Short-term costs of relocating a territory in a Caribbean damselfish, *Stegastes diencaeus*

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ABSTRACT

Little is known about the costs of relocating a territory into an established neighbourhood. In this study we investigated short-term costs of relocation in the longfin damselfish, *Stegastes diencaeus*, on a fringing reef in Barbados. Experimental removals of residents created vacancies, and focal observations over two days examined the intensity and duration of behavioural changes in the newcomers. Newcomers used smaller territories than original residents, and exhibited increased movement, increased agonistic behaviour and decreased foraging. The behavioural changes suggest that energetics are a major cost to relocation, but that opportunity costs, predation risk and injuries are also important. Differences between strangers and expanding neighbours support the concept of 'dear enemy' recognition, but familiarity does not influence the agonistic behaviour initiated by these newcomers. The costs reported here represent important limitations to the mobility of individuals and provide insights into the stability of fish territories.

RÉSUMÉ

Peu d'information est connue sur les coûts reliés à la relocalisation d'un territoire vers un quartier établi. Dans cette étude, nous enquêtons sur les coûts à court terme liés à la relocalisation du démoiselle noire *Stegastes diencaeus*, sur des récifs coralliens aux Barbade. Les déplacements expérimentaux des résidents ont créé des places vacantes, et des observations visuelles, sur une période de deux jours, ont examiné l'intensité et la durée des changements comportementaux chez les nouveaux venus. Les nouveaux venus ont utilisé des territoires plus petits que les résidents originaux et ont démontré plus de mouvements, plus de comportements agonistiques et une diminution de recherche alimentaire. Les changements comportementaux sugèrent que la perte d'énergie est un coût majeur à la relocalisation, mais que les coûts d'occasion, les risques de prédation et les blessures sont aussi importants. Les différences entre les étrangers et les voisins prenant de l'expansion soutien le concept de reconnaissance du "cher ennemi", mais la familiarité n'influence pas le comportement agonistique initié pas ces nouveaux venus. Les coûts rapportés dans cette étude représentent des limites importantes à la mobilité et fournissent des perspicacités dans la stabilité de territoires de poisson.

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throughout my 26 years of curiosity

CONTRIBUTIONS OF AUTHORS

I planned the study in collaboration with my supervisor, who is second author on the manuscript. I was responsible for the collection of the data, the analyses, and for writing the first draft in consultation with my supervisor. Together we collaborated on the editing and polishing of the manuscript, producing the following work, which is planned for submission to the journal Animal Behaviour.

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ABSTRACT

Relocation of territories is important for ontogenetic shifts in habitat preference and establishing patterns of population distribution in the reef system. However, relocation occurs relatively rarely, suggesting that it may be costly. Although the costs of movement between social groups are well studied, the costs of movement between territories remain poorly documented. We investigated the short-term costs incurred by newcomers settling into an established neighbourhood of longfin damselfish, *Stegastes diencaeus*, on a fringing reef in Barbados. Experimental removals of residents created vacancies, and focal observations over two days examined the intensity and duration of behavioural changes in the newcomers. Newcomers used smaller territories than the original residents, and exhibited increased movement, increased agonistic interactions and decreased foraging. Differences from original residents gradually declined over the two-day period, except for space use, which changed little. The behavioural changes suggest that energetics are a major cost to relocating territories, but that opportunity costs, predation risk and injuries are also important. Differences between strangers to the neighbourhood and expanding neighbours in behavioural changes support the concept of 'dear enemy' recognition. However, familiarity did not affect the number of agonistic events initiated by newcomers. The costs observed in this study represent important limitations to the mobility of individuals settling into a vacancy, yet are relatively small compared to the costs of evicting a territorial owner. This study offers a first look at the costs of individual mobility in a territorial system, and could provide insight into the stability of fish territories.

INTRODUCTION

An important influence on the mobility of animals may be the costs associated with becoming familiar with a new physical, biotic and social environment. Sociobiologists have long recognized the role of aggression in establishing the dominance hierarchies that exist in many social groups (Wilson 1975). Because of this, previous studies have focused on measures of increased aggression and decreased rank associated with movement between social groups. These include theoretical (Pagel & Dawkins 1997; Broom 2002) and empirical studies in both the laboratory (Blanckenhorn 1992; Moore et al. 1993; Alley & Fordham 1994; Cristol 1995) and the field (Baker & Dietz 1996; Drews 1996). Despite the numerous studies on movement between groups, remarkably few studies have investigated the social costs of moving between territories. Work on movement in territorial systems has focused on the mechanisms involved in establishing a territorial mosaic (Getty 1981; Stamps 1992; Stamps & Krishnan 1994a; Stamps & Krishnan 1994b), and little work relates specifically to the dynamics of immigration into established neighbourhoods.

Relocation to a new territory is potentially associated with an increased predation risk and the allocation of time and energy to acquiring information and to establishing social relationships with new neighbours (Kramer & Chapman 1999; Stamps 2001). If large, such costs might make relocation uneconomical and contribute to site fidelity in territorial animals. Very few studies have examined the magnitude or duration of potential costs of relocation, although the limitations that they place on the mobility and behaviour of relocating individuals are implied in a number of studies through measures such as switching residency, differences in behaviours types of floaters and territory owners and changes to territory area due to removals and introductions (Krebs 1971; Boutin & Schweiger 1988; Shutler & Weatherhead 1991; Stamps & Krishnan 1995; Stamps & Krishnan 1997; Tobias 1997; McMann 2000; Meadows 2001).

Behavioural measures indicating significant potential costs to relocation have been reported in studies focused on other questions. Investigations of increased predation risk associated with unfamiliarity with the home range (Clarke et al. 1993; Larsen & Boutin 1994; Waser et al. 1994) have never discussed movement of individuals between neighbourhoods. Similarly, studies of resource use (Pusenius et al. 2000) and movement (Jacquot & Solomon 1997) in immigrant voles (*Microtus* sp.) made no inferences about fitness costs for individuals attempting to establish a new territory. The phenomenon of 'dear enemy' recognition is the basis of a well-developed body of literature that documents an increase in agonistic interactions during encounters between unfamiliar individuals. A number of different taxa exhibit 'dear enemy' recognition, including fish (Hojesjo et al. 1998; Leiser & Itzkowitz 1999; Leiser 2003), amphibians and reptiles (Jaegar 1981; Husak & Fox 2003), birds (Eason & Hannon 1994; Hyman 2002), and insects (Langen et al. 2000). Eason & Hannon (1994) considered implications of 'dear enemy' for settling in a new territory, but their study only considered behavioural changes from the perspective of the neighbours.

We found only two studies that measured the intensity and duration of costs associated with the arrival of a newcomer to an established neighbourhood of territories. Both studies were designed to address other issues, so the actual impacts of the relevant costs were not fully discussed. Tobias (1997) studied the 'owners always win' convention in European robins, *Erithacus rubecula*. The study observed decreased foraging and increased territorial singing in newcomers, and suggested that lower costs to newcomers would accelerate a shift in residency (Tobias 1997). Meadows (2001) investigated differences between territories on the edge and territories in the middle of a reef spur neighbourhood of threespot damselfish, *Stegastes planifrons*. The study considered recolonization time as a measure of territory quality, and observed increased chase behaviour in settling newcomers (Meadows 2001).

Many studies have proposed that territorial relocations of post-settlement individuals play an important role in determining the structure and function of the reef system through such processes as ontogenetic shifts in habitat preference and recovering population distributions after mortality events (Robertson 1988; Jones 1991; Lirman 1994; Frederick 1997b; Kramer & Chapman 1999). However, it is generally accepted that certain reef fish are strongly philopatric (Sale 1978), which would suggest that the natural rates of movement are low, and that the costs of relocation are potentially high. The current study presents the results of a series of removal experiments that investigate the short-term costs of settling into an established territorial neighbourhood. We accomplish this by examining the magnitude of changes in the behaviour of longfin damselfish, *Stegastes diencaeus*, over a 2-day period following relocation into experimentally created vacancies in preferred habitat. If relocation decisions are dependent upon the benefits and costs of moving, vacancies in preferred habitat are expected to generate immigration, even if the costs of moving are high. The removals simulate a vacancy created by a predation event or emigration from the neighbourhood.

Longfin damselfish are highly territorial benthic herbivores that form a mosaic of territories across much of the substrate on fringing reefs in Barbados. Herbivorous damselfish are recognized as highly site-attached fish (Sale 1978), yet territory relocation does occur in this species (McDougall 2000; Cheney & Côté 2003). Previous studies indicated that reef spurs are preferred habitat with high densities of adult fish, while rubble grooves are secondary habitat with lower densities, more juveniles and fewer and smaller adults (McDougall 2000). With contiguous territories averaging only 1 m^2, the longfin damselfish makes an ideal subject for neighbourhood-level studies of territoriality.

We expected that newcomers to an experimental vacancy in a territory mosaic would incur costs associated with learning feeding and shelter sites, establishing relationships with owners of neighbouring territories, and defending the territory against both expansions by neighbours and other potential immigrants. We assumed that such costs were measurable through quantifiable changes in space use, movement, agonistic behaviour, and feeding. Furthermore, we predicted that differences from original residents would gradually diminish as the newcomer became established in the new territory.

METHODS

Study Population and site

We studied longfin damselfish on North Bellairs and South Bellairs Reefs, fringing reefs located on the west coast of Barbados, West Indies, described by Lewis (1960), and contained within the Folkestone Marine Park and Reserve. Focal observations provided initial estimates of territory boundaries based on space use.

Although space use indicates the home range boundaries and not the actual defended area, home ranges and territories appeared equivalent in area for our population. A similar relationship occurred in a related species studied by Meadows (2001), but see also Robertson et al. (1981).

PTM and an assistant collected data using SCUBA and underwater dive slates during daylight hours from March 1 to July 1 2002. Damselfish are generally active only between dawn and dusk (Collette & Talbot 1972). We used a modified cast-net to catch individuals for marking, using an injection of Visual Implant Fluorescent Elastomer (VIE, Norwest Marine Technologies) tagging product under the scales (Frederick 1997a). Individuals were also sexed by in situ examination of the shape of the genital papillae (Thresher 1984) and measured (total length in mm). All marking, sexing and measuring took place underwater.

Removal experiments

In reef spur habitat, we identified 20 neighbourhoods consisting of six to nine adjacent territories of adults where one or two large, central individuals had neighbours on all sides. In some cases, one neighbour, but never more, was the dusky damselfish, *Stegastes dorsopunicans*, a closely related species that also holds non-overlapping territories on the reef substrate. Duskies did not recolonize vacated territories and contributed little to the agonistic interactions of the neighbourhood. They are included in the conspecific totals for the analysis of agonistic behaviour. Selection of the neighbourhoods was haphazard, except that egg-guarding males were excluded from the central positions. We captured, marked, sexed and measured all but the central individuals of the neighbourhoods. We then mapped out the territories of the centrally located individuals using a grid system of 25 cm by 25 cm squares, marking the points of intersection with small bleached coral pebbles. These measurements were completed at least 18 hours prior to the first focal observations. In preliminary trials, the behaviour of the residents of the neighbourhoods had returned to normal levels by this time.

Preliminary trials also suggested that fish might have difficulty occupying a single vacated territory so treatments involved removing either one or two adjacent fish. Each data block consisted of a control neighbourhood (observations by PTM), a single removal neighbourhood (observations by PTM) and a double removal neighbourhood (observations by assistant) all located in the vicinity of one another. The number of individuals contained in the neighbourhood depended on the treatment type. A total of 10 blocks were completed. Each block lasted approximately three days, with three periods of focal observations per day (0900 hours, 1200 hours and 1500 hours). The first focal observations of the period started at 0900, and the second started 20 minutes afterwards. Each focal period included four focal observations, one for each central territory (one control, one single removal and two double removals), resulting in a total of 12 focal observations per day, and 36 focal observations per block.

We performed focal observations on the original residents (N = 29) (the eighth block consisted of two single removals instead of a single and a double removal) and controls (N = 10) during the first day of the data block. At the end of the first day of observations, the original residents were removed from the single and double-removal neighbourhoods, measured, sexed and euthanized, and the neighbourhoods were left undisturbed. All removals occurred prior to 1700 hours. Newcomers arrived by the first focal period of the following day. Neighbours frequently expanded into the vacated territory, effectively excluding unfamiliar newcomers from the neighbourhood. Studies report similar patterns in other removal experiments (Paterson 2002; Cheney & Côté 2003). Therefore newcomer type, stranger or expanding neighbour, was included as a treatment as well. We performed six focal observations on each of these newcomers over a span of two days. The data block was concluded when six consecutive focal observations on a newcomer were successfully completed. In three instances strangers arrived at the start of the second post-removal day, and successfully evicted the expanding neighbours who had occupied the focal territory during the previous day. In these cases, the six focal observations counted from the beginning of the second-post removal day. Two newcomers without a full complement of six focal observations were omitted from the analysis. The final sample sizes consisted of 12 strangers and 15 expanding neighbours.

Focal observations consisted of observations made at 5-sec intervals for a total of 20 minutes (240 intervals per focal observation). Each interval included a record of the location of the focal fish on the grid, and measures of movement, agonistic behaviour and foraging during that interval.

Space use

Space use is a measure of the functional territory area of the focal fish during a 20-min focal observation. The measure of space use is based on the total number of grids that an individual visited over the course of a 20-min focal observation. When a focal fish occupied two grids during one interval, we assigned the visit to the grid that the fish used the most. When a fish occupied three or more grids in one interval, we recorded it as movement and did not record a grid location. The measure of space use was the number of grids visited divided by the total number of grids in the territory. The total number of observations varied slightly as a result of differences in movement and in time spent outside of the territory. Space use data were normally distributed so no transformations were performed.

Movement

The movement index is a measure of non-aggressive and non-foraging activity of the focal fish. We recorded movement when a focal fish visited three or more grid squares during a single 5-sec interval, and did not engage in agonistic or foraging behaviour. Movement was not recorded when individuals were outside of the focal territory and therefore off of the grid system. The movement index consisted of the number of intervals of recorded movement in the 20-min focal observation divided by the number of minutes the fish was present in the territory and multiplying by 20 (maximum of 240). The data required a $\log_{10}$ transformation in order to satisfy assumptions of normality.

Agonistic behaviour

Agonistic behaviour of the focal fish included chases, displays and fights with conspecifics and duskies, as described by Rasa (1969) and Myrberg (1972). We recorded the identities of both participants in an agonistic event, and categorized the events as chases by focal fish, displays by focal fish, fights, chases by conspecifics, and displays by conspecifics. Multiple fights, chases or displays could occur in one interval, provided that each event was distinct. A chase or display simultaneously directed at more than one individual was counted as a single event. We only counted one event if an action lasted for the duration of the 5-sec interval, but we recorded a second, separate event if the action lasted into a second interval. The measure of agonistic behaviour included events from off of the grid area. This was most important in the case of expanding neighbours defending their original territories. We estimated the total number of agonistic events during the data series by assuming 12 hours of activity per day, and using behavioural rates measured for the three different periods of the day to extrapolate an overall daily total. To satisfy assumptions of normality, we used a square root (x + 3/8) transformation.

Injury and scarring

We recorded damage to the body and fins of the newcomers just prior to the first post-removal focal observations in order to identify individuals over the course of the data block. These records described the placement of key distinguishing scars and provided a qualitative description of the condition of the individual. We updated the descriptions if additional scarring occurred over the course of the data block. We ranked individuals on a qualitative scale of 0 to 3 where 0 was equivalent to no evidence of damage to either fins or body and 3 represented heavy scarring and/or fraying of the fins. Scars consisted of whitish marks on the body surface and were generally larger than a single missing scale. Fraying was heaviest on, but not restricted to the inter-ray tissue of the caudal and dorsal fins. We observed pectoral fin and anal fin damage at lower frequencies. Analysis of the injury/scarring data used a non-parametric Kruskal-Wallis test.

Foraging rate

Foraging rate was measured as the number of bites at the substrate per minute. Longfins feed primarily on the thin algal film covering hard surfaces. Feeding bites consisted of a sharp jab at the substrate along with a jerking of the body, similar to the "feeding snaps" described by Rasa (1969) and the "nips" described by Myrberg (1972). Each 5-sec interval included a count of the foraging bites taken by the focal fish. The foraging rate consisted of the total number of bites in the 20-min focal observation divided by 20 to give a rate of bites per minute. The measure of foraging included bites outside of the focal territory, most notably for expanding neighbours who often foraged on their original territories. We estimated total foraging bites taken during the data block by assuming 12 hours of activity per day, and using bite rates measured for the three different periods of the day to extrapolate an overall daily total. We performed a $\log_{10}$ transformation of the data in order to satisfy assumptions of normality.

Analysis using a General Linear Model Repeated Measures test (GLM RM) indicated a significant difference between PTM and the assistant in the recording of foraging rate in the 29 original residents. We calculated the mean difference between observers, and corrected the measurements of the assistant to those of PTM by subtracting the mean difference (Price & Grant 1984). (Please see Appendix II for further explanation.)

Statistical analysis

We analyzed all behavioural measures using the same series of statistical tests, unless otherwise indicated. The first test consisted of a GLM RM investigating the effects of time, fish size, type of newcomer (stranger or expanding neighbour) and type of removal (single or double) on the behaviour of newcomers across the six post-removal focal observations. We included fish size as a covariate because previous studies demonstrated an important effect of size on the behaviour of damselfish (McDougall 2000). A subsequent GLM RM investigated the difference between the two separate days of newcomer observations. We then performed a set of two GLM RMs that compared the first and second days of post-removal focal observations of newcomers separately to the pre-removal focal observations of original residents. A post-hoc Bonferroni test identifying differences between the three fish types (strangers, expanding neighbours and original residents) followed each test. Removal type was not included in this analysis because there were no significant effects in the first set of tests for any of the behaviours (see Table 1). An identical set of analyses comparing newcomers with controls is included as an appendix (Appendix III). Original residents represent a spatial control to the newcomers, while control fish represent a temporal control for effects of the observer, and changing environmental conditions.

A last GLM RMs involved just the focal observations of the controls and original residents. It investigated the effects of gender and fish size on the pre-removal behaviour of controls and original residents, and also determined the significance of any differences between the two types of fish. Gender and fish size rarely had significant effects on the behaviour of original residents and controls (Appendix IV), and fish size did not have a significant effect on the behaviour of newcomers (see Table 1), so neither will be discussed further. Similarly, there were no observed differences between controls and original residents (Appendix IV).

An outlier in the agonistic behaviour was removed from the analysis. A single stranger in the fifth post-removal focal observation fought 16 times when all others had a total count of zero. The data point was more than three standard deviations away from the mean, and the point was the highest fight total for any other fish at any other time by a factor of three.

RESULTS

Size and sex of replacements

Newcomers (108.0 ± 11.5 mm) were consistently smaller than original residents (114.9 ± 6.7 mm) by a mean difference of 6.9 ± 7.8 mm or 6% of original residents' size (Paired sample t-test: t = 4.467, df = 26, $P < 0.001$). Strangers (109.8 ± 13.7 mm) and expanding neighbours (106.5 ± 9.5 mm) did not differ significantly in size (Two sample t-test: t = 0.627, df = 25, $P = 0.536$) or in the size difference between newcomer and original resident (strangers: 7.0 ± 9.0 mm; expanding neighbours: 6.8 ± 7.2 mm; Two sample t-test: t = 0.065, df = 25, $P = 0.949$). Furthermore, size of the original resident did not have an effect on newcomer type (residents replaced by strangers: 116.8 ± 7.5 mm; residents replaced by expanding neighbours: 113.3 ± 5.8 mm; Two-sample t-test: t = 1.306, df = 25, $P = 0.204$). Newcomers (108.0 ± 11.5 mm) were significantly larger than the mean size of the neighbouring individuals (101.7 ± 8.7 mm; Paired sample t-test: t = 2.362, df = 26, $P = 0.026$).

Females recolonized territories originally held by females at a greater frequency than expected if recolonization was due to random selection by newcomers (12/15; X^2 with Yates correction = 6.30, df = 1, $P < 0.025$). Males demonstrated a similar pattern (11/12; X^2 with Yates correction = 4.95, df = 1, $P < 0.05$). There was however, no pattern to suggest that strangers were more likely to recolonize male territories (6/12) or female territories (6/15) than expected by chance (X^2 with Yates correction: Male = 0.009, df = 1, $P > 0.90$; Female = 0.008, df = 1, $P > 0.90$).

Expanding neighbours spent the least amount of time inside of the focal territory (77.8%) as compared to strangers (96.4%), original residents (98.2%) or controls (99.2%) [ANOVA: F = 67.085, $R^2 = 0.762$. $P < 0.001$; Post-hoc Tukey: $P < 0.001$ for all pair wise comparisons with expanding neighbours; all other fish types were not significantly different ($P > 0.5$)].

Space use

Strangers visited significantly less of the focal territory than did original residents (Fig. 1, Table 2). During the first post-removal focal observation, they visited 72% of the total number of grids (75% of the grids that original residents typically visited; Fig. 1). By the second observation, the average proportion of grids was slightly higher (78%) and remained unchanged over the next four observations (Table 1). Levels did not change significantly across either post-removal day (Table 2), nor were the first and second post-removal days significantly different from one another (GLM RM: F = 0.023, df = 1, $P > 0.75$). During the final observation period, strangers visited 80% of the total territory, which was roughly 15% less than original residents and controls. Comparisons with control fish show the same pattern (Appendix III).

Expanding neighbours visited 88% of the focal territory during the first focal observation, 7% less than original residents (Fig. 1). This difference was marginally non-significant over the first day of post-removal observations ($P = 0.068$), but was significant over the second day (Table 2). The difference between the strangers and the expanding neighbours was not significant on either the first or second post-removal days, although the difference in the first focal observation following removal was significant (Two sample t-test: t = 2.2, df = 26, $P = 0.037$).

Movement

Strangers moved around the territory much more than either original residents or controls (Fig. 2, Table 2). During the first observation period, they moved three times as much as original residents. The rate of movement decreased during both the first and second days following removal of the original residents. By the second post-removal day, movement was less than on the first day (GLM RM: F = 10.3, df = 1, $P < 0.01$), and slightly but not significantly greater than original residents (Table 2) or controls (Appendix III).

Expanding neighbours exhibited a movement index that was roughly 3.6 times the levels observed in original residents during the first observation period (Fig. 2). Movement in expanding neighbours did not decrease as greatly over the first day of observations, or between the first and second days, as indicated by the interaction between Time and Fish Type for the newcomers (Table 1). The difference between strangers and expanding neighbours was not significant on the first day following removal, but was over the course of the second day, when expanding neighbours showed more than twice as much movement as strangers (Table 2). The patterns were the same for expanding neighbours when compared with control fish (Appendix III).

Agonistic behaviour and injuries

Strangers exhibited a large increase in aggressive behaviour. In the first focal observation following the removal of original residents, strangers performed on average 10.9 chases, 7.4 displays, and 1.0 fight per 20-min period. This corresponds to 10-fold, 17-fold and 15-fold respective increases over original resident and control behaviours (Table 2, Fig. 3a, b, c). Strangers also experienced an average of 3.7 chases and 2.9 aggressive displays by conspecifics in the same period. This corresponded to 11-fold and 15-fold respective increases from baseline levels (Fig. 3d, e). Most chases and displays involved neighbours, but the majority of fights involved unidentified longfins apparently seeking to occupy the focal territory.

At the first observation on the morning following removal of original residents, strangers occupying the territory already exhibited heavy scarring and shredding of fins (2.5 on a scale of 3.0). This indicates that elevated levels of aggression had occurred prior to the first focal observation, despite a maximum of only four hours of daylight since the experimental removal occurred (approximately an hour in the evening post-removal and three hours pre-observation in the morning).

Agonistic levels in strangers declined over the course of the first day following the removals, yet remained significantly higher than values of original residents (Table 2). The decline in fighting over the first post-removal day was not significant, but the decline over the six post-removal focal observations was significant (Table 1). In general, the decrease in agonistic behaviours had leveled out by the second post-removal day, and in all behaviours except fights, the second post-removal day was lower than the first post-removal day (GLM RMs: Chases by focals: F = 5.2, df = 1, $P < 0.05$; Displays by focals: F = 14.1, df = 1, $P < 0.001$; Fights: F = 2.6, df = 1, $P > 0.05$; Chases by conspecifics: F = 6.3, df = 1, $P < 0.05$; Displays by conspecifics: F = 16.3, df = 1, $P < 0.001$). Strangers maintained elevated agonistic levels through the last three focal observations of the data series, although the difference was not significant in the case of chases by focals (Table 2). We observed similar patterns when comparing strangers to controls (Appendix III).

Over the two-day period following the removals, strangers on average performed approximately 400 chases and 280 displays, were the target of about 150 chases and 115 displays, and participated in approximately 30 fights. This compares to control counts of 100, 25, 20, 15 and 0, respectively, over the same time period. These estimates are probably conservative since they do not account for the potentially intense rate of aggression during the first few hours of settlement.

Like strangers, expanding neighbours showed an increase in agonistic behaviour as compared to original residents and controls (Fig. 3). During the first observation following the removals, expanding neighbours performed 7.3 chases, 6.6 displays and 0.44 fights on average. Like strangers, they exhibited scarring and shredding of the fins, although the level of injury was significantly lower (0.9 out of 3.0, Kruskal-Wallis: U = 176.0, $P < 0.001$). Over the course of the first post-removal day, expanding neighbours performed more chases, displays and fights than original residents or controls, although the difference in fights was not significant in the comparison with controls (Table 2, Appendix III). On the other hand, chases and displays received from conspecifics, although higher on average, were not significantly different from original residents and controls. However, they were significantly lower than agonistic levels observed in strangers across both days of observations (Table 2). As a departure from the above patterns, expanding neighbours performed significantly more chases than both original residents and strangers over the second post-removal day (Table 2).

Overall, differences between the two newcomer types tended to be greatest in agonistic events received as compared to events initiated. On the second post-removal day, the rates of agonistic behaviour of expanding neighbours had decreased to levels roughly equivalent to original residents and controls. Significant differences only remained in chases and displays initiated by the expanding neighbour.

Foraging rate

All four fish types exhibited strong diurnal patterns of foraging, characterized by low morning rates followed by sharp increases in the noon and afternoon rates (Fig 4, highly significant effect of time in Table 2). Strangers and expanding neighbours did not differ significantly in their foraging rates across the six post-removal focal observations (Table 1) and exhibited very similar values, so they will be considered together.

Newcomers foraged at a reduced rate as compared to original residents and controls (Fig. 4). They exhibited a drop of 25% in the first observation period following the removal, and this difference persisted over the first day (Table 2, Appendix III). On the second post-removal day, foraging rates in newcomers had returned to normal on the first observation period, but remained slightly, though not significantly lower at approximately 85% of original resident values during the last two periods. Newcomers exhibited an overall foraging rate 10% lower than original resident levels for the second post-removal day. The difference between the two days was marginally non-significant (GLM RM: F = 3.1, df = 1, $P = 0.084$).

Based on average foraging rates over the two days, newcomers are estimated to have taken 8600 bites compared to the 10,250 bites of controls during the same time period. That corresponds to 1650 fewer bites, or a 16% decrease.

Correlations

We did not observe significant correlations between foraging rates and total agonistic events across any of the three pre-removal focal observations of original residents and controls combined (Table 3). Neither did we observe significant correlations between foraging rates and movement, except for a marginally significant correlation during the third focal observation. However, significant positive correlations existed between total agonistic events and movement (Table 3). Similar patterns were evident in the strangers across the six observations, although correlations between movement and agonistic events generally had associated probabilities slightly higher than the alpha of 0.05 ($P < 0.08$), despite similar correlation coefficients (Table 4). This was perhaps due to differences in sample size. Although not a strong pattern, the trend is different than the same set of correlations in expanding neighbours. Furthermore, in five of the six post-removal focal observations of expanding neighbours, foraging rate was strongly and negatively correlated with agonistic events (Table 4).

DISCUSSION

Behavioural Changes

Space use

In our study, strangers held a smaller territory than the previous occupants. Two studies that performed removals on the same species observed boundaries that remained similar after recolonization by newcomers (McDougall 2000; Cheney & Côté 2003). This difference may result from the fact that the first two studies were not designed for fine scale measurements of recolonized territory area. One of the few other studies that considered space use was a study by Tobias (1997) that reported a 60% decrease in territory size of European robins when original residents resettled after a temporary removal in spring. Encroachment by neighbours was suggested as the cause of this loss. This was much more than the initial 25% decrease from original resident territory area observed in our study, yet the cause of the space reductions are likely the same. It is unlikely that 25% of a vacant territory would remain unused by the newcomer as well as the surrounding fish. Expanding neighbours also end up using a smaller territory area than the original occupants by approximately 8%. However, the fact that expanding neighbours also hold their original territories suggests that the substantial encroachment of other neighbours observed with strangers does not occur to the same degree for both newcomer types. Familiarity of the newcomer may play a role in determining how much of the original territory is lost to encroachment by individuals of the neighbourhood.

The observed decrease in space use could result from the confounding effect of movement. Since space use excludes measures of movement, individuals that spend more time moving have fewer overall measures of space use and this could result in a smaller observed territory area. However, this cannot be the sole cause of the observed difference because the territory area of strangers remains lower than that of original residents on the final day of observations, despite equivalent levels of movement. Furthermore, strangers moved 6% less than expanding neighbours, despite the fact that expanding neighbours used 19% more of the territory over the first post-removal observation.

A second potentially confounding effect is the smaller size of newcomers. Since territory size is correlated with body size in this species (McDougall 2000), the smaller area could be an effect of the smaller size of newcomers. However, analysis of the number of grids occupied as a function of body size showed that strangers held a smaller territory than original residents or controls when controlling for size.

Two factors that might contribute to the persistence of this reduced territory area are prior residency and the highly territorial nature of the longfin. Regardless of the mechanisms of residency, an individual that holds a space is better at defending it (Alcock & Bailey 1997; Hardy 1998). Furthermore, a stranger that has initially lost 25% of its potential territory to surrounding neighbours is likely to reduce the probability of regaining that area the longer it remains at the reduced level. Tobias (1997) reported that robins were unable to regain control of 75% of their original territory after five days of absence. Similarly, Meadows (2001) observed a 25% increase in the territory areas bordering a number of removal sites. The increases occurred between one and seven days following the large-scale removals, and individuals were able to hold this enlarged territory beyond the 22 days of observation (Meadows 2001). In this system, as in others, gaining resident advantage appears to be a fairly rapid process.

Individuals acquire space through agonistic interactions, and in particular, through persistent and repeated interactions with neighbours (Stamps & Krishnan 1995). Longfins are considered one of the most aggressive and territorial damselfish species on the reef (Robertson 1995, 1996), so it is likely that the persistence required to reclaim lost territory would carry with it substantially elevated levels of agonistic behaviour. The decreases observed in the agonistic behaviour of strangers in the current study do not reflect the pattern expected by persistent attempts to reacquire lost space. This suggests that over the first two days of post-removal observations, strangers are most concerned with consolidating their current territory against further encroachment by neighbours. It is possible that the expansion of the territory to encompass the total area held by the original resident is a delayed process. It is also possible that the newcomer will remain restricted to a smaller than optimal territory area until another disturbance in the neighbourhood frees up more space.

Movement

Strangers moved at higher rates than original residents as they attempted to establish a new territory. We have not found any previous studies that measured movement following territory relocation; however, two studies investigated the differences in movement between familiar and unfamiliar rodents when introduced into an enclosure. Twelve hours after relocation, unfamiliar prairie voles, *Microtus ochrogaster*, moved twice as much as familiar individuals as measured by trail length in 0.1 ha outdoor enclosures (Jacquot & Solomon 1997). Unfamiliar meadow voles, *Microtus pennsylvanicus*, were 7.5 and 5 times as mobile during two intra-trapping periods, as measured by movement of individuals between patches of vegetation in the 40 m by 40 m enclosure (Pusenius et al. 2000).

Movement may be required to gain information about a new territory. However, exploration of a 1-m^2 territory by a 130 mm-long fish would not be expected to require much time. It is therefore likely that movement in the current situation relates more to patrolling the territory than to exploration. Movement tended to be positively correlated with agonistic behaviour in our study. Furthermore, other studies on damselfish have described patrolling behaviour throughout a portion of the territory (Horne & Itzkowitz 1995; Itzkowitz 2000).

For strangers, the rate of movement declined quite rapidly, approaching levels observed in original residents by the end of the second day. This may relate to reduced intrusion and greater familiarity with the territory. Unlike other behavioural measures, the movement index of expanding neighbours was generally higher than that of strangers, and remained at significantly elevated levels throughout the second post-removal day. This pattern only represents movement on the new territory, and is possibly a result of patrolling the additional space while still occupying their original territory. It is likely that presence plays a large role in establishing occupation, and so with a greater amount of time absent from the newly acquired space, expanding neighbours may need to patrol more than strangers in order to maintain the territorial boundaries.

Agonistic behaviour

A significant increase in the agonistic behaviour of strangers occurred as they attempted to establish a new territory. A recent study by Meadows (2001) on a congeneric species, the threespot damselfish, observed a six-fold increase in chase behaviours of newcomers. The elevated chase levels decreased with time in much the same pattern as observed in the current study. The protocols of the two studies differed primarily in that Meadows recorded the first observations one hour after the removals, as compared to roughly three hours of active time in the current study. After three hours, Meadows (2001) reported an increase of roughly 4.5 times baseline values as compared to the 10.0- and 6.6-fold increases in strangers and expanding neighbours respectively. This highlights newcomer type as a second possible cause of the different chase levels observed in the two studies, since in our study expanding neighbours initiated fewer chases than strangers. Meadows (2001) reported that the majority of newcomers in his study consisted of expanding neighbours, which is much closer to the increase in expanding neighbours observed in our study. Density is probably not a contributing factor, as Meadows reported territory areas of approximately 0.3 m^2, and inferred that territories were contiguous. Territories in the current study were closer to 1 m^2, with no overlap evident between neighbours.

The study by Tobias (1997) on European robins reported that newcomers to a territory exhibited a two-fold increase in territorial singing as compared to other members of the population, but did not report any other behaviour. The newcomer robins exhibited increased levels of territorial singing over a period of five to six days, which is potentially longer lasting than the elevated levels of agonistic behaviour in the current study.

Our findings parallel numerous studies demonstrating a higher rate of aggression in unfamiliar animals establishing a dominance hierarchy than with familiar animals in an established hierarchy (Pagel & Dawkins 1997; Broom 2002). Furthermore, 'dear enemy' literature suggests that territorial individuals will increase agonistic behaviours against an unfamiliar neighbour (Eason & Hannon 1994; Husak & Fox 2003), although none of these studies examine the agonistic behaviour of the newcomer.

The declines in the agonistic behaviours of newcomers are relatively consistent across all five measures in the current study. This pattern of decline likely represents the gradual establishment of mutually exclusive boundaries. In a study on *Anolis aeneus* lizards, Stamps & Krishnan (1997) demonstrated that neighbours that fought were more likely to establish mutually exclusive territories than territories with large overlapping areas. Similar mechanisms could function with longfin damselfish, where newcomers that fight early on in the settlement process are able to rapidly establish territory boundaries. The highly territorial nature of the damselfish system could result in this rapid demarcation of borders, as compared to a longer process reported by Tobias (1997) in territorial robins.

Strangers performed more than twice as many displays and chases as they received from neighbours and other conspecifics. This contrasts with the expectation that on average, fish in a stable territorial system should perform and receive about the same number of aggressive acts. However, since both original residents and controls also performed more chases and displays than they received, this does not represent any particular shift in the agonistic behaviour of newcomers. This is not likely to be an artifact of the observer missing some behavioural actions by neighbors because of greater attention on the focal fish; chases by other fish involved fleeing by the focal subject and thus were quite apparent. A likelier explanation is that focal individuals are larger than their neighbours, and therefore more likely to perform more aggressive acts than they receive (McDougall 2000).

Foraging rate

Newcomers had lower foraging rates than original residents and controls. Only Tobias (1997) investigated initial decreases in foraging time, reporting 16% and 44% initial decreases for spring and winter, respectively, that are comparable to the 25%

decline observed in the first day of our study. Tobias (1997) reported that foraging levels remained low for five to six days following the arrival of newcomers. However, we observed a more rapid recovery in foraging rate. On the second day newcomers no longer differed significantly from original residents, although their rates averaged about 10% lower.

The diurnal pattern of low foraging rates in the morning followed by a sharp increase to midday and afternoon levels that we observed in newcomers was present in the original residents and controls as well. Studies on other damselfish species support this temporal pattern (Montgomery 1980; Robertson 1984; Polunin & Klumpp 1989), suggested to be a response to the diurnal pattern of photosynthate accumulation in turf algae (Polunin & Klumpp 1989).

In general, reduced foraging rates might be expected in a new territory holder as a result of lack of knowledge about local resources and appropriate foraging sites (Pusenius et al. 2000) or a lack of food availability as a result of increased foraging by intruders following removal of the original resident (Meadows 2001). Time budget constraints might also result in an observed decrease, where time is devoted to higher priority activities, like territorial defence (Breau & Grant 2002; Grant et al. 2002). For a benthic algal grazer with a small territory, the first two possibilities are more likely to result in a decrease in quality of foraging locations, rather than a decrease in the overall bite rate. A time constraint due to agonistic behaviour is an unlikely cause of the reduced foraging by strangers because foraging rates did not correlate negatively with agonistic events. Furthermore, the foraging rates of newcomers over the two post-removal days differed only slightly, in contrast with a large change in the agonistic behaviour. Stronger negative correlations between aggression and foraging in expanding neighbours suggest a more limited time budget due to increased movement required to patrol both the old and new territories. Since expanding neighbours foraged inside of their old territory as well, limitations on their foraging rates are not likely to be related to lack of information. It is difficult, however, to identify a specific explanation for the reduced foraging.

Short-term costs of relocation

The behavioural changes observed in the current study represent indirect measures of fitness costs. Each behavioural measure consists of a number of component costs that affect an individual's decision to relocate. The fitness costs can take the form of energetic costs, opportunity costs, increased risk of predation, injury and mortality, and reproductive costs.

Increased agonistic interactions, increased movement, and decreased foraging rates all contribute to a reduced energy budget. Strangers exhibited approximately four times as many chases as control fish over two days, and an estimated 30 fights as compared to none in controls. Chases in damselfish involve rapid acceleration and swimming at high speeds, which are recognized as incurring substantial energetic demands in fish (Brett 1964; Beamish 1978). Chellappa and Huntingford (1989) reported that fights between male sticklebacks, *Gasterosteus aculeatus*, lasting more than a few seconds resulted in substantial decreases in body glycogen levels. Although defence costs are considered to carry energetic costs in a variety of systems: fish (Hixon 1980; Chellappa & Huntingford 1989), crustaceans (Sneddon et al. 1999), and insects (Hack 1997), some disagreements remain about the relative importance of these costs. A study on the *Agelenopsis aperta* spider argued that the energetic costs of fighting proved low relative to the costs incurred by an increased risk of predation during bouts of fighting, a loss of feeding time and by injury and mortality (Riechert 1988). Furthermore, a study on two congeneric species, *S. planifrons* and *S. dorsopunicans*, reported no increase in oxygen consumption when confronted with intruders (Cleveland 1999). The small impacts of energetic costs in these studies are likely related to the observed behaviours. Cleveland (1999) reported that defence behaviours in her study consisted of static displays next to a partition. Differences in foraging strategies and predation rates between spiders and the current system likely contribute to the low relative impact of energetic costs in the Riechert (1988) study.

In addition to the increased movement associated with higher levels of chases and fights, newcomers score higher in the movement index. Energetic costs of swimming increase linearly with duration (Brett 1964; Beamish 1978), and when combined with a reduced energy intake due to a lower foraging rate newcomers likely experience a large energy constraint. The majority of studies investigating the impact of short-term cessation of foraging in fish report that fitness costs are relatively minor (Angradi 1992; Booth & Hixon 1999), although when combined with large increases in energy output, a reduction of any magnitude in energy input may be more likely to have deleterious effects. Previous studies on the cessation of foraging have not focused on a territorial species in a state of increased activity and aggression.

Strangers also occupied a smaller territory area than original residents, representing a potentially long-term cost associated with lost resources. The costs associated with a 25% reduction in space use are difficult to quantify, but in a system of such high densities of territories, it is likely that individuals hold less than optimal territory areas to begin with. The rapid expansion of individuals into any available space supports this assumption. Assuming that the newcomer's old territory was the size expected by the body size-territory area relationship, the new territory is roughly 25% smaller than the old territory. That corresponds to a 25% decrease in available resources, a potentially large cost. However, the willingness of strangers to remain in a reduced territory area seems to indicate that the costs associated with the lost resources may not be that large. Maintaining persistent levels of agonistic interactions is a viable strategy for acquiring space (Stamps & Krishnan 1995), and it is possible that the benefits of gaining back 25% of the territory are initially outweighed by the costs of the required aggressive interactions. The low apparent benefit of regaining the 25% translates to a low cost of establishing a territory at 75% of the previous occupant's area. However, it is likely that the longer this reduction persists, the greater the limitations will be on the individual occupying fewer resources.

Expanding neighbours effectively gain the resources associated with a second territory, despite the slight reduction as compared to the area occupied by the original residents. Meadows (2001) suggests that this situation for expanding neighbours can persist for extended periods of time. On the other hand, the strength of the body size-territory area relationship suggests that the expanding neighbours eventually lose these resources to a newcomer or to gradual encroachment by other individuals in the neighbourhood.

Opportunity costs generally apply to time-budget restrictions for lost foraging time. Lost foraging time is not likely much of a factor in the current study as behavioural correlations suggested that time budgets were not limited in original residents, controls or strangers. A similar conclusion about unrestricted time budgets was reached by Meadows (2001). However, systems where time budgets are limited, energy maximizers for example (Hixon 1982), would likely exhibit much higher opportunity costs.

Individuals in an unfamiliar environment are frequently associated with an increased risk of predation. Due primarily to a lack of knowledge about appropriate escape routes and shelters (Clarke et al. 1993), increased predation risk also results from increases in activity (Werner & Anholt 1993) and decreases in vigilance during agonistic interactions (Brick & Jakobsson 2002). A model of increased foraging activity resulted in a 10% decrease in fitness resulting from a two-fold increase in movement speed (Werner & Anholt 1993). The study considered movement speed as similar in effect to time spent moving, which is a closer approximation of the movement index reported in our study. Furthermore, with the reported increases in chases and fights for newcomers, a resulting decrease in vigilance could incur significant increases in predation risks.

We observed no predation events during focal observations, although attempted predation events by yellowtail snappers, *Ocyurus chrysurus,* occurred on two separate occasions. The presence of the observer in close proximity to the focal territory possibly deterred potential predators from attacking. Furthermore, shelter sites are not limited in the current system (Robertson 1979), and so numerous available refuges likely reduce the predation risk.

Injury and mortality costs represent relatively straightforward decreases in fitness. Considerable fin damage from agonistic behaviour in steelhead trout, *Oncorhynchus mykiss*, contributed significantly to depressed growth rates (Abbott & Dill 1989). Furthermore, Rasa (1969) observed substantial damage to individuals after fighting bouts, inferring significant fitness costs. The fighting bouts infrequently led to the death of the subordinate fish, although the few instances occurred as a result of confining the individuals in an enclosure with no means of escape (Rasa 1969).

We did not observe any mortality as a result of agonistic interactions. However, it is possible that damage to certain individuals was severe enough to be life threatening over a longer time scale. There are few studies that report the healing time required for damage of this nature to reef fish, although a study on injuries resulting from damselfish attacks on redlip blennies, *Ophioblennius atlanticus*, does suggest a healing time of under two weeks (Reynolds & Côté 1995). In addition to the effect on mortality, injury also represents costs associated with tissue repair and increased risks of infection.

No direct measure of reproductive output occurred in this study, but the potential exists for a substantial cost to newcomers. Resident male variegated pupfish, *Cyprinodon variegatus*, exhibited a reduced number of spawnings when confronted with unfamiliar intruders (Leiser 2003). Furthermore, it can be argued that excess energy budgeted for agonistic interactions and increased activity reduce the energy available for growth and reproductive output.

Energetic costs likely compose the highest proportion of total relocation costs for newcomers, as changes in the majority of the measured behaviour result in a shift in energetics. Furthermore, the duration of the increased levels of agonistic behaviour suggest that energetic costs might be the longest lasting, with the exception of the opportunity costs of lost resources. Relocation in other systems may incur costs that differ in relative importance. Systems where shelter is limited or predation events more frequent would likely involve much higher costs associated with predation risk than we observed here. However, each of the costs discussed above can contribute to a decrease in fitness, representing a trade-off for the benefits of relocating a territory.

Implications for 'dear enemy' recognition

As a result of interest in the 'dear enemy' phenomenon, as described by Wilson (1975), more studies have examined increases in the aggression of established residents directed at newcomers, than the aggression of newcomers directed at established residents. Residents attacked unfamiliar intruders between three and fives times as much as neighbours in salamanders, lizards, and fishes (Jaegar 1981; Husak & Fox 2003; Leiser 2003). Little is understood how familiarity acts from the intruder's perspective.

Familiarity of the expanding neighbours with respect to the surrounding neighbourhood was a key difference between the two newcomer types. An expanding neighbour is expected to be more familiar with the neighbours surrounding a vacated territory than would be a stranger. True to the concept of 'dear enemy' recognition, this familiarity may explain why expanding neighbours did not receive significantly more chases or displays than original residents, while strangers received 11 and 15 times more chases and displays, respectively. Furthermore, strangers had incurred significantly more damage than expanding neighbours by the time of the first observation.

A study in willow ptarmigan, *Lagopus lagopus*, reported similar findings, such that unfamiliar new neighbours resulted in an increase in the time spent fighting (Eason & Hannon 1994). However, Husak and Fox (2003) reported that in collared lizards, *Crotophytus collaris*, familiar neighbours intruding in a part of the territory where they were not commonly found elicited equivalent reactions from the residents as did unfamiliar intruders. The expanding neighbours of the current study are out of context with their familiar neighbours, yet are attacked significantly less than unfamiliar strangers. This suggests that the mechanisms dictating 'dear enemy' recognition are more complicated than previously reported.

Of particular interest, agonistic behaviour initiated by newcomers was unaffected by differences in familiarity. When attempting to establish a new territory, newcomers did not appear to be less aggressive towards familiar versus unfamiliar individuals. Although some differences between strangers and expanding neighbours existed in the number of initiated chases, this was likely a result of fewer attacks by neighbours. Chases were frequently observed as responses to attacks by conspecifics. A likely assumption in the strategy of recolonization by expanding neighbours is the reduced cost of agonistic behaviour due to familiarity. This study provides evidence that familiarity only reduces the costs associated with received aggression, and not the costs of initiated aggression. This situation offers the potential for asymmetrical interactions, where the benefits of familiarity are one-sided. Expanding neighbours receive fewer attacks from conspecifics because of 'dear enemy' familiarity, yet the neighbours receive just as many attacks as if the newcomer was a stranger.

Consequences for mobility

The costs listed above represent relatively significant departures from the everyday costs incurred by original residents and controls. Based on the durations of the various behavioural changes, agonistic interactions likely represent the greatest costs to newcomers establishing a new territory. The energetic costs of aggression along with the associated injuries and risks of mortality combine to represent a significant potential decrease in fitness. It is likely for this reason that aggression is so well represented in the literature when dealing with the social mobility of individuals.

Despite the large increases discussed above, it is important to note that these represent the costs associated with the relocation of an individual to a vacant territory. Relatively large compared to the assumed costs of such a strategy (Dunham et al. 1995), they still represent relatively low costs when compared with a strategy involving the eviction of an original resident. Studies from numerous territorial species reflect this through discussions of the benefits that residency imparts in territorial contests and the various strategies for taking over a territory (Itzkowitz et al. 1995; Karino 1996; Alcock & Bailey 1997; O'Connor et al. 2000).

Differences between the costs of strangers and expanding neighbours offer two different strategies to territorial relocation, each with different associated costs. We assumed that expanding neighbours incurred very few costs when initially occupying a vacancy in a neighbouring territory. Although strangers incur the greater costs in the short-term for the two newcomer types, expanding neighbours still incur significant costs beyond those involved with the long-term occupation of the territory. The initial changes in behaviours experienced by expanding neighbours were significant, and represented significant costs required to gain residency over the vacated territory. Both of these strategies must be considered when addressing issues of territorial relocation.

The rates of relocation in territorial systems on the reef and elsewhere are primarily limited by the rate at which vacancies are created in the territorial mosaics. This study provides some of the first measures of the behavioural changes and associated costs that constrain the mobility of individuals once these vacancies are present. Understanding the costs involved in the decision to relocate a territory is the first step in understanding the mechanisms that drive the relocation of territorial species.

CONCLUSIONS

The short-term costs of relocating a territory into an established neighbourhood of longfin damselfish primarily involve energetic costs associated with increased agonistic behaviour, but costs associated with injuries and lost resources also play an important role. In general the mobility of territorial individuals between established neighbourhoods is constrained by settlement costs even when employing a strategy involved with settling into a vacancy. We believe that the costs associated with evicting a territorial resident prior to settling would be prohibitive, and so we assume that movement on the reef is limited by the natural creation of vacancies. Future research needs to incorporate these relocation costs into discussions of mobility, and further study is required to measure the direct fitness costs that result from the observed behavioural changes in this study.

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Table 1. The effect of time over six focal observations (focals four to nine), newcomer type (strangers, N = 12 and expanding neighbours, N = 15), removal type (single versus double removals) and fish size o n the behaviour of longfin damselfish

	F-value[1] and Significance[2]				
Behaviour	Time	Fish Type	Time x Fish Type	Removal Type	Size
Space Use	0.086	1.4	2.2	1.4	0.26
Movement Index	6.3***	9.4**	3.6**	0.98	0.060
Chases by focals	8.5***	0.013	3.1*	0.93	$3.3^{0.081}$
Displays by focals	5.3***	1.5	0.53	0.96	1.8
Fights	2.8*	5.2**	0.77	0.072	0.001
Chases by conspecifics	$2.0^{0.083}$	5.6*	1.7	1.9	3.0
Displays by conspecifics	$2.1^{0.073}$	9.6**	0.21	$3.3^{0.083}$	$3.7^{0.069}$
Foraging rate	28.3***	0.25	0.31	0.082	1.3

[1] GLM RM with Fish Type and Removal Type as factors and Fish Size as covariate

[2] *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$; exact probabilities are shown when $0.05 < P < 0.1$

Table 2. The effect of time of day (0900, 1200, 1500), fish type (original residents, OR, N = 29; strangers, S, N = 12, expanding neighbours, EN, N = 15) and their interaction on the behaviour of longfin damselfish over two days of observations

		F-value[1] and Significance[2]			Comparisons between fish types[2,3]		
Behaviour	Day	Time	Fish Type	Time x Fish Type	S vs OR	EN vs OR	S vs EN
Space Use	2	1.2	10.2***	2.8*	***	*0.068*	NS
	3	0.75	10.1***	0.81	***	*	NS
Movement index	2	6.9**	28.9***	$2.3^{0.059}$	***	***	NS
	3	3.7*	20.7***	2.6*	NS	***	***
Chases by focals	2	13.0***	30.0***	4.0**	***	***	*
	3	3.7*	7.4***	1.7	NS	***	NS
Displays by focals	2	7.5**	26.6***	2.9*	***	***	NS
	3	0.49	9.7***	0.09	***	**	NS
Fights	2	1.9	9.1***	1.7	***	*	NS
	3	1.1	5.7**	0.12	**	NS	*
Chases by conspecifics	2	4.4*	19.1***	2.7*	***	NS	***
	3	0.67	4.0*	1.2	*	NS	NS
Displays by conspecifics	2	6.5*	20.1***	2.0	***	*0.069*	***
	3	0.26	8.7***	0.38	***	NS	*
Foraging rate	2	87.1***	15.3***	0.30	***	***	NS
	3	67.3***	2.4	1.8	NS	NS	NS

[1] GLM RM comparing original residents from day 1 with newcomers on days 2 and 3

[2] *$P \le 0.05$, **$P \le 0.01$, ***$P \le 0.001$; exact probabilities are shown when $0.05 < P < 0.1$

[3] Post-hoc Bonferroni comparisons between fish types

Table 3. Pearson correlations with significance[1] between the three behavioural measures from combined original residents and controls (N = 39)

Correlations	Focal 1	Focal 2	Focal 3
Foraging rate vs Movement index	-0.180	-0.011	-0.328*
Foraging rate vs Agonistic events	-0.236	0.007	-0.196
Agonistic events vs Movement index	0.390**	0.533***	0.349*

[1] **P ≤0.05, **P ≤0.01, ***P ≤0.001*; exact probabilities are shown when $0.05 < P < 0.1$

Table 4. Pearson correlations with significance[1] between three behavioural measures from strangers (S, N = 12) and expanding neighbours (EN, N = 15)

Correlations	Fish Type	Focal 4	Focal 5	Focal 6	Focal 7	Focal 8	Focal 9
Foraging rate vs	S	-0.613*	-0.260	-0.376	0.020	0.227	-0.196
Movement index	EN	-0.441	-0.255	-0.323	-0.724**	$-0.480^{0.060}$	-0.506*
Foraging rate vs	S	$-0.565^{0.056}$	0.219	0.199	0.312	0.012	-0.424
Agonistic events	EN	-0.336	-0.785***	-0.807***	-0.578**	-0.557*	-0.529*
Agonistic events vs	S	$0.573^{0.051}$	$0.562^{0.057}$	$0.524^{0.080}$	$0.567^{0.055}$	0.223	$0.538^{0.071}$
Movement index	EN	0.230)	0.278	0.390	0.623**	$0.455^{0.077}$	0.654**

[1] **P ≤0.05, **P ≤0.01, ***P ≤0.001*; exact probabilities are shown when $0.05 < P < 0.1$

Figure 1. Proportion of total territory visited by longfin damselfish (number of grids visited divided by number of grids in the focal territory) during a given 20-min focal observation. Focal observations 1, 2, and 3 represent 0900, 1200 and 1500 hours on the pre-removal day of observations. Focal observations 4 to 6 and 7 to 9 represent the equivalent times for the first and second days following the removals. Symbols: (●) controls (N = 10), (▼) original residents (N = 29), (□) strangers (N = 12), and (◊) expanding neighbours (N = 15). Error bars are ± 1 S.E.M.

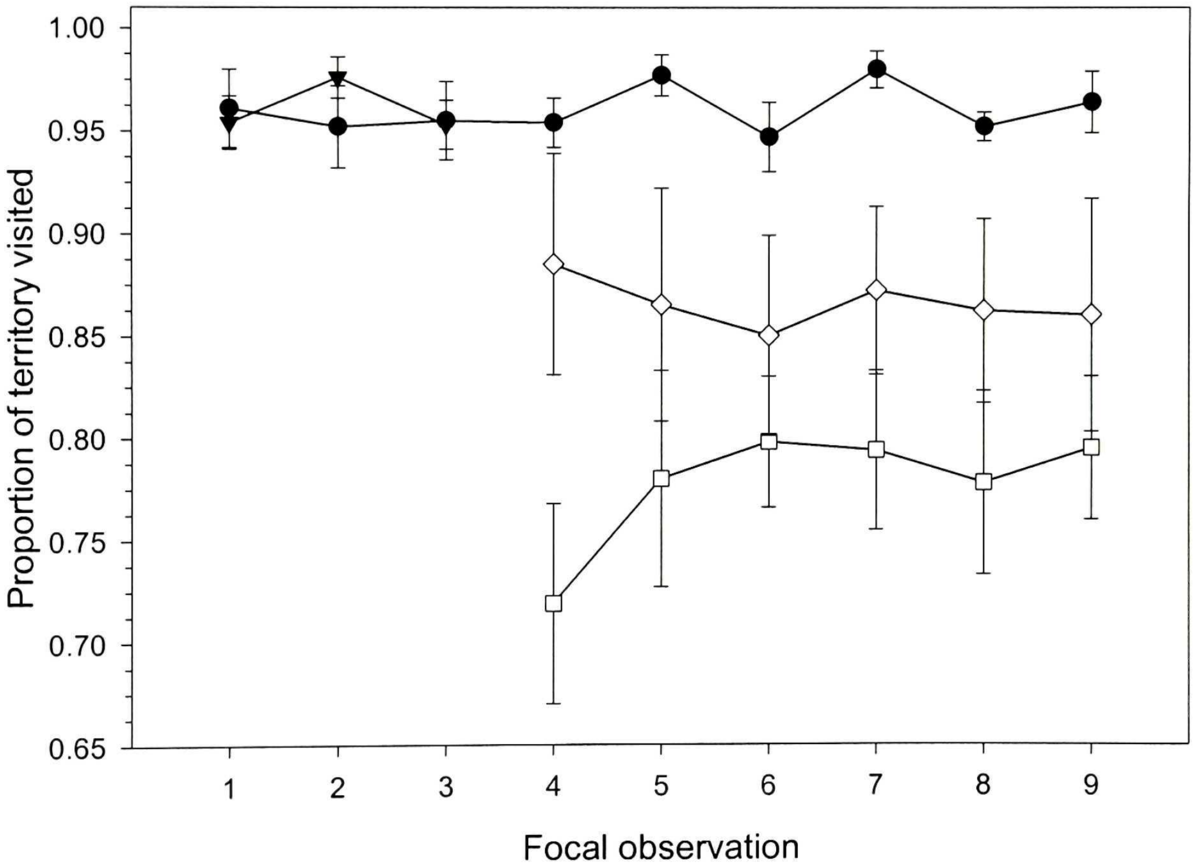


Figure 2. Movement Index (number of 5-sec intervals of movement per 20-min focal observation with a maximum value is 240) for each of nine focal observations. Symbols are the same as in Figure 1.

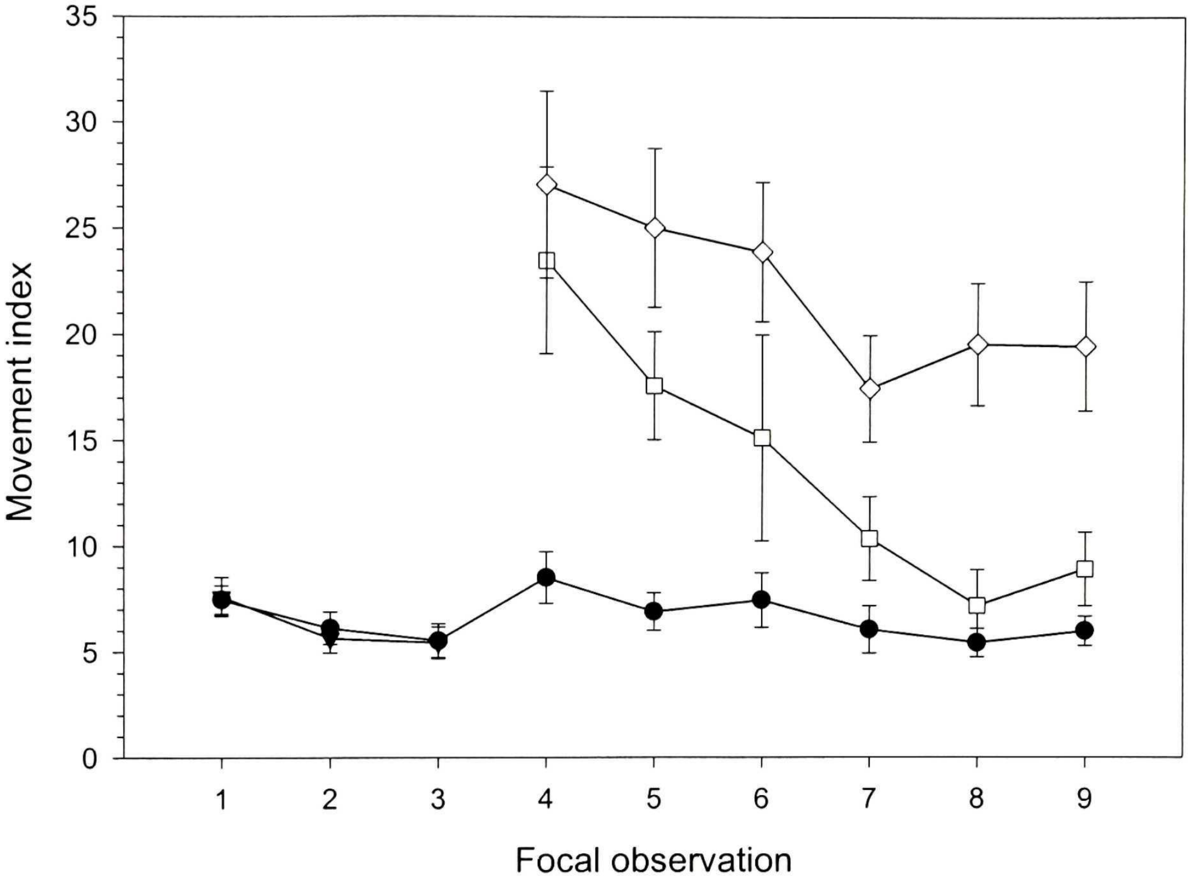


Figure 3. Number of agonistic events per 20-min focal observation divided into (a) chases by focal fish, (b) displays by focal fish, (c) fights, (d) chases by conspecifics, and (e) displays by conspecifics in relation to each of nine focal observations. Symbols are the same as in Figure 1.

Figure 3

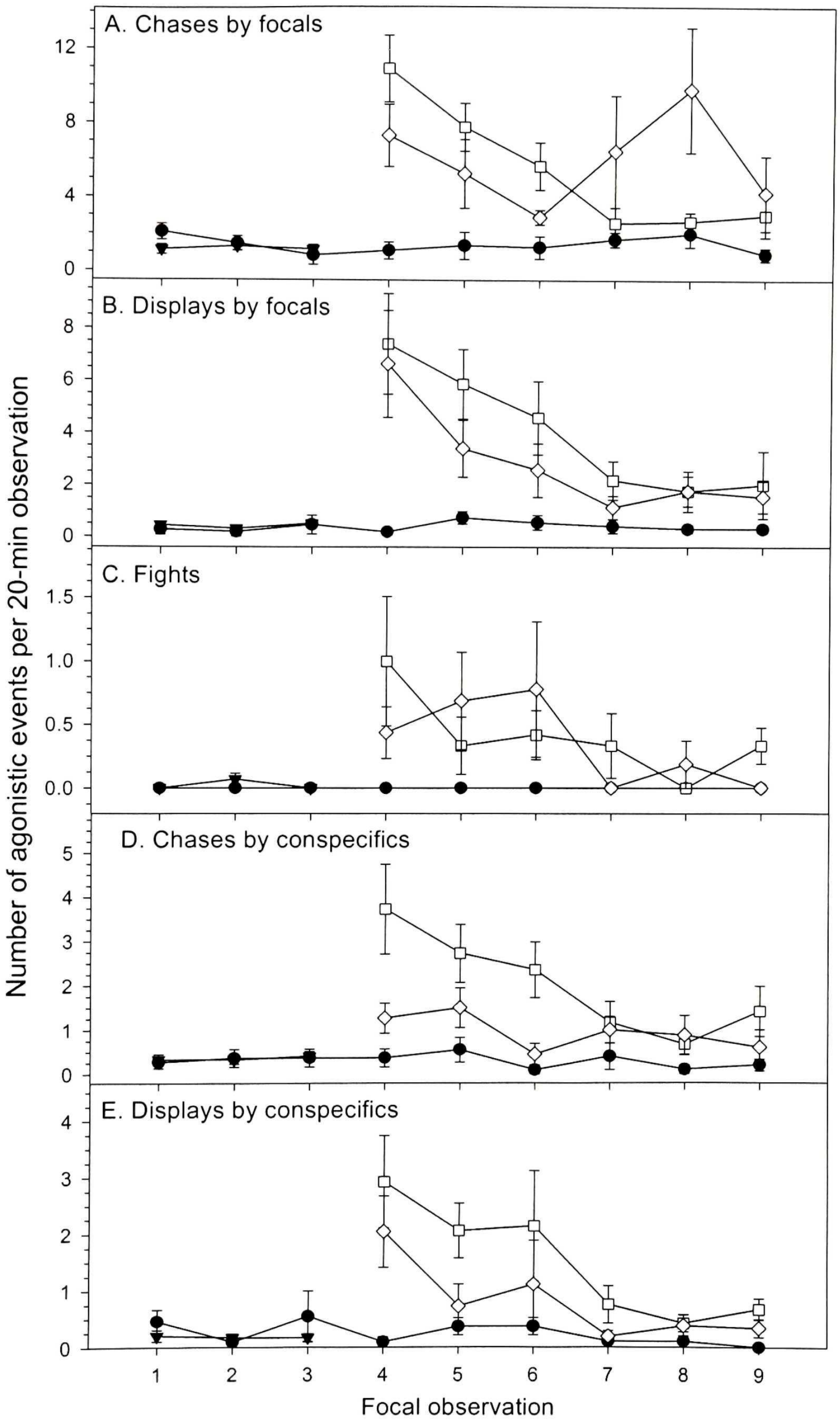
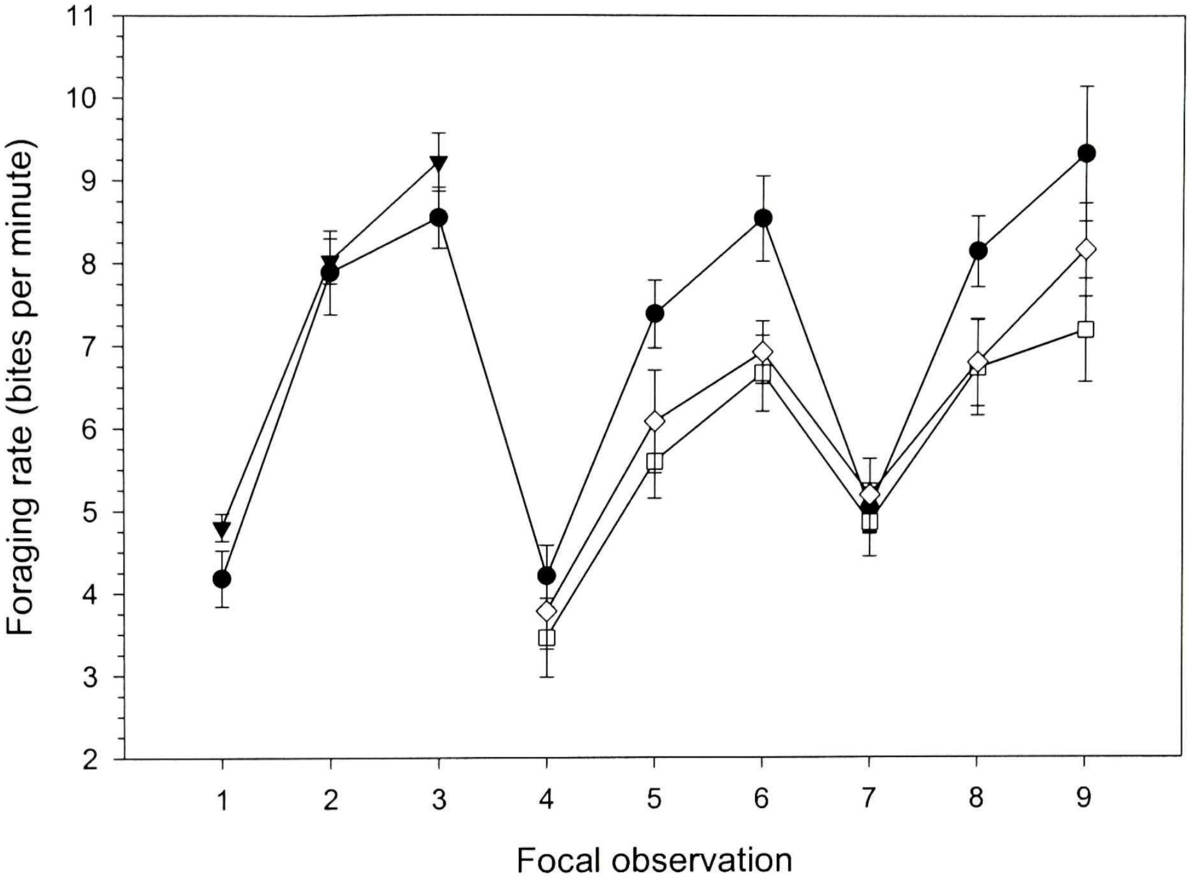

A. Chases by focals
12
8
4
0
B. Displays by focals
8
6
4
2
0
C. Fights
1.5
1.0
0.5
0.0
D. Chases by conspecifics
5
4
3
2
1
0
E. Displays by conspecifics
4
3
2
1
0
1
2
3
4
5
6
7
8
9
Focal observation
Number of agonistic events per 20-min observation

Figure 4. Foraging rate (bites per minute) in nine focal observations. Symbols are the same as in Figure 1.



APPENDIX I: Turnover Rates on Territories of Longfin Damselfish

We investigated the natural rate of turnover in longfin damselfish, *Stegastes diencaeus,* on North Bellairs and South Bellairs reefs where the main study occurred. We designed an observational study to record the rate at which territory vacancies occurred, whether through migration events or mortality. The study involved monitoring a total of 64 individuals over a period of 70 days.

We haphazardly selected seven neighbourhoods in the spur and rubble groove habitats. Each neighbourhood consisted of seven to fourteen residents including both adult- and juvenile-coloured individuals, ranging in size from 35 mm to 122 mm in total length (TL). Individuals were captured, tagged using Visual Implant Fluorescent Elastomer (VIE) tagging product, sexed, measured and released back into their territories. The total tagging period lasted for about two weeks, and the 70 days of observations were staggered for each neighbourhood depending on when the last fish of the neighbourhood was tagged. Monitoring took place at approximately two-week intervals and involved using SCUBA for close observation to permit identification of individuals. Identification generally required only visual observations from a distance of about 1 m. However, recaptures were frequently required in order to retag individuals when tags became difficult to identify.

We only included individuals in the study if they were present at the first census, approximately one week after tagging (only one individual was excluded for this reason). We counted adults as replacements if they occupied territories previously held by a departed individual. This restriction did not apply in the case of juveniles, as they often settle in between the territories of adults and often do not strictly defend a territory.

More vacancies occurred in the rubble groove habitat (7/18) than in the spur habitat (1/35) (X^2 with Yates correction = 8.07, df = 1, $P < 0.01$). Furthermore, the juvenile vacancy rate (6/11) was higher than the adult rate (8/53) juveniles (X^2 with Yates correction = 4.83, df = 1, $P < 0.05$). A trend suggested that more males (7/32) than females (1/21) vacated their territories, but the difference was not significant, due most likely to a sex ratio bias of 3:2 males to females in the study population (X^2 with Yates correction = 1.35, df = 1, $P > 0.1$).

The most important conclusion from this preliminary study is that vacancies do occur on the reef, although at one departure in 25 individuals over 70 days, the frequency of vacancies is rare in the spur habitat. McDougall (2000) reached the conclusion that spur habitat was preferred habitat compared to the rubble groove, which is supported by the differences in the replacement patterns observed between the two habitats. The very high relocation rates of juveniles suggests that the costs of settling are not high, which is supported by observing settlement between the borders of territorial adults. Although predation is likely to contribute to a greater proportion of the turnover rates in juveniles than in adults, most of the juveniles measured more than 50 mm and are large enough to experience similar predation rates as adult-coloured individuals of a similar size. This preliminary study supports the use of preferred spur habitat as the location for removals investigating the costs of territory relocation in adults.

Appendix I. Table 1. Turnover rates in territories of longfin damselfish

Habitat	Gender	No. Present	No. Departed[1]	No. Arrived	% Turnover	% Replacement
Spur	Male	17	1	1	5.9	100
	Female	18	0	0	0.0	---
	Juvenile	3	1 (3)	3	33.3	300[2]
Rubble groove	Male	15	6	3	40.0	50
	Female	3	1	1	33.3	100
	Juvenile	8	5	0	62.5	0

[1] Brackets represent late arrivals in the study neighbourhood that subsequently departed before the end of the study

[2] Three juvenile-coloured individuals (TL < 45 mm) were observed establishing territories where previously there had been no resident

APPENDIX II: Observer Differences in Behavioural Measures

A set of GLM RMs on the 29 original residents of the main study was performed on all behavioural measures to determine whether observers were consistent. The difference between observers was statistically significant only in the foraging rate, but was consistent over the three pre-removal focal observations (see table below). The assistant consistently observed foraging rates 0.046 ± 0.008 $\log_{10}$ (bites per min) higher than the rates observed by PTM. We corrected the measurements of the assistant by subtracting this mean difference from each observation.

Since PTM performed the observations on control fish, whereas both observers were responsible for the observations on the original residents, the observer difference resulted in a significant difference between the recorded foraging rates of controls and original residents before correction. This effect was observed in the GLM RM of controls and original residents over the first 3 focal observations (Fish Type: F = 8.465, df = 1, $P = 0.006$). However, the difference between fish types did not change across the three focal observations (Time x Fish Type: F = 0.426, df = 1.541, $P = 0.603$). When the observer difference was corrected by subtracting the mean difference, the observed difference between controls and original residents was no longer significant.

Appendix II. Table 1. The effect of observer and the interaction with time over three focal observations (0900, 1200, 1500) for original residents (N = 29) from a GLM RM

Behaviours	F-value[1] and Significance[2]	
	Observer	Time x Observer
Space use	1.4	1.0
Movement index	0.26	0.43
Chases by focals	2.9	0.87
Displays by focals	0.38	0.39
Fights	1.3	1.3
Chases by conspecifics	0.00	0.31
Displays by conspecifics	0.727	2.0
Foraging rate[2]	6.3*	0.73
Foraging rate[3]	0.075	0.58

[1] $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$

[2] Values calculated from original foraging rate

[3] Values calculated from corrected foraging rate, taking into account observer differences

APPENDIX III: Analysis Comparing Newcomers to Controls

The main analysis included in the text involved a comparison with the original residents, which represent a spatial control for the characteristics of the focal territories. The following are the results from an identical analysis involving a comparison with control individuals, which represent a control for temporal effects over the course of the data block (see table below). The GLM RM used below includes that same factor of fish type as described in the Methods section, and the results can be compared to the F-values and significances reported in Table 2 of the main results. The results are presented as comparisons separated by day (first and second post-removal days) to consider the effect of time and fish type with post-hoc Bonferroni probabilities for differences between fish types. The patterns of behavioural differences are the same, with only a few minor decreases in significance in expanding neighbours, such as Displays by focals on the second day, Fights over the second day, and in strangers for Fights on the second day.

Appendix III. Table 1. The effect of time of day (0900, 1200, 1500), fish type (controls, C, N = 10; strangers, S, N = 12; expanding neighbours, EN, N = 15) and the interaction on the behaviour of longfin damselfish in a GLM RM with post-hoc Bonferroni comparisons

		F-value and Significance[1]			Comparisons between fish types[1]	
Behaviour	Day	Time	Fish Type	Time x Fish Type	S vs C	EN vs C
Space Use	2	0.8	4.2*	$2.4^{0.059}$	**	NS
	3	1.4	4.6*	0.37	**	*
Movement index	2	3.9*	10.2***	$2.3^{0.067}$	**	***
	3	0.74	16.9***	$2.1^{0.093}$	NS	***
Chases by focals	2	7.9***	11.0***	3.1*	***	**
	3	3.4*	3.6*	1.1	NS	*
Displays by focals	2	3.7*	9.9***	1.4	***	**
	3	0.11	4.3*	0.23	*	*0.088*
Fights	2	0.97	3.8*	0.91	*	NS
	3	0.37	3.4*	0.10	*0.084*	NS
Chases by conspecifics	2	4.6*	9.9***	0.64	***	NS
	3	0.82	3.3*	0.62	**	NS
Displays by conspecifics	2	2.1	8.1***	1.5	**	NS
	3	0.033	7.9**	0.44	***	NS
Foraging rate	2	60.4***	4.4*	0.534	*	*
	3	40.6***	1.3	0.567	NS	NS

[1] $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$; exact probabilities are shown when $0.05 < P < 0.1$

APPENDIX IV: Effects of Fish Size and Gender on the Behaviour of Baseline Individuals

This analysis was based on the pre-removal focal observations (focals 1, 2, and 3) of both the original residents (N = 29) and the controls (N = 10) in order to look for possible effects of size and gender on behaviour of unmanipulated individuals. Reported below are the F-values and the associated probabilities of the covariate and the two factors. Included in the GLM RM are fish size (Log_{10} fish total length) as a covariate, and gender (male vs. female) and fish type (control vs. original residents) as two factors.

The directions of the significant relationships are that larger fish move less, are chased more frequently by conspecifics and tend to forage at a higher rate than smaller fish. The trend observed in displays by conspecifics was due to a slightly higher count in controls during the third focal observation.

Appendix IV. Table 1. The effect of size, fish type (controls, N = 10; original residents, N = 29) and gender (male, female) on the behaviour of unmanipulated longfin damselfish in a GLM RM

	F-value and Significance[1]		
Behaviours	Size	Gender	Fish Type
Space use	2.645	0.200	0.137
Movement	6.345*	0.037	0.134
Chases by focals	0.010	1.381	1.321
Displays by focals	0.030	0.685	0.504
Fights	1.927	0.393	0.483
Chases by conspecifics	4.304*	2.099	0.004
Displays by conspecifics	0.096	2.984	$3.892^{0.057}$
Foraging rate	$3.303^{0.078}$	1.077	1.381

[1] $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$; exact probabilities are shown when $0.05 < P < 0.1$

B level

McGill University
Animal Use Protocol – Research
Guidelines for completing the form are available at
www.mcgill.ca/rgo/animal

Protocol #: 4549
Investigator #: 378
Approval End Date: MARCH 31, 2003
Facility Committee: SCI

☐ **Pilot** ☒ **New Application** ☐ **Renewal of Protocol #** ____

Title Cost of home range relocation in a coral reef damselfish, Stegastes diencaeus
(must match the title of the funding source application)

1. Investigator Data:

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Name:		Work #:		Emergency #:	
Name:	Peter McDougall	**Work #:**	(514) 398-6725	**Emergency #:**	(514) 931-3341
Name:	Kelsey Abbott	**Work #:**	N/A	**Emergency #:**	(978) 526-7447

3. Funding Source:

External ☒
Source (s): NSERC grant to D.L.Kramer
er Reviewed: ☒ YES ☐ NO**
Status : ☒ Awarded ☐ Pending
Funding period: 04/98 - 03/03

Internal ☐
Source (s): ____
Peer Reviewed: ☐ YES ☐ NO**
Status: ☐ Awarded ☐ Pending
Funding period: ____

ACTION	✓	DATE
P.I.	✓	Ap 3 '02
FACC	✓	〃
RGO	✓	〃
VET	✓	〃
DB		
approved		

**** All projects that have not been peer reviewed for scientific merit by the funding source require 2 Peer Review Forms to be completed . e.g. Projects funded from industrial sources. Peer Review Forms are available at www.mcgill.ca/fgsr/rgo/animal/**

Proposed Start Date of Animal Use (d/m/y): 24/02/02 **or ongoing** ☐

Expected Date of Completion of Animal Use (d/m/y): 30/09/02 **or ongoing** ☐

Investigator's Statement: The information in this application is exact and complete. I assure that all care and use of animals in this proposal will be in accordance with the guidelines and policies of the Canadian Council on Animal Care and those of McGill University. I shall request the Animal Care Committee's approval prior to any deviations from this protocol as approved. I understand that this approval is valid for one year and must be approved on an annual basis.

Principal Investigator's signature: Donald L Kramer **Date:** 13 Feb 2002

Approval Signatures:

Chair, Facility Animal Care Committee:		**Date:** MAR 2 5 2002
University Veterinarian:		**Date:** 4/2/02
Chair, Ethics Subcommittee(as per UACC policy):		**Date:**
Approved Period for Animal Use	**Beginning:** April 1, 2002	**Ending:** MARCH 31, 2003

☐ This protocol has been approved with the modifications noted in Section 13.

MAR 28 2002