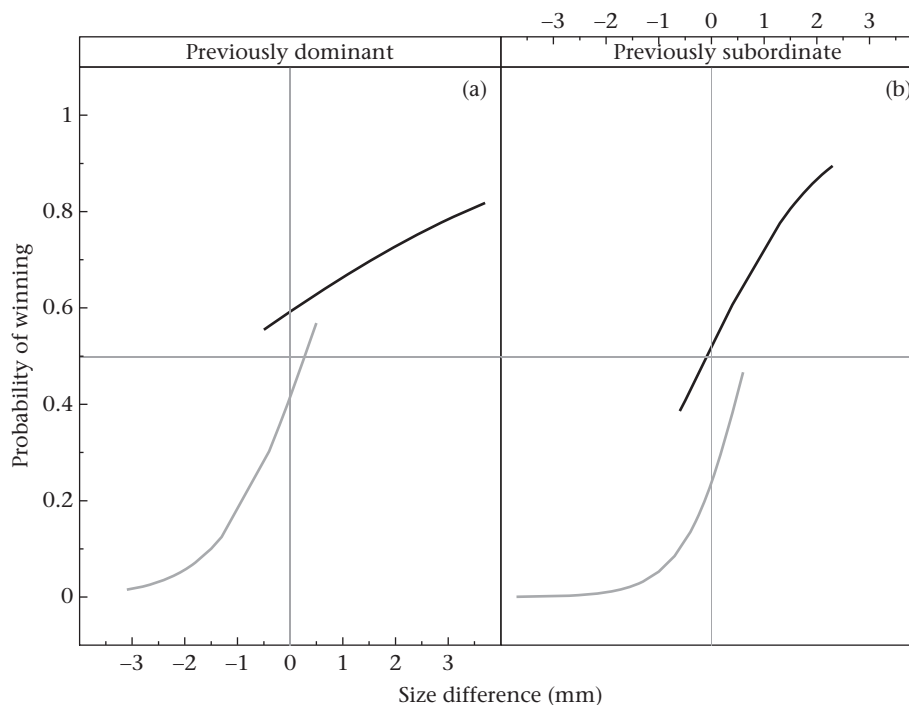


Figure 1. Logistic regression showing the probability of winning a paired encounter as a function of size difference, residency and behavioural history in coral reef damselfish, *Pomacentrus amboinensis*. Black lines represent residents, and grey lines represent intruders. Behavioural history is shown for (a) previously dominant and (b) previously subordinate individuals.

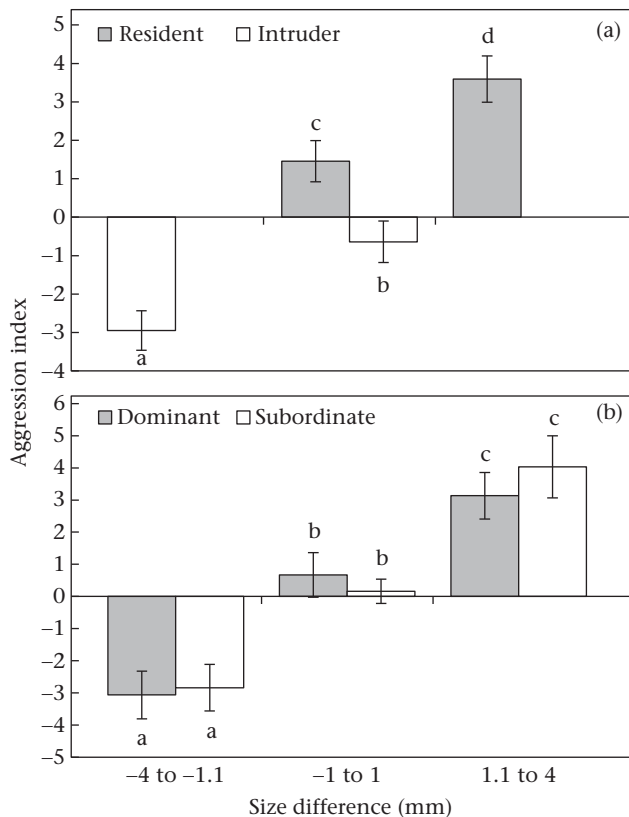


Figure 2. Mean \pm SE level of aggression during encounters between fish that were smaller than (-4 to -1.1 mm), of similar size to (-1 to 1 mm SL), or larger than (1.1 to 4 mm SL) their opponent: (a) residents and intruders; (b) fish that had been dominant or subordinate in previous encounters. A positive value means the individual 'won' the competitive interaction, and a negative value means they lost. Letters above or below bars represent Tukey HSD post hoc groupings of means.

compared to individuals with a substantial size difference (Tukey tests: $P < 0.001$; Fig. 3).

Residents did not venture as far away from the patch as intruders regardless of size differences ($F_{1,243} = 11.056$, $P = 0.001$), yet the relative difference in distance ventured was not affected by prior encounter outcome (Fig. 4). Larger dominants and subordinates, however, stayed closer to the patch than smaller individuals, and pairs that were similar in size did not venture far from one another ($F_{2,243} = 6.183$, $P = 0.002$; Fig. 4).

DISCUSSION

To understand what determines the successful acquisition of space on a habitat patch and to be able to predict what factors drive community structure, it is necessary to examine the outcomes of context-specific competitive interactions. Our study illustrates the importance of size advantages and residency in determining the success of intraspecific encounters in the damselfish *P. amboinensis*, but it also suggests that success in previous encounters has limited influence on winning future contests. Size had an overwhelming influence on the outcome of behavioural interactions at this vulnerable life stage, and a small size advantage of just 7% was enough to promote success regardless of interaction history or prior residency.

Size-related advantages are commonplace in many communities of organisms, but species differ in the extent to which size influences the outcome of competitive interactions (Chellappa et al., 1999; Jackson & Cooper, 1991). Our findings reveal that size greatly affects the outcomes of intraspecific interactions in

P. amboinensis, such that, as the size difference increased, it became the key factor accounting for winning the interaction despite the presence of other asymmetrical factors (residency and/or behavioural history). Even size differences of less than 1 mm ($\sim 7\%$ of mean length) could influence the outcome of a social interaction. This influence of small size differences is similar to the findings for this species when it competes with a congeneric at settlement (McCormick & Weaver, 2012), and for intraspecific interactions in several species of cichlids (Barlow, Rogers, & Fraley, 1986; Enquist & Jakobson, 1986; Turner & Huntingford, 1986). These studies suggest damselfishes may be as sensitive to size differences as other fishes, but it is unclear how they compare to other organisms (for example, insects or amphibians) because so few studies examining size effects report the exact size differences examined.

The influence of size on behaviour suggests that size is important to an individual's success. Our results demonstrated that larger individuals were more aggressive and were on average located closer to the habitat patch than smaller individuals, which ventured further away from the patch where they were at a higher risk of predation (Holbrook & Schmitt, 2002). Although we suggest this may have been a result of smaller individuals being chased to the edges (McCormick, 2009), it might have also been a result of the efforts of small fish to gain access to food (Webster, 2004). Most theory would suggest, and many other studies have found, that individuals that are similar in size are generally more aggressive towards one another than those differing in size (e.g. Chellappa et al., 1999; McCormick, 2009; Turner & Huntingford, 1986). This is contrary to our findings for damselfish, where aggression was

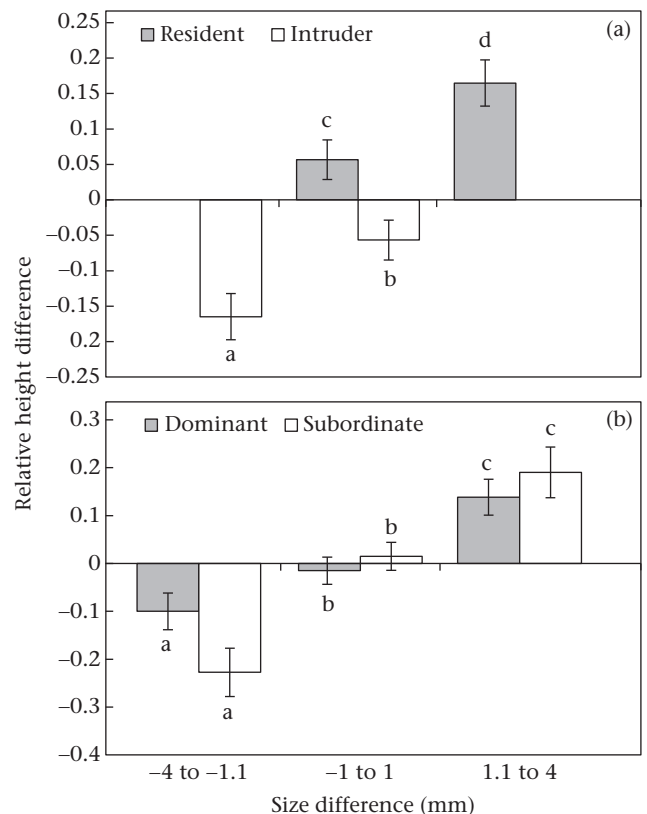


Figure 3. Mean \pm SE relative difference in height on the habitat patch during paired encounters between individuals that were smaller than (-4 to -1.1 mm), of similar size to (-1 to 1 mm SL), or larger than (1.1 to 4 mm SL) their opponent: (a) residents and intruders; (b) dominants and subordinates. A positive value means the individual was on average higher on the patch than their competitor, and a negative value means they were lower on the patch. Letters above or below bars represent Tukey HSD post hoc groupings of means.

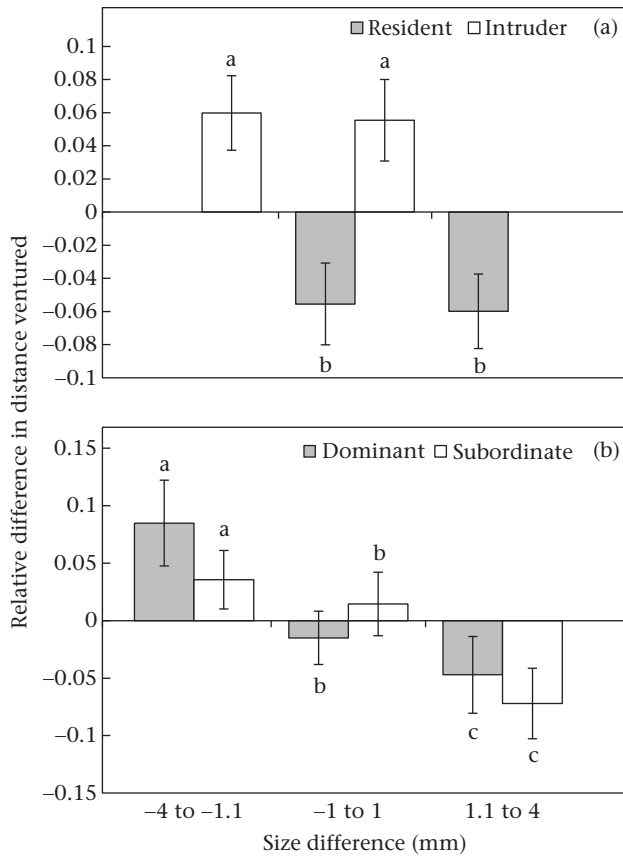


Figure 4. Mean \pm SE relative difference in distance moved away from the habitat patch during paired encounters between individuals that were smaller than (-4 to -1.1 mm), of similar size to (-1 to 1 mm SL), or larger than (1.1 to 4 mm SL) their opponent: (a) residents and intruders; (b) dominants and subordinates. A positive value means the individual was on average further away from the patch than their competitor, and a negative value means they were closer to the patch. Letters above or below bars represent Tukey HSD post hoc groupings of means.

lower for similarly sized opponents, and to the findings of Evans and Shehadi-Moacdieh (1988) for prawns, *Palaemon elegans*, where stalemates were more frequent between size-matched individuals. It is possible that this could be because size-matched individuals may take longer to establish a winner, forcing them to interact more frequently (Evans & Shehadi-Moacdieh, 1988), resulting in a longer but less intense fight. We found that size-matched individuals shared similar areas of the patch and were often observed closer to one another, suggesting that their encounters were more evenly balanced. Our findings demonstrate that size contributes more to monopolization of space and high social rank in *P. amboinensis* than other asymmetries examined. We also demonstrated that the level of aggression was important in determining space acquisition, which was more profound when size asymmetries existed.

In competitive scenarios where no size asymmetries exist, there are other factors that drive individual success and resulting community dynamics (Beaugrand et al., 1996). The present study demonstrates the importance of prior residency effects, whereby residents had an ecological advantage through prior knowledge of the habitat. For organisms with complex life cycles (Wilbur, 1980), such as most fishes and amphibians, individuals experience ontogenetic niche shifts, and the ability to time these shifts to optimize fitness is vital for future success. Therefore, the order in which individuals arrive at a habitat has important consequences for the establishment of social hierarchies and affects their chances of

survival. While research demonstrates that prior residency has growth and survival benefits (Geange & Stier, 2009; Shorrock & Bingley, 1994; Tupper & Boutilier, 1995), the underlying behavioural mechanisms involved are not well understood. In our study, residents that were more aggressive also occupied higher areas of the habitat. This may have resulted from a covariance of aggression and activity, with residents spending more time at the top of the habitat patch simply because they were more active. Previous studies of planktivorous damselfish have also found that dominant individuals often occupy areas higher and further out into the current where they achieve higher feeding rates (Forrester, 1990; Meekan, von Kuerthy, McCormick, & Radford, 2010). This suggests that the initial prior residency advantage can be maintained through the aggressive assertion of dominance, which leads to higher feeding rates, growth and subsequently size advantages (O'Connor, Metcalfe, & Taylor, 2000).

The outcome of context-specific scenarios may change as a result of differing temporal scales of priority effects. The priority period of 3 h in our study, similarly to Beaugrand et al. (1996), was enough time for individuals to establish themselves on the habitat patch, as this is done rapidly in damselfishes (Almany, 2003), which would otherwise face death (McCormick & Weaver, 2012). Studies of a variety of species that have examined priority effects over more than one temporal scale have found that the strength of interactions increases as the priority period increases (Geange & Stier, 2009; Hodge, Arthur, & Mitchell, 1996; Sandell & Smith, 1991). It is likely that the relative importance of priority effects will depend on the magnitude of the prior residency period because individuals more experienced with a habitat may have a greater propensity to engage in more aggressive interactions (Geange & Stier, 2010). The relative importance of priority effects found in the present study, while ecologically relevant to newly recruiting or migrating individuals, are likely to be contingent on the relative length of the priority period used.

In our study, prior winning or losing experience only influenced the probability of winning an encounter when both individuals arrived at a habitat patch about the same time and were similar in size. Ecologically, this is important because damselfishes arrive in pulses during the breeding season, like many other organisms (amphibians, insects, marine invertebrates; Pechenik, Wendt, & Jarrett, 1998; Vonesh, 2005), so individuals arriving together will be similar in size. At this time, their recent history of behaviour will be important in potentially determining their future success. Our findings show that previously subordinate intruders needed to be closer in size to their competitor than previously dominant intruders in order to have an equal chance of winning. These results are similar to those of Beacham (1988) and Beaugrand, Goulet, and Payette (1991) for a freshwater fish, and may be explained by the disadvantage of their subordinate behavioural history, suggesting small size differences would neutralize this behavioural history effect. This concept was more strongly demonstrated by Harwood, Griffiths, Metcalfe, and Armstrong (2003) in juvenile Atlantic salmon, *Salmo salar*, where the effects of residency and previous dominance rank are equally important, such that previously dominant intruders and previously subordinate residents have similar success. The mechanisms by which previous encounters prime a winner for future wins can be explained in part by learning or by changes in endocrinology, such as increased testosterone in winners (Johnsen & Zuk, 1995). This leads to behavioural changes such that an individual with a history of winning has a greater probability of attacking in future encounters (Hsu, Earley, & Wolf, 2006). In California mice, *Peromyscus californicus*, increased testosterone levels reinforce the 'winner effect', whereby an individual's testosterone level significantly increases after it has won two encounters and increases the probability of winning future

encounters when it has won three previous encounters (Oyegbile & Marler, 2005). Previously observing an encounter can also produce similar results, such as in fighting fish, *Betta splendens*, where individuals act more aggressively towards individuals that they had observed winning in a previous encounter against another individual (McGregor, Peake, & Lampe, 2001; also see Earley, Tinsley, & Dugatkin, 2003). It is clear that a history of winning encounters is beneficial for success in many organisms, and despite our results suggesting that behavioural history is important only when all else is equal (owing to residency status and size having stronger effects), the 'winner effect' has significant behavioural implications for future encounters.

Size, prior residency and behavioural history all influenced the outcome of interactions, but they differed in their relative importance depending on the level of asymmetry expressed in the other traits. An intruder (residency disadvantage) with a size advantage was just as likely to win an encounter as a resident (residency advantage) with a size disadvantage. It is clear that contest outcomes are highly dependent on who the individual is competing against, such that species identity has been shown to influence the outcome and strength of competitive interactions (Geange & Stier, 2009). Intense asymmetric competition plays a key role in determining the structure of social hierarchies (Geange, Stier, & Shima, 2013), which will ultimately influence the future success of individuals. Predation is often considered as the primary cause of mortality in newly recruited organisms (Almany & Webster, 2006; Petranka, 1983), but it is the competitive hierarchies present in communities of organisms that can influence an individual's risk of predation through differential activity patterns and space use (McCormick & Weaver, 2012). Rather than the selective loss of individuals of a particular phenotype (e.g. size) occurring through phenotypic selection by the predator, the selection can be mediated through competitive interactions causing differential exposure to predators that may be nonselective within the particular size range that they are morphologically constrained to eat (McCormick, 2009).

The present study highlights some of the key behavioural mechanisms that affect the small-scale distribution and composition of communities and circumstances under which conflict for space is intensified. It also recognizes that animal size and priority of access to resources are two particularly important traits that will influence the outcome of contests. Size differences, priority effects and behavioural history were all important, but to varying degrees, and acted in a hierarchical way to affect an individual's future success. These findings place emphasis on the deterministic factors at play immediately after arrival to the reef community. Further research is required to understand the relative importance of size, priority and behavioural history at higher densities of conspecifics, whether the relative importance of these factors are likely to change with ontogeny, and the extent to which the outcome is modified as habitats change.

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Appendix

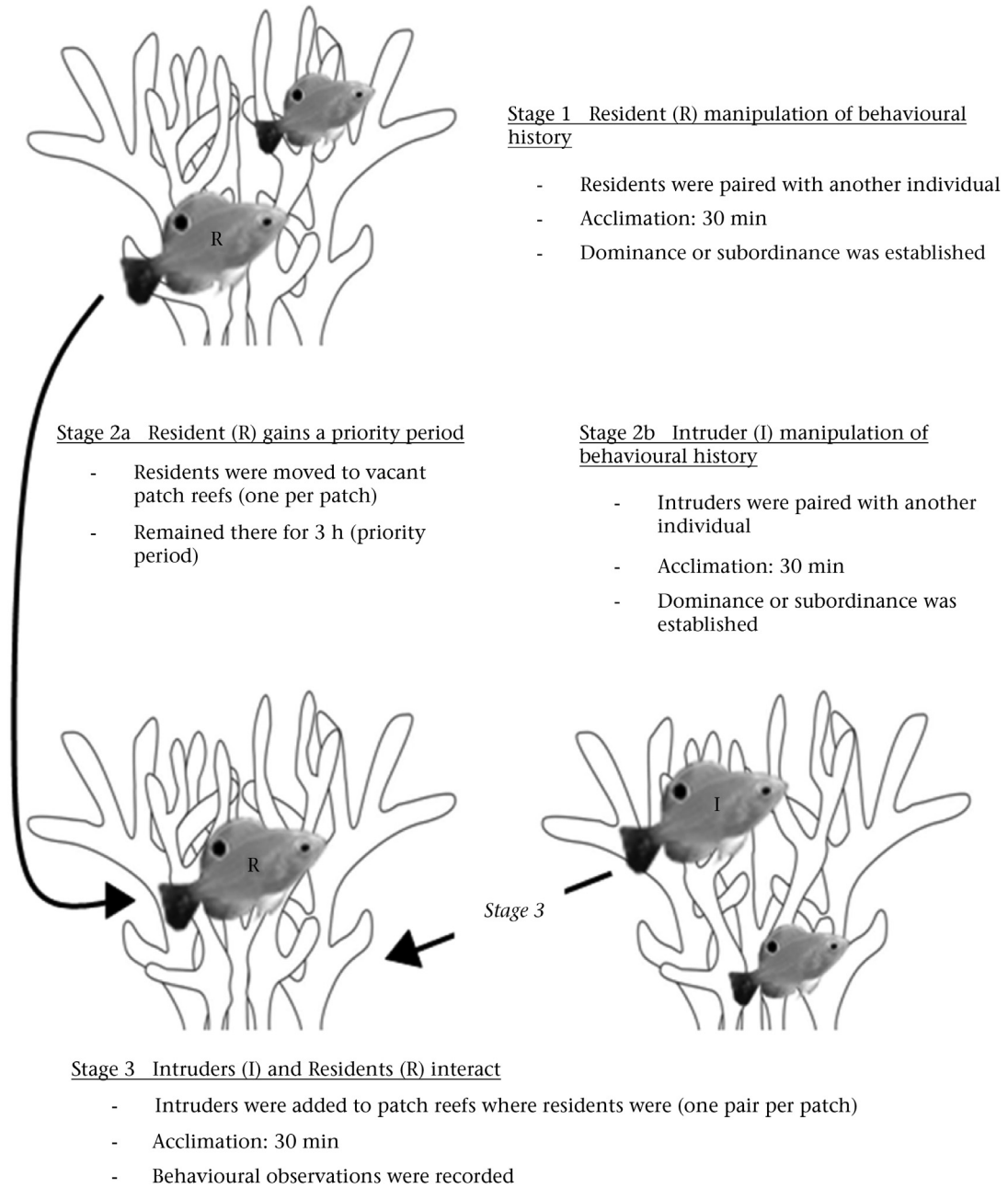


Figure A1. Flow diagram of methodology illustrating manipulation of behavioural history for residents and intruders, and priority period for residents, before they interacted.

Table A1

Pilot study results indicating that dominance or subordination status was quickly established

Pair	Individual	Positive (+) or negative (-) aggression index			Dominance ranking retained? (Y/N)
		30 min	1 h	4 h	
1	1a	+	+	+	Y
	1b	-	-	-	Y
2	2a	-	-	-	Y
	2b	+	+	+	Y
3	3a	+	+	+	Y
	3b	-	-	-	Y
4	4a	+	+	+	Y
	4b	-	-	-	Y
5	5a	+	+	+	Y
	5c	-	-	-	Y
6	6a	-	-	-	Y
	6b	+	+	+	Y

Dominant or subordinate status was quickly established from a positive or negative aggression index, respectively, where a positive index means the individual won the interaction. Dominance rankings determined after 30 min remained the same after 4 h (Yes/No represented by Y/N). Individuals in each pair were size-matched (<0.4 mm difference in standard length) and entered the patch reef simultaneously.