

Short-term behavioral consequences of territory relocation in a Caribbean damselfish, *Stegastes diencaeus*

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Home-range relocation occurs during natal and breeding dispersal, ontogenetic habitat shifts, and the maintenance of resource- or density-dependent patterns of distribution. Relocating animals are expected to change their behavior to compensate for limited familiarity with the new home range and with neighboring conspecifics; such changes may indicate some of the costs of relocation. Little is known, however, about the magnitude and duration of the changes or about the types of behavior affected. We investigated the short-term (2 day) behavioral changes associated with relocation in the highly territorial longfin damselfish, *Stegastes diencaeus*. We compared the behavior of newcomers settling into experimentally created vacancies in an established neighborhood with that of the original residents of the same territories. The greatest difference was an increase in the rate of agonistic interactions. Newcomers also used smaller territories, moved more, and fed less. Neighboring damselfishes were less aggressive toward neighbors that expanded into vacant territories than toward “strangers” that relocated from elsewhere. The behavior of newcomers approached that of original residents within 2 days but territory size did not. These observations suggest that relocating a territory increases energy expenditure and decreases energy intake. Such costs could explain the philopatry of reef fish when alternative locations are of uncertain quality or are only slightly better. Nevertheless, they are unlikely to outweigh the long-term benefits of obtaining a superior territory—especially for individuals from adjacent territories. *Key words*: aggression, dear-enemy, dispersal, foraging, Pomacentridae, postsettlement movement. [*Behav Ecol* 18:53–61 (2007)]

Animals that move to a new home range may obtain long-term benefits from improved quality and/or quantity of food, mates, shelter, nest sites, and other resources, as well as a reduced risk of predation on themselves and their offspring (Greenwood and Harvey 1982). This relocation, however, may also result in short-term fitness costs. For example, unfamiliarity with the distribution of important resources may temporarily reduce food intake and increase predation risk, as well as require the expenditure of additional energy and time to gain the information needed to use the new home range effectively (Greenwood and Harvey 1982; Kramer and Chapman 1999; Stamps 2001). For territorial animals, the lack of established relationships with the owners of adjacent territories is likely to increase the rate of aggressive interactions (Temeles 1994), resulting in increased energy expenditure and risk of injury. If reductions in the net rate of energy gain, reproductive success, or survival are large or long-lasting, natural selection will favor philopatry—the tendency to remain on an established home range—even when alternative, higher quality locations are available. Thus, information on the costs of relocation is important for understanding how environmental and social variables may affect the stability of spatial organization and the timescale over which animal distributions can be expected to track changes in resource distribution. Most studies of the consequences of dispersal, however, obtain long-term average values for survival and reproduction that may not reveal the relative importance of relocation in the cost of dispersal. Short-term measures of survival and of reproduc-

tion, where the latter occurs soon after relocation, will reveal some but not all of these costs. Behavioral changes in activity, foraging, antipredator behavior, aggression, and space use are likely to provide a more sensitive measure of short-term changes than mortality and reproductive rates. This sensitivity renders the behavioral measures better suited to indicate the magnitude and duration of possible energetic costs and the risk of injury.

The literature on natal dispersal supports the widespread assumption that moving through unfamiliar terrain lowers survival (Johnson and Gaines 1990), but the costs associated with settlement on a new home range are mostly unknown (Bowler and Benton 2005; Burns 2005). The only examination of short-term survival after relocation to a new home range of which we are aware found that survival of red squirrels, *Tamiasciurus hudsonicus*, was lower during the first 10 days after settlement than during dispersal (Larsen and Boutin 1994). No one to our knowledge has focused a study directly on a broad range of behavioral changes associated with relocation, although several studies addressing other questions have provided some useful information. In a study of the resident advantage in defense of space by European robins, *Erithacus rubecula*, Tobias (1997) examined the behavior of territorial replacements. He found that newcomers sang more than established residents in both winter and spring trials, although chases and fights were rare. Replacements also spent less time foraging than residents did, but the difference was only significant in winter. These differences lasted about 3–6 days. In a study of the effect of spatial position on territorial behavior in three-spot damselfish, *Stegastes planifrons*, Meadows (2001) found higher rates of aggression in individuals reoccupying vacant territories as compared with the original owners. The effect was strongest in the first hour after removal but persisted for at least 48 h on territories in preferred locations. Movement and space use after relocation

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Received 30 August 2005; revised 1 August 2006; accepted 13 August 2006.

do not appear to have been directly investigated. Some studies of voles, *Microtus* spp., suggest that animals transferred to unfamiliar enclosures exhibit higher movement rates (Jacquot and Solomon 1997) and larger home ranges (Pusenius et al. 2000) than animals remaining in familiar enclosures. Whether these animals had settled in a new home range or were still attempting to “disperse” or return to their original range, however, was not certain. Burns (2005) translocated white-footed mice, *Peromyscus leucopus*, to examine the effects of the habitat originally occupied and the presence of established residents in the new location. She found that residents reduced the probability of successful establishment. Furthermore, individuals relocated in the presence of residents lost weight on average whereas residents did not, but relocated individuals did not differ from established residents in their access to an artificial food source.

The present study documents behavior immediately after territory relocation in a highly territorial coral reef fish, the longfin damselfish, *Stegastes diencaeus*. Our main goal was to examine the magnitude and duration of changes in activity related to the energy budget, space use, and interactions with neighbors. Damselfishes of the genus *Stegastes* are an excellent system for such studies because they are abundant, strictly diurnal, and occupy small territories in clear, shallow water. Many adult reef fishes, including damselfishes, are considered strongly philopatric (Sale 1978), possibly indicating high costs of relocation. On the other hand, reoccupation often occurs within hours for territorial vacancies in preferred habitat (e.g., Meadows 2001; Cheney and Côté 2003) and frequently involves intense aggression among several individuals (McDougall PT and Kramer DL, unpublished observations). This suggests a strong net benefit to moving that would allow us to document any short-term costs of moving.

Natural relocation of territories by adults is infrequent in this system (see below), so we created attractive vacancies by removing relatively large territory owners in areas with contiguous territories. We believe that the territories were highly attractive because in this system size influences competitive ability (Robertson 1995), and territories held by larger individuals are recolonized more quickly, both of these strongly suggesting that they are preferred locations (Cheney and Côté 2003; Turgeon K, personal communication). Furthermore, the speed of recolonization in this study was similar to that of recolonization of preferred habitat by other damselfish species (Wellington and Victor 1988; Meadows 2001). Our approach allowed us to determine the length of time required before the newcomer's behavior became similar to that of the former resident—an approach that is not possible in studies following a focal individual during dispersal. By measuring all individuals and comparing the original occupants with the replacements after they had adjusted to the new location, we were able to check whether differences in size or behavioral characteristics of the replacements rather than relocation itself could explain observed differences. For example, if replacements were, on average, more aggressive individuals, we would expect aggression to remain above premanipulation levels. In addition to original residents, we included simultaneous controls on similar territories to check for effects of repeated observations or temporal changes in the environment. We were unable to compare the behavior of individuals before and after relocation because tens to hundreds of potential immigrants would have had to be marked and observed before creating the vacancy.

We predicted that newcomers would initially use less space than original residents because they might be safer by restricting their movements to only part of the territory and then gradually expanding the area used with increasing familiarity. On the other hand, the need to gain information about the

new territory was expected to increase the level of exploratory activity in the space that was used. We predicted that the rates of aggression both performed and received would increase after relocation because the newcomer would have to defend the territory from other potential immigrants as well as establish relationships with the owners of neighboring territories. We predicted a reduction in the foraging rate because of the number of competing activities and because of a potential lack of information about the best feeding sites. Because predators large enough to threaten an adult *Stegastes* were rarely seen and because this species does not have morphology that would allow it to directly kill a rival, we did not anticipate detectable reductions in survival during the observation period, but we thought it is possible that newcomers would remain closer to shelter and more wary until they were established. Such patterns are often seen in translocated animals (e.g., Burns 2005, p. 900). All these changes were expected to be most intense immediately after relocation and to gradually decline with time. Activity and space use would be the exception to this pattern, because newcomers might initially exhibit relatively low values, followed by a period of relatively high values before returning to normal levels once the new home range was established; this is the pattern observed in captive voles, *Microtus rossiaemeridionalis*, released into their natural habitat (Banks et al. 2002).

Preliminary trials suggested that a 2-day period would be sufficient to record most of the change. These preliminary trials also suggested that when only 1 territory owner was removed, a neighbor was very likely to expand into the vacancy. To increase the likelihood of relocation by non-neighbors, we included a treatment in which fish were removed from 2 adjacent territories. The presence of neighbors that expanded their territories to include the vacancy as well as “strangers” moving from outside the immediate neighborhood allowed us to examine the effect of familiarity with the new location. We expected that expanding neighbors would exhibit behavioral differences of lesser magnitude than those of strangers.

METHODS

Study population and site

We studied longfin damselfish on North Bellairs and South Bellairs Reefs (Lewis 1960), fringing reefs located on the sheltered west coast of Barbados, West Indies (13°10'N, 59°38'W), within the Folkestone Marine Park and Reserve (Barbados Marine Reserve). Longfin damselfish are very common on fringing reefs in Barbados and mature at about 85 mm total length (TL), with males reaching at least 128 mm and females at least 122 mm at our site. Both sexes vigorously defend feeding territories of about 1 m² in which they graze microscopic algae and detritus from nonliving hard substrates (McDougall PT and Kramer DL, unpublished observations). Males care for eggs laid on a cleared patch of substrate within their territory. After hatching, the larvae drift in the plankton for about 3 weeks before settling to the reef as juveniles (Wellington and Victor 1989), so individuals are unlikely to be closely related to their neighbors. Adult territories are contiguous on spurs (finger-shaped seaward projections of the reef), the apparently preferred habitat. In adjacent grooves (gaps between the spurs), densities are lower, adults are smaller, and juveniles form a higher proportion of the population (McDougall PT and Kramer DL, unpublished observations). Adult longfin damselfish at our site are highly site attached, especially in preferred habitat. We have seen no evidence of nonterritorial “floaters.” Among 53 territories observed over a 70-day period, there were only 8 disappearances and 5 arrivals, among which there was only a single replacement in

the 35 territories on spurs (McDougall PT and Kramer DL, unpublished observations). Previous studies of longfin damselfish have examined competition for space (Robertson 1995) and the effects of territory characteristics on the latency to reoccupy (Cheney and Côté 2003).

General protocol

All data were collected between 1 March and 1 July 2002 by P.T.M. and an assistant using SCUBA. We identified 30 neighborhoods on spurs, each consisting of 6–9 adjacent territories of adults where 1 or 2 large, central individuals (excluding egg-guarding males) had neighbors on all sides. In some cases, one neighbor, but never more, was a dusky damselfish, *S. dorsopunicans*—a very similar species that is interspecifically territorial with longfin damselfish (Robertson 1995). Ten 3-day data blocks were completed consecutively. Each block included 4 focal territories in 3 neighborhoods: a single removal, a double removal, and a control. Initial observations of the 3 neighborhoods revealed the territorial boundaries as indicated by space use—home ranges and defended areas are equivalent in this system—and “forays” (Bartels 1984) off the territories were easily distinguished. We captured all individuals adjacent to the focal territories using a modified cast net, then measured (TL in mm), sexed (based on shape of the genital papilla [Thresher 1984]), and marked (by injecting Visual Implant Fluorescent Elastomer, Northwest Marine Technology, Shaw Island, WA) under the scales [Frederick 1997]) them *in situ*. We established a grid of 25×25 cm squares on the focal territories, marking the intersections with bleached coral pebbles. On day 1, at least 18 h after marking the neighbors, we made observations (see below) of the 4 focal territory residents, from 0900 to 1000, 1200 to 1300, and 1500 to 1600 h. Then, from 1600 to 1700 h, we captured, measured, sexed, and removed the owners of the 3 territories designated for removal (original residents) using the same techniques described above. Controls were not disturbed at this time. By the morning of day 2, all territories of removed individuals had been reoccupied. Between 0900 and 1000 h, we recorded whether the newcomers were marked (expanding neighbors) or unmarked (strangers) and noted any damage to the body and fins to assist in identifying individuals in subsequent observations. We then made 6 observations of the newcomers and controls over days 2 and 3 in the same time periods as on day 1. In 3 cases, strangers were present at the start of day 3, having displaced an expanding neighbor that initially occupied the vacated territory. In these cases, we made the 6 observations over the course of days 3 and 4. Control territories never changed ownership. The final data set consisted of 29 original residents (one single removal replaced a double removal for logistical reasons, resulting in 11 single, 18 double), 12 stranger newcomers, 15 expanding neighbor newcomers (2 newcomers were missing because 1 had incomplete data and 1 territory had multiple changes of ownership), and 10 control fish. After the sixth focal observation, we captured, measured, and sexed all newcomers and controls. We selected the observation times of 0900–1000, 1200–1300, and 1500–1600 h to cover a broad sample of the midday period and to allow sufficient time between removal and the first observation the next morning for newcomers to establish control over the territory. Note that original residents were euthanized after removal, using an overdose of carbon dioxide.

Each focal observation consisted of 240 behavioral records of a single individual fish taken at 5-s intervals over a 20-min period. Each record included the primary grid location of the focal fish during the time interval, the number of agonistic events during the interval (all chases and displays directed toward or received from conspecifics or dusky damselfish, as

described by Rasa (1969) and Myrberg (1972), all fights with conspecifics or dusky damselfish, whether on or off the grid), and the number of feeding bites at the substrate (on and off the grid) during the interval. We recorded movement for the interval if the fish had passed through three or more cells without engaging in agonistic or foraging behavior.

From the behavior records, we derived measures of space use, movement, and agonistic and foraging behavior. Space use was the proportion of the original territory used during the focal observation, calculated by dividing the number of grid cells visited by the total number of cells in the original territory. The movement index—a measure of activity on the grid possibly associated with information gain and patrolling—was the number of intervals with movement as defined above divided by the proportion of the observation period that the focal fish spent in the focal territory. The measure of agonistic behavior was the number of agonistic acts of each type per 20 min. Foraging rate was the mean number of bites per minute. Expanding neighbors spent some of their time on their original territory. Space use and movement measurements were dependent on the grid so were calculated only for time on the focal territory and not for time on the original territory in the case of expanding neighbors. Agonistic behavior and feeding were recorded for the newcomer whether on the original or new territory. In addition, we ranked body and fin condition of all newcomers on a qualitative scale from 0 (no damage) to 3 (heavy scarring of body and/or fraying of the fins).

Statistical analyses

We analyzed all behavioral measures using a series of General Linear Model Repeated Measures (GLM RMs) tests. It was not possible to include all potential factors in a single test because certain combinations of factors would contain too few subjects. We used transformations to achieve normality for movement and foraging (\log_{10}) and agonistic behavior ($\sqrt{x+(3/8)}$). To determine whether sex affected the behavioral measures, we used a series of GLM RMs on data from the first 3 observation periods (preremoval) with sex and category (original residents and controls) as factors and size as a covariate. Neither sex nor category was significant (summarized in McDougall [2003, Appendix IV]), so we excluded sex as a factor in all further tests. Because size was significant for 2 behavioral measures (movement and chases by conspecifics), and longfin damselfish behavior is often related to size (McDougall PT and Kramer DL, unpublished data), we included size (\log_{10} transformed for normality) as a covariate in all further tests. We tested for an effect of relocation on each behavioral measure by comparing both categories of newcomer (strangers, expanding neighbors) with the original residents. Using original residents as the comparison group accounts for variation associated with the specific location of the territory. Using separate tests for the data collected on the first and second day of relocation, we included time of day, fish category (original residents, strangers, expanding neighbors), and their interactions as factors. Removal treatment (single, double) was not included in these tests because it was not significant for any measure in tests for behavioral changes in newcomers (see below). Post hoc pairwise comparison tests using estimate marginal means with Bonferroni correction identified differences between categories. As suggested by the figures (see below), previous analyses of this data set showed that using the controls as the comparison group to account for changing environmental conditions and potential effects of multiple observation sessions on individual behavior yielded nearly identical results except for reduced power due to fewer controls than original residents

(McDougall 2003). We only present statistical comparisons with original residents from this set of analyses.

To examine the effect of time since relocation on newcomer behavior, we ran an additional set of GLM RMs, using all 6 postremoval focal observations and including time, newcomer category (stranger, expanding neighbor), and removal treatment (single, double) as factors. When there was a significant effect of time, we followed up with a GLM RM comparing controls to strangers and expanding neighbors, separately, to confirm that the observed pattern was not due to temporal patterns that similarly affected controls. We expected a temporal effect to be reflected in a significant interaction between fish type and time. To compare the time spent out of the focal territory among categories, we performed an analysis of variance (ANOVA) with a post hoc Tukey test. We used SPSS® v. 10.1 and v. 14.0 for Windows® for all statistical analyses. Means are presented \pm standard deviation.

Ethical note

We euthanized removed individuals using an overdose of carbon dioxide in seawater. The alternative of moving fish to new locations was not successful because the fish returned after displacements in preliminary trials. Our previous studies suggested that all suitable habitats were saturated and that there were no nonterritorial floater adults. Thus, fish moved to new locations were unlikely to survive unless they displaced another individual. We therefore considered euthanasia the most humane approach. Longfin damselfish are very abundant in Barbados, with densities approaching 1 adult per m^2 in the widespread preferred habitat, so removal of 30 individuals would not put the population at risk.

RESULTS

Size and sex of newcomers

Newcomers (108.0 ± 11.5 mm) were smaller than original residents (114.9 ± 6.7 mm; paired sample $t = 4.467$, degrees of freedom [df] = 26, $P < 0.001$). Strangers (109.8 ± 13.7 mm) and expanding neighbors (106.5 ± 9.5 mm) did not differ significantly in size ($t = 0.627$, df = 25, not significant [NS]); but strangers were larger than the average size of their neighbors (100.8 ± 9.0 mm; paired sample $t = 2.326$, df = 11, $P < 0.05$), whereas expanding neighbors were not significantly larger than the average of their neighbors (101.2 ± 8.2 mm; paired sample $t = 1.417$, df = 15, NS). Of the fish occupying single removals, 5 of 11 (45%) were strangers, whereas of the fish occupying double removals 7 of 16 (43%) were strangers. The number of territories bordering the focal territory was similar for strangers (5.4 ± 1.0) and expanding neighbors (5.1 ± 1.1). However, expanding neighbors also had an undetermined number of additional neighbors on their own original territory. Females occupied territories originally held by females at a greater frequency than expected by chance (12/15; $\chi^2 = 4.95$ with Yates correction, df = 1, $P < 0.025$), and the same was true for males (11/12; $\chi^2 = 6.30$ with Yates correction, df = 1, $P < 0.05$).

Space use

Focal territories averaged 18.8 ± 3.9 cells (range 12–28 cells; about 1.12 ± 0.25 m^2 , 0.75–1.75). Strangers used 24% less of the focal territory than did original residents, visiting 72% of the cells during the first postremoval focal observation as compared with 95% visited by original residents (Figure 1). Overall, strangers used less space than original residents and this was not explained by their smaller size (Table 1). Space

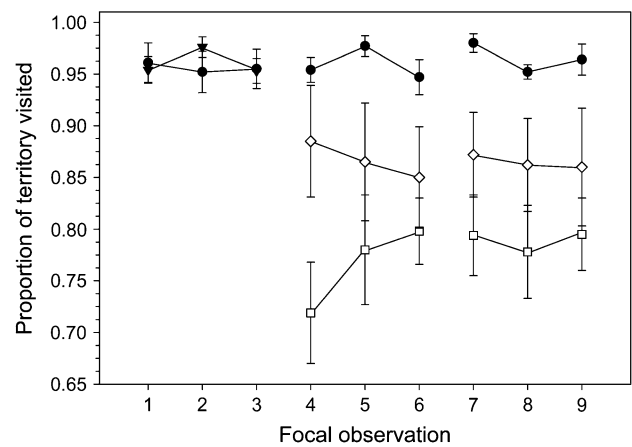


Figure 1

Proportion of total territory visited by longfin damselfishes (number of cells visited divided by number of cells in the focal territory) during a given 20-min focal observation. Focal observations 1, 2, and 3 represent 0900, 1200, and 1500 h on the preremoval day of observations. Focal observations 4–6 and 7–9 represent the equivalent times for the first and second days after the removals. Symbols: controls (filled circle) ($N = 10$), original residents (filled inverted triangle) ($N = 29$), strangers (open square) ($N = 12$), and expanding neighbors (open diamond) ($N = 15$). Error bars are ± 1 standard error of the mean.

use did not change significantly over the course of the observations and averaged 79% on day 3 (Table 1, no effect of time of day; Table 2, no effect of time, i.e., observation number).

Expanding neighbors, on average, used less of the vacated territory during the first focal observation (88%) than the original residents had (95%) and continued to do so throughout the observation sequence (Figure 1), averaging 86% over the course of day 3. Overall, this pattern was not significantly different from space use by either original residents or strangers (Table 1). Expanding neighbors also spent less time in the focal territory (77.8%) than did strangers (96.3%) or original residents (98.8%; ANOVA: $F = 177.391$, df = 3, $R^2 = 0.621$, $P < 0.001$; post hoc Tukey comparisons: $P < 0.001$ for both pair-wise comparisons involving expanding neighbors, $P > 0.1$ between strangers and original residents).

Movement

The movement index of strangers was 3 times higher than that of original residents on the first postremoval focal observation, decreasing over the course of the 6 observations (Figure 2; Table 2). By day 3, movement was only slightly and not significantly greater than that of original residents (Table 1). The 2-way comparison between strangers and controls over all 6 observations confirmed that fish type affected movement ($F = 4.210$, df = 1, $P < 0.05$). A significant interaction between fish type and time ($F = 3.103$, df = 5, $P < 0.05$) demonstrated that temporal changes of strangers differed from those of controls. Expanding neighbors exhibited 3.6 times as much movement as did original residents during the first observation and slightly but not significantly more movement than strangers (Figure 2; Table 1). Movement by expanding neighbors did not diminish to the same extent over time as that of strangers; on day 3, expanding neighbors were still moving more than twice as much as strangers (Figure 2; Tables 1 and 2). Thus, the comparison of expanding neighbors with controls over time showed a highly significant effect of fish type ($F = 36.112$, df = 1, $P < 0.001$) but no significant interaction between fish type and time ($F = 0.426$, df = 5, $P > 0.1$).

Table 1

The effect of time of day (0900, 1200, 1500 h), fish category (original residents [OR], $N = 29$; strangers [S], $N = 12$; expanding neighbors [EN], $N = 15$), fish size, and their interactions on the behavior of longfin damselfish over 2 postremoval days

Behavior	Day	<i>F</i> -value ^a and significance ^b					Comparisons between fish categories ^{b,c}		
		Time of day	Fish category	Fish size	Time × fish category	Time × fish size	S versus OR	EN versus OR	S versus EN
Space use	2	0.046	9.0***	0.046	2.7*	0.040	***	NS	NS
	3	0.14	9.2***	0.015	0.74	0.15	***	0.056	NS
Movement index	2	0.66	23.6***	0.009	2.5*	0.64	***	***	NS
	3	0.57	15.8***	0.99	2.0	0.62	NS	***	**
Chases by focals	2	0.55	46.3***	16.5***	4.2**	0.63	***	***	*
	3	3.0 ^{0.052}	6.8**	0.10	1.4	3.0 ^{0.056}	NS	**	NS
Displays by focals	2	0.15	28.8***	3.0 ^{0.090}	2.5*	0.14	***	***	NS
	3	0.76	9.6***	0.51	0.31	0.76	**	**	NS
Fights	2	2.6 ^{0.078}	9.5***	1.0	2.5*	2.7 ^{0.072}	**	*	NS
	3	2.0	5.3**	0.35	0.076	2.0	*	NS	*
Chases by conspecifics	2	0.37	25.0***	8.4**	2.0 ^{0.094}	0.33	***	**	**
	3	0.21	3.4*	0.023	1.0	0.22	*	NS	NS
Displays by conspecifics	2	2.9 ^{0.058}	18.6***	0.055	0.76	2.8 ^{0.068}	***	NS	**
	3	0.076	7.8**	12.9**	0.40	0.079	**	NS	**
Foraging rate	2	5.02**	14.2***	0.30	1.1	5.9**	***	***	NS
	3	6.1**	2.6 ^{0.080}	0.56	0.94	7.0**	NS	NS	NS

^a GLM RM comparing OR from day 1 with newcomers on days 2 and 3.

^b * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; exact probabilities are shown when $0.05 < P < 0.1$.

^c Post hoc comparisons with Bonferroni corrections between fish categories.

Agonistic behavior and injuries

Newcomers exhibited large increases in aggressive behavior. In the first focal observation, strangers performed on average 10.9 chases, 7.4 displays, and 1.0 fight per 20-min period, respectively, 10, 17, and 15 times more than original residents (Figure 3A,B,C; Table 1). Strangers also received an average of 3.7 chases and 2.9 aggressive displays in the same period, corresponding to 11- and 15-fold increases over rates in original residents (Figure 3D,E). Approximately 80% of chases

and displays of focal individuals involved neighbors, but 75% of their fights were with unidentified longfin damselfish apparently seeking to occupy the focal territory. Although the rates of agonistic behavior of strangers declined over time (Table 2), they remained significantly higher than those of original residents on day 3, with the exception of chases (Table 1). Comparisons between stranger and controls showed highly significant effects of fish type for chases ($F = 23.127$, $df = 1$, $P < 0.001$), displays ($F = 29.477$, $df = 1$, $P < 0.001$), fights ($F = 9.389$, $df = 1$, $P < 0.05$), chases received ($F = 21.497$, $df = 1$, $P < 0.001$), and displays received ($F = 19.486$, $df = 1$, $P < 0.001$). The interaction between fish type and time was significant for chases ($F = 15.409$, $df = 5$, $P < 0.001$) and displays ($F = 4.173$, $df = 5$, $P < 0.01$) performed, as well as chases ($F = 2.538$, $df = 5$, $P < 0.05$) and displays ($F = 2.923$, $df = 5$, $P < 0.05$) received but not for the fights ($F = 0.406$, $df = 5$, $P < 0.05$).

Expanding neighbors, like strangers, showed a large increase in agonistic behavior as compared with original residents. During the first observation, they performed 7.3 chases, 6.6 displays, and 0.44 fights on average, corresponding to 7-, 15-, and 7-fold increases over original residents, respectively (Figure 3A,B,C; Table 1). Overall, they averaged slightly fewer aggressive acts than strangers on day 2, significantly so for chases. As with strangers, the majority (69%) of the chases and displays involved neighboring damselfish, but the fights mostly (75%) involved non-neighbors. The amount of aggression received by expanding neighbors on day 2 was notably less than that received by strangers. In the first observation, expanding neighbors received 1.3 chases (a 4-fold increase over original residents) and 2.0 displays (a 10-fold increase). For the rest of day 2, the number of chases received remained low and significantly different from strangers but not significantly different from original residents. Similarly, displays decreased quickly resulting in a highly significant difference from strangers but not from original residents (Figure 3D,E; Table 1). Larger newcomers performed and received more chases on day 2 than smaller newcomers did, but they received fewer displays on day 3 (Table 1, size). In general, the 2-way

Table 2

The effect of time (observations 4–9), newcomer category (strangers, $N = 12$ versus expanding neighbors, $N = 15$), removal treatment (single versus double removals), and fish size on the behavior of longfin damselfish relocating to vacated territories

Behavior	<i>F</i> -value ^a and significance ^b				
	Time	Newcomer category	Time × newcomer category	Removal treatment	Fish 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

^a GLM RM with newcomer category and removal treatment as factors and fish size as covariate.

^b * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; exact probabilities are shown when $0.05 < P < 0.1$.

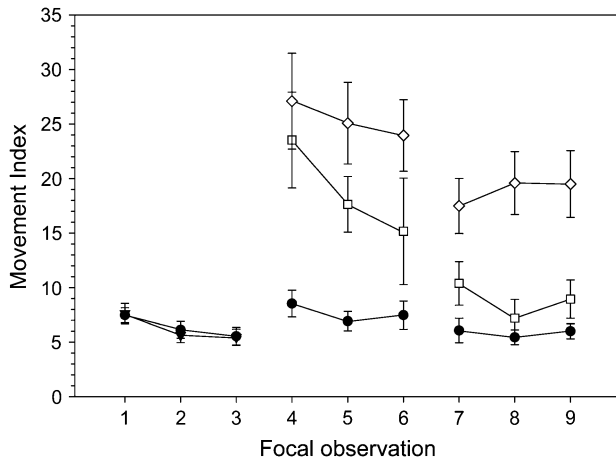


Figure 2

Movement index (number of 5-s intervals of movement per 20-min focal observation with a maximum value of 240) for each of 9 focal observations. Symbols are the same as in Figure 1.

comparison between expanding neighbors and controls over time showed lower F -values for the effect of fish type than the similar comparison between strangers and controls: significant for chases ($F = 7.744$, $df = 1$, $P < 0.01$) and displays performed ($F = 13.183$, $df = 1$, $P < 0.01$) as well as chases received ($F = 7.503$, $df = 1$, $P < 0.05$) but not for fights ($F = 3.175$, $df = 1$, $P > 0.05$) or displays received ($F = 1.492$, $df = 1$, $P > 0.1$). The interaction between fish type and time was significant only for displays performed ($F = 2.530$, $df = 5$, $P < 0.05$) and not for any of the other measures of agonistic behavior (all $F < 1.584$, all $P > 0.1$).

Strangers had heavy scarring and shredded fins on the first observation after the removal of original residents. Their damage index (median, 25th–75th percentile, range = 3, 2–3, 1–3) was much greater than the damage index for expanding neighbors (1, 0–2, 0–3; Mann–Whitney $U = 176.0$, $P < 0.001$).

Foraging rate

The damselfish exhibited strong and highly significant diel patterns of foraging, characterized by low morning rates, sharply higher rates at noon, and a small additional increase in the afternoon (Figure 4; Table 1, time of day). Strangers and expanding neighbors did not differ significantly in their foraging rates across the 6 focal observations (Table 2) and exhibited very similar values, so will be considered together. Newcomers foraged at about 75% of the rate of original residents over day 2, a significant difference (Table 1). By day 3, they had returned to about 90% of original resident rates and this difference was no longer significant (Figure 4; Table 1). Larger newcomers fed at a higher rate during the afternoon peak than smaller newcomers did (Table 1, time by size interaction). Comparing the combined newcomers with controls indicated a significant effect of fish type ($F = 5.612$, $df = 1$, $P < 0.05$) but no significant interaction between fish type and time ($F = 0.440$, $df = 5$, $P < 0.1$), probably because of the confounding effect of the strong diel pattern.

DISCUSSION

Behavioral changes and associated costs of relocation

To examine the behavioral changes associated with relocation, we focus primarily on the strangers. We do this because some of the changes observed in the behavior of expanding neigh-

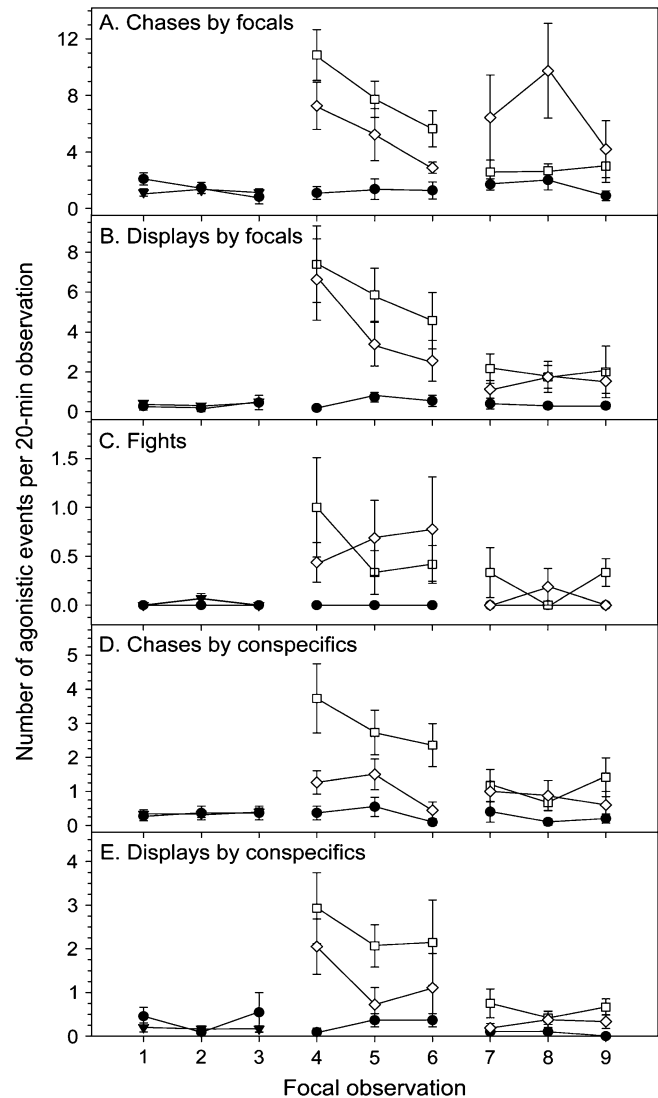


Figure 3

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 9 focal observations. Symbols are the same as in Figure 1.

neighbors may have been associated with maintaining their original territories in addition to the new focal territory. Furthermore, expanding neighbors are likely more familiar with the focal territory than are strangers, so we expected the magnitude of the observed changes to be less than that of strangers. Subsequently, we compare the 2 newcomer types to provide insight into the origin of the observed patterns.

The behavior of strangers was strikingly different from that of original residents. In the first observation after removals, strangers increased agonistic behavior more than 10-fold and movement more than 3-fold, and decreased space use and foraging by about 25% as compared with original residents. Rates of behavior at the final observation were very similar to those of both original residents and controls, which suggests that intrinsic differences—such as aggressiveness or activity—between newcomers and original residents were not responsible for the initial behavioral differences. Size difference rarely had a significant effect on any of the behavioral measures, in particular for space use, where home-range size and fish size

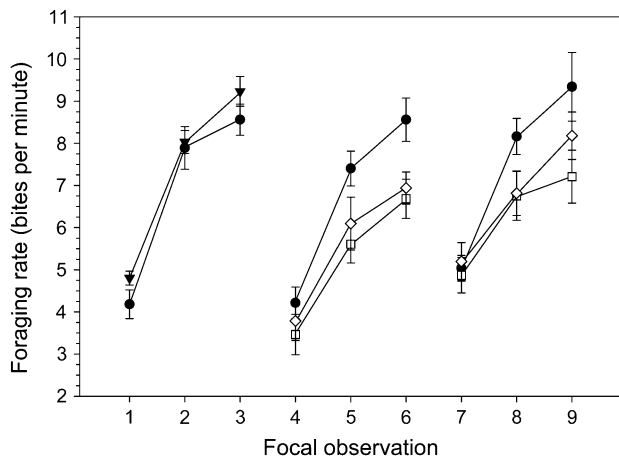


Figure 4
Foraging rate (bites per minute) in 9 focal observations. Symbols are the same as in Figure 1.

are positively correlated over a broader size range (McDougall PT and Kramer DL, unpublished data).

The increases that we observed in the rates of aggression performed by relocating longfin damselfish were considerably greater than those observed in the previous studies of aggression in relocating animals. In three-spot damselfish, Meadows (2001) observed an initial increase in aggression that diminished over time, but the difference was only 6-fold. This lower initial increase may have been due to a difference in newcomer type because Meadows reported that most newcomers in his study were expanding neighbors. We observed a similar 7-fold increase in agonistic behavior of expanding neighbors. In European robins, overt aggression by relocating individuals appeared to be rare, but they did sing at 1.5–2 times the rate of residents, with higher rates in winter (Tobias 1997). Nevertheless, in contrast to the patterns observed in damselfishes, robins taking over territories in winter were quiet during their first day on the territory and did not begin to sing at high rates until their second day (Tobias 1997).

High levels of aggression appear to be necessary when establishing a territory; individuals acquire space through persistent and repeated agonistic interactions with neighbors (Robertson 1995; Stamps and Krishnan 1995). One likely contribution to the high rates of aggression in our study was the lack of information that strangers had about territorial boundaries. This lack of information would have resulted in accidental border transgressions and a consequent increase in attacks by neighbors (Stamps 1987). Additionally, established individuals often direct more aggression toward strangers than toward established residents, a pattern termed the “dear-enemy phenomenon” (Temeles 1994). These increases in attack rates may precipitate retaliatory chases by the stranger. A third reason for the increased aggression of strangers is that their short time on the territory provided little resident advantage in aggressive interactions (Huntingford and Turner 1987). This lack of resident advantage would result in increased attempts by neighbors to expand their territories and by other intruders to take over the territory.

Relocating animals must explore to learn the location of feeding sites (e.g., Noda et al. 1994), refuges (Clarke et al. 1993; Markel 1994), sleeping sites (Robertson and Sheldon 1979), and other important resources and threats on their home range. On the other hand, movement may be riskier in unfamiliar terrain, inhibiting activity immediately after relocation (Norrdahl and Korpimäki 1998; Banks et al. 2002).

The amount of movement after relocation could depend on the relative strength and temporal pattern of these effects. In our study, the index of movement on the new territory—which did not involve foraging or agonistic behavior—was higher for strangers during the first observation even though the amount of space used was less. Unlike some observations on relocating rodents that seem to hide and move very little at first (e.g., comment in Burns 2005, p. 900), newly relocated strangers did not hide but moved about actively. This pattern suggests a predominant function of exploration. Nevertheless, the higher level of movement in expanding neighbors compared with strangers implies that at least some of the increase in movement could be an increase in patrolling to detect intruders (Home and Itzkowitz 1995). We expect exploratory movement to be higher in species with relatively larger home ranges and patrolling to be higher in species with larger territories and more intrusion. To our knowledge, however, there are no previous studies of activity in relation to relocation with which we can directly compare our findings.

In the case of strangers, it is likely that part of the original territory was lost to surrounding neighbors because the prolonged pattern of reduced space use was not due to the newcomer remaining hidden throughout the observation period. Territory size in this species is generally correlated with body size when a broad size range is examined (McDougall PT and Kramer DL, unpublished observations), so the lack of a significant effect of body size on territory size in this study is probably due to the small size range of focal fish. Because our statistical analysis showed that size difference between newcomers and original residents could not explain the reduced territory area occupied by the strangers, it is likely that the territory obtained by the relocating individual was smaller than the one it originally vacated. If the reduction in size of the territory were long-lasting, the territory obtained by a relocating individual would not be of the same value as the one vacated. We are not aware of any other study that has compared territory or home-range sizes before and after relocation.

Newcomers exhibited the diel cycle of foraging characteristic of many damselfishes and other herbivorous reef fishes (Montgomery 1980; Robertson 1984; Polunin and Klumpp 1989), albeit initially reduced by about 25% from that of original residents. This may have been a result of more time devoted to other activities or a reduction in the availability of food. A reduction in food availability could result indirectly from a lack of information about local resources or more directly through foraging by intruding damselfish and other herbivores after the removal of original residents (e.g., Meadows 2001). Although the amount of algae ingested per bite was not known, a lower foraging rate likely represents a reduction in food intake—especially considering that newcomers used less space, had less information about food availability, and may have had a lower standing crop of algae due to grazing by intruders. Tobias (1997) observed similar decreases in foraging, where time allocated to foraging by newcomer European robins dropped to 82% and 62% of the rates of original residents in spring and winter, respectively. Burns (2005) further highlighted a link between relocation and nutrient intake, reporting that relocated mice lost weight whereas residents in the same habitats did not, although access to artificial feeders did not appear to differ.

Our behavioral results suggest that relocating longfin damselfish experience substantial, though brief, increases in energy expenditure. Chasing requires rapid acceleration and high swimming speeds, both of which incur substantial energetic demands (Brett 1964; Beamish 1978). Similarly, fighting is a very vigorous activity that should require a similar or greater expenditure. Cleveland (1999) failed to detect a cost

of territory defense in 2 other damselfish species, but hers was a laboratory study in which fish were confined to small chambers that limited the potential for chases and may have inhibited normal territorial defense. Torn fins and lost scales were not recorded in original residents or controls but because such damage is rarely observed in stable territorial situations (McDougall PT and Kramer DL, unpublished observations), we infer that the difference between strangers and original residents was even greater than that recorded between strangers and expanding neighbors. The damage observed in newcomers would have increased the energy and nutrient requirements for tissue repair, as well as a potential mortality risk from infection. Furthermore, the increases in energy and nutrient expenditure coincided with decreases in nutrient intake. A sustained reduction in the net gain of energy and nutrients would ultimately affect fitness through effects on growth, fecundity, and survival. In addition to an energy cost, we can infer increased opportunity costs; as a result of time spent on agonistic behavior and movement, damselfish may have less time to find, assess, and monitor potential mates (e.g., Sikkell 1998), to defend their territory from heterospecific herbivores, and to visit cleaning stations to have ectoparasites removed (Cheney and Côté 2001). Such time budget demands could magnify the effects of energy budgets on reproduction and survival if they were long lasting. Without a detailed energy and time budget, however, we cannot quantitatively assess the magnitude of such fitness costs. Because the large changes in behavior generally lasted less than several hours, with patterns of most activities approaching baseline levels within 2 days, it seems unlikely that these short-term effects have a major effect on the long-term fitness of relocating fish. Although risk of predation or mortality through intraspecific conflict may be a substantial cost of relocation in some systems, we found no evidence for increases in either effect in longfin damselfish.

Benefits of familiarity and implications for philopatry

In many taxa, including fishes, prior residence greatly increases the probability of winning an aggressive encounter in that location (Huntingford and Turner 1987). Experimental studies show that the longer a newcomer resides in a vacancy, the lower the chance that an original resident can reclaim its original territory (Tobias 1997). Studies in birds and lizards indicate that resident advantage for winning territorial disputes applies not only to territory owners but also to floaters and neighbors that seek to occupy a newly vacant territory (Stamps 1987; Zack and Stutchbury 1992; Bruinzeel and van de Pol 2004). The occupation of 15 out of 27 vacated territories by expanding newcomers, despite large numbers of other territorial longfin damselfish in the population, suggests that a resident advantage applies in our system. Although other studies of replacements on territories of removed damselfishes did not mark the neighbors, observations suggested that most replacements were neighbors (Robertson 1995; Meadows 2001; Cheney and Côté 2003).

Explanations for the predominance of neighbors as replacements include suggestions that territories are more valuable to familiar individuals which results in a greater willingness to fight (Tobias 1997), that prior information improves success in competition (Stamps 1987), and that familiarity decreases defensive costs (Eason and Hannon 1994; Höjesjö et al. 1998; Leiser and Itzkowitz 1999; Utne-Palm and Hart 2000). In our study, expanding neighbors received levels of aggression intermediate between those received by strangers and original residents, probably related to their intermediate level of familiarity with surrounding neighbors. Previous studies show that aggression directed at a “dear-

enemy” neighbor increases when the neighbor occupies a new location (e.g., Husak and Fox 2003). Our study, however, indicates that even in a new position, neighbors receive less aggression than strangers. To what extent this relates to familiarity among the neighbors and to what extent it is due to fewer boundary transgressions are uncertain. Both newcomer types, however, initiated similar levels of aggression, which implies that familiarity rather than the number of border transgressions played a stronger role in the pattern of received aggression. Furthermore, lower levels of agonistic behavior in expanding neighbors as compared with strangers cannot be explained by expanding neighbors having fewer adjacent territories because expanding neighbors and strangers were similar in that respect. Thus, our study supports the concept that familiar individuals are likely to have lower short-term costs and greater benefits of relocation overall. Additionally, our findings suggest that this effect of familiarity may function in an incremental fashion, where intermediate levels of familiarity result in intermediate levels of aggression.

The short-term costs of relocation that we observed might be sufficient to favor site fidelity, by reducing the advantages of relocating when the difference in quality among territories is small, variable, or difficult to assess. Overall, however, they did not appear to be sufficient to outweigh the benefits of even a moderate improvement in territory quality. The rapid onset of vigorous competition that we observed after removal of a territory owner from apparently high-quality habitat suggests that longfin damselfish are aware of vacancies and are willing to relocate. Similar patterns have been observed in other studies of longfin damselfish (Cheney and Côté 2003) and congeners (e.g., Meadows 2001). If a number of individuals are willing to relocate, and the costs of relocation are relatively small, why then are damselfish so philopatric? Given the low rate of movement, it seems unlikely that every individual is in the best territory it can defend. Rather, the resident’s advantage in competition over space may be so strong that a takeover is very difficult to achieve, especially when combined with the increased aggression of neighbors toward a potential newcomer. As long as mortality rates of established adults are also low, turnover of territory owners will be slight.

CONCLUSIONS

Optimal habitat selection and frequency-dependent models like the ideal-free distribution assume the ability of animals to relocate their home ranges in order to track changing needs or fluctuations in resources and competitor densities (Kramer et al. 1997; Kramer and Chapman 1999). Although the lack of such relocation movements is often observed, relatively little attention has been devoted to understanding why relocation might not take place. In a system of small, contiguous territories, social constraints may be the most important limiting factors. For species with large home ranges and higher predation risk, relocation costs may be sufficient to negate any benefits achieved. When suitable habitat is patchy at a large scale, lack of information about alternatives may be the critical problem. Understanding large-scale distributions may be aided by comparing behavioral responses to home-range relocation in species with a diversity of space-use patterns.

We are indebted to Kelsey Abbott for assistance in the field and for editorial comments on various drafts of this paper. J. Stamps, P. Sikkell, K. Cheney, A. Hendry, G. Brown, K. Turgeon, and 2 anonymous reviewers also provided many helpful comments. Denis Réale and Daniel Sol offered statistical advice. The staff of the Bellairs Research Institute gave on-site support. Waddell Aquatics, Montréal, Québec supplied a valuable discount on diving equipment and services. The

principal financial support for this study came from Natural Sciences and Engineering Research Council Canada through a Postgraduate Scholarship to P.T.M. and a research grant to D.L.K. We are grateful to them all. Procedures were approved by the McGill Animal Care Committee (Animal Use Protocol #4549) and the Director of the Bellairs Research Institute, Barbados.

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