ORIGINAL ARTICLE

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Distance to neighbours influences the trade-off between hiding after disturbance and defending food patches in convict cichlids (*Archocentrus nigrofasciatus*)

Abstract Territories are often aggregated. Because of this, distance to neighbours should influence how territory-holders balance safety from predators with the use and defence of resources. I examined the influence of distance to a neighbour on refuge use by pairs of convict cichlids (*Archocentrus nigrofasciatus*) faced with a conflict between hiding and defending food patches. Neighbours could reduce the rate of intrusions by strangers as a by-product of their own resource defence. This should allow fish with near neighbours to spend more time in the refuge. Neighbours could also steal from patches that are left undefended. This should lead to a reduction in use of the refuge. When one fish was confined to its refuge (so that its patch was undefended), theft by the other increased as inter-patch distance decreased. Distance between patches did not influence the rate of intrusion by non-territorial fish. When both fish defended patches, body mass influenced the effect of inter-patch distance on refuge use. Large fish rarely used the refuge, but small territory-holders spent more time in the refuge when patches were close together, as predicted. However, when one fish was dominant at both patches, distance between patches did not influence refuge use. These results suggest that, despite increased opportunity for theft, there is no realised foraging or defensive benefit to settling near neighbours that are of similar competitive ability.

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Introduction

Avoiding predators often conflicts with other activities, such as searching for food or mates (Lima and Dill 1990) or defending resources (Diaz-Uriarte 1999). Faced with such a conflict, an animal must balance safety with the benefits of searching for or defending resources. For example, barnacles and tubeworms will emerge from hiding sooner after a disturbance when expected foraging gains are greater (Dill and Gillett 1991; Dill and Fraser 1997). Where animals are aggregated, allocation of time and effort to anti-predator behaviour should also be influenced by distance to neighbours, who may reduce the risk of predation but are also competitors for food.

Territorial animals are often aggregated because defendable resources are aggregated or because of conspecific attraction (Stamps 1988). One potential benefit of aggregation is that neighbours may detect, dilute or deter intruders (Hart 1987) and predators (Turner and Pitcher 1986) as a by-product of their own territorial defence, so that a territory-holder settling near others may reduce its own risk of mortality and energetic and injury costs of defence. I refer to this defence by near neighbours as "by-product defence", to highlight that such defence is not altruistic or driven by reciprocity, but is a consequence of selfish defence by neighbours.

By holding territories near those of others, animals may also benefit from stealing their neighbours' resources. In birds, settlement in high-density colonies often allows greater opportunity for extra-pair matings. In many studies, the majority of extra-pair sires are immediate neighbours (e.g. Tobias and Seddon 2000; Webster et al. 2001), and long distances between territories may increase the costs of extra-territorial movements to seek matings (Norris and Stutchbury 2001). In lekking systems, males display to attract more mobile females (Hö-

glund and Alatalo 1995). Poor quality males may settle near higher quality ones and attempt to mate with females attracted to these ('hotshot' model; Beehler and Foster 1988; but see Bednekoff 2002).

The converse of this relationship is that near neighbours also represent potential intruders. Although aggression against familiar neighbours may be reduced, particularly on multi-purpose territories (Temeles 1994), neighbours are well-situated to take advantage of temporary lapses in territorial defence (Tobias and Seddon 2000), such as when a territory-holder is hiding or interacting with others. Thus, even if escalated aggression among neighbours is rare, the presence of close neighbours may require greater vigilance against intrusion, and reduced allocation of time to other activities. For example, in high-density situations, male birds may spend more time guarding mates at the cost of reduced foraging effort (Komdeur 2001). I refer to the potential gain from and loss to neighbours as "opportunity for theft".

Both by-product defence and opportunity for theft may influence the relative payoffs of defending a territory versus other activities that conflict with defence (including hiding) and the allocation of time to each. When these effects are present, territorial defence is a game among neighbours. It is not the aim of this paper to describe this game in full. Instead, I present verbal predictions of the influences of by-product defence and opportunities for theft on the activities of a pair of neighbours of equal competitive ability, assuming that they use a mixture of hiding, foraging, defence and theft from neighbours. An increase in the potential for by-product defence, with no change in opportunities for theft, should allow each individual to increase its allocation of time to other activities, as each member of the pair attempts to shift some of the costs of defence onto the other. Increased opportunity for theft should result in reduced allocation of time to hiding or foraging. A territory-holder that is hiding or foraging on (but not defending) its own territory cannot benefit from stealing from its neighbour and is itself vulnerable to theft. Therefore, when opportunities for theft are high, each individual should spend more time defending its own patch or attempting to steal from its neighbours.

Both by-product defence and opportunity for theft may be related to distance between defended patches. Either or both of these effects are likely to decrease as the distance between patches increases. If opportunity for theft decreases with increasing distance between defended patches, then the time that territory-holders spend hiding (or otherwise not defending the patch) should increase with distance, controlling for the effect of by-product defence. If by-product defence decreases with increasing distance between patches, then allocation of time to hiding or foraging on (but not defending) the patch should decrease with distance, controlling for the effect of opportunities for theft.

Previous experimental studies have found that risk-taking increases with the density of competitors in nonterritorial systems (e.g. Grand and Dill 1999). To my knowledge, there have been no previous experimental studies on the effect of neighbours on risk-taking by territorial animals, even though territorial defence can conflict with avoiding predators (e.g. Diaz-Uriarte 1999), the influence of neighbours is pervasive in territorial systems and the density of neighbours does influence guarding (e.g. Komdeur 2001). In territorial species, high-density situations are characterised by both larger numbers of potential intruders and shorter distances among patches. In this experiment, I examine the influence of distance between defendable patches on refuge use independent of the effects of competitor number.

I used convict cichlids (*Archocentrus nigrofasciatus* - formerly *Cichlasoma nigrofasciatum*) to test the general prediction that distance between patches will influence by-product defence, opportunity for theft, or both, in the absence of defence by a neighbour. I then used these results to predict how refuge use should change with inter-patch distance. Convict cichlids fish have long been used in experimental investigations of aggression and feeding territoriality (e.g. Breau and Grant 2002; Grant et al. 2002; Grand and Grant 1994). Both male and female breeding convict cichlids defend nest sites (caves) against other breeding pairs (Wisenden 1994). They also defend free-swimming young that are outside of the nest site from predators (Wisenden 1994). While these fish have not been observed to defend feeding patches in the field, they, like many tropical freshwater fish, will readily do so in aquaria when presented with spatially predictable, defendable patches (Barlow 1993). The lack of feeding territoriality in the wild likely reflects the lack of spatially and temporally defendable food resources there. Numerous experiments demonstrate that they alter defence of food as predicted by models of economic defendability (e.g. Breau and Grant 2002; Grant et al. 2002; Grand and Grant 1994). In the field, hiding behaviour is very rare in convict cichlids (B.D. Wisenden, personal communication), and fish might be expected to trade off time spent defending with other activities, such as foraging. However, in the laboratory, fish will readily use a refuge, particularly after a disturbance (personal observation). In this experiment, I heightened perceived predation risk by disturbing fish immediately before observations. Thus, I expected that, if fish could reduce the time that they allocated to defence, they would increase the time that they spent hiding.

Methods

Experimental subjects

A total of 80 juvenile convict cichlids (20 groups of 4 fish) was obtained from laboratory stocks. These fish were descendants of crosses between laboratory fish and wild fish captured in Costa Rica at least five generations previous. For each replicate, I haphazardly selected four juvenile cichlids. Two of these fish were relatively large (1.0–2.0 g), and were from the same brood. These fish were selected so that the mass of the smaller individual was at least 92.5% that of the larger fish. The other two fish were selected so that the mass of each one was 25–33% of the mean mass of the
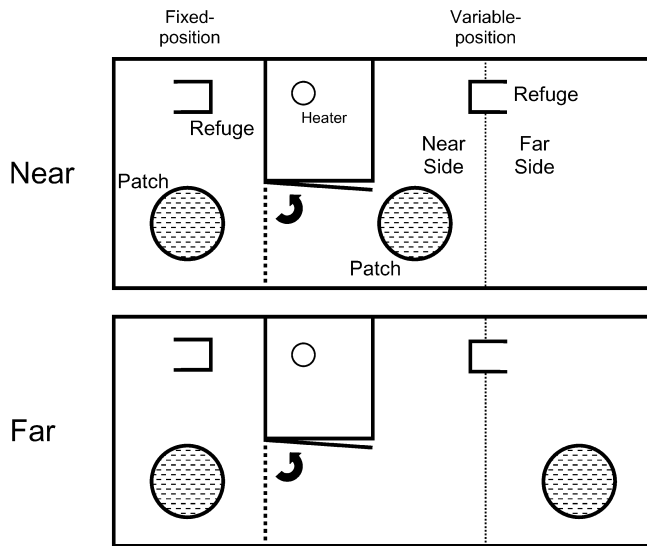
Fig. 1 Layout of experimental tanks, including patches, refuges, fixed-position side and the near and far sections of the variable-position side. The *black arrow* represents the doorway between the sides of the tanks

two large fish. These fish were obtained from different broods than the large fish, and were unfamiliar to the larger fish, although they may have been full or partial siblings. The size asymmetry was created to produce two territory-holding fish and two non-territorial potential intruders that could easily be evicted.

The two largest fish were tagged by attaching red or blue pre-made tags (Chapman and Bevan 1990) through the musculature anterior to the dorsal fin. The two smaller fish were not tagged.

Experimental procedures

The experiment was conducted in five replicate 75×30×40-cm (l×w×h) tanks. Each tank was filled to a depth of approx. 3 cm with gravel and equipped with a heater and two airstones. Tanks were divided into two unequal-sized compartments with black Plexiglas (Fig. 1). This divider was situated 15 cm from one (randomly-determined) side of the tank. The smaller side is hereafter referred to as the "fixed-position" side, because the food patch in this side was never moved among treatments. The larger side is the "variable-position" side, because the food patch could be moved. A door in the divider could be opened so that fish could move between sides. The area of the tanks that was behind this door, when it was open, was blocked off by black Plexiglas (Fig. 1). The heater was placed in this blocked-off section of the tank. The sides and back of the tank were covered in white paper so that fish could not observe neighbouring tanks and to minimise disturbance.

Each side of the tank was equipped with a refuge, which consisted of one inverted cell from a blue plastic ice-cube tray, weighted with a glass marble and with one side removed to provide an entry. These provided refuges of approx. 4×3×3 cm. Preliminary observation indicated that fish of the size range used in this experiment would hide in these when alarmed. Each refuge was placed 5 cm from the back of the tank. On the fixed-position side, the refuge was placed 7.5 cm from the side of the tank; on the variable-position side, the refuge was placed 25 cm from the side of the tank, which positioned it equidistant to the patches in the near and far treatments (see below).

Each tank was filled to within 10 cm of the top using aged tap water, and maintained at 28–29°C. One day after filling, one large and one small fish were introduced to each side, with the door closed. The colour and side assigned to each fish were randomly determined, with one red-tagged and one blue-tagged fish per tank.

Fish were allowed to acclimate for a day before being trained to use the food patches.

Food patches consisted of Petri dishes weighted with two glass marbles attached to the underside of the dish. On the first day of training, I placed 24 "Fry Feed Kyowa" pellets (1,000 μm diameter; proximate composition: crude protein not less than 55%, crude fat not less than 10%, crude fibre not less than 44%, and crude ash not more than 17%) into the Petri dish, which was covered and lowered onto the gravel 10 cm in front of the refuge. The cover was then carefully removed so that food did not float out of the dish.

The food was replaced twice per day, with 2-h intervals between presentations. After 2 days of this procedure, food was presented as 24 pellets mixed with fine coral sand, and a further 12 pellets scattered on the surface of the sand in the dish. This was presented as before for another 2 days.

The following day, food was presented as before, but without the pellets on the surface. After the first presentation of food, the door between the sides was opened and the fish allowed to interact for 1 h. Fish were then returned to their original side (the two small, non-territorial fish were randomly redistributed between sides), and the door was closed. Food was presented once more after this. By the end of this presentation, the large fish in all tanks had learned to search through the sand to find the food.

Experimental treatments began the following day. There were a total of five treatments per tank, which were presented in random order. In one of these, the door was closed as during the preliminary training period. I refer to this treatment as the "alone" treatment (although a small, non-territorial fish was present).

For the other four treatments, the door between the fixed-position and variable-position sides was open. As well, the location of the patch in the variable-position side was changed. The patch could either be moved closer to the fixed-position patch or further away. In the "far" treatment, the centre of the patch was 12.5 cm from the side of the tank (and 55 cm from the fixed-position patch; Fig. 1), while in the "near" treatment, it was 37.5 cm from the side of the tank (and 30 cm from the centre of the fixed-position patch; Fig. 1).

Because I was interested in the effects of neighbours on an unguarded patch, I included two treatments in which the fish on the variable-position side was confined to its refuge, using an opaque plastic cup placed over the refuge while the large fish was hiding within. Again, the food patch on the variable-position side could be near the fixed-position patch or further away from it.

For all trials, food was placed on each side of the tank (in random order) and I then swept each side of the tank with two sweeps of an aquarium net to increase perceived danger. I then opened the door (and closed it again in the alone treatment), and allowed the fish to forage and interact for 20 min. I videotaped the behaviour of these fish with a camera mounted directly overhead. To reduce disturbance to the fish, no observers were present during the trials. After 20 min, the fish were returned to the appropriate side of the tank (if they had moved). I conducted two trials per day, one in the morning and one in the mid-afternoon, for 2 days, with the fifth trial taking place in the morning of the third day. After all trials were finished, fish were left for at least 3 h, removed and weighed.

A total of 16 pairs of territory-holders was used in this experiment. For one pair, I was unable to obtain any data except for refuge use and interactions with neighbours for the fish on the fixed-position side of one of the tanks during the far treatment (because of the positioning of the video camera). Therefore, the sample size for some comparisons differs from 16.

Patch and refuge use

Patch and refuge use were obtained from the videotapes. Beginning 40 s after the door was opened, the location of each large fish was noted every 20 s, for a total of 20 min. After 40 s, most fish had emerged from hiding after this disturbance, even if they immediately returned to the refuge, and therefore had the opportunity to gather information regarding the location of their neighbour. Lo-

cations were divided into seven categories: the fixed-position patch, the variable-position patch, either refuge, the fixed-position side of the tank (excepting the patch), and the variable-position side of the tank (excepting the patch) divided into two sections ("near" and "far") by a line bisecting the refuge (Fig. 1). There was a small space behind the door where fish would occasionally hide; use of this space was included as refuge use.

The location of the fish was defined as the location of its head, except for fish on the food patches. A fish foraging on the patches used fin-digging (see Wisenden et al. 1995) to find food, and then would turn to feed on uncovered. Their heads were often just outside the patch as they turned to feed, so I assigned fish to a food patch if any portion of their body was on that patch.

Smaller, non-territorial fish could not be seen when they were not on the patch. However, I was able to record the location of the small fish as on the fixed-position patch, on the variable-position patch or on neither patch each 20 s.

Chases

I recorded the number and location of chases performed by the fixed- and variable-position fish towards the small, non-territorial fish over the 20-min period. I also recorded the number and location of chases between large fish, as well as the identity of the fish that initiated the chase. Locations were categorised as the fixed-position side, the near section of the variable-position side and the far section of that side.

Some interactions between the large fish were not chases of short duration, but escalated contests, which often yielded no clear winner. During my measurements of patch and refuge use (above) I noted if and where the fish were engaged in such a contest.

Data analysis

My predictions assume the presence of two territorial fish, which win most of the contests that occur at the patch on which they were trained. Of the 16 replicates of the experiment, there were 8 in which each large fish initiated most of the chases on the side of the tank in which it was trained. I refer to these as 'equal-status' tanks. In the other 8 replicates, one of the large fish was dominant to the other (i.e., it initiated most of the chases between large fish on both sides of the tank). Invariably, it was the fish from the fixed-position side that was dominant. In the following, I refer to these as "unequal-status" tanks. Because only equal-status tanks fit the assumptions of my model, I analysed the data from these separately from those from unequal-status tanks, which I report here because they may represent a more natural situation (see Discussion).

My predictions also depend upon the relationships between inter-patch distance and opportunities for theft or by-product defence. I tested these using the data from trials in which the fish at the variable-position patch was confined to its refuge. I compared the ln-transformed use of near and far patches by the fish from the fixed-position side using one-tailed paired t-tests. I used one-tailed tests because I was testing the directional prediction that opportunities for theft would increase as inter-patch distance decreased. I used two-tailed paired t-tests to test whether treatments differed in the time that fish spent on their own patch.

To test whether inter-patch distance influenced by-product defence, I used Wilcoxon signed-rank tests to compare between treatments the number of chases performed by the unconfined fish in the section of the tank containing the variable-position patch, and the total number of chases performed by that fish. I used non-parametric tests because these data were not normally distributed, even after transformation. I used one-tailed tests to compare the number of chases in the section of the tank containing the variable-position patch, because I predicted that there would be more chases on this side when it was near. This was because I expected there would be both increased by-product defence and increased use of that side by fixed-position fish. For comparisons of the total number of chases, in all sections of the tank, I did not have a di-

rectional prediction, so I used a two-tailed test. I used paired t-tests to compare between treatments the square-root transformed number of observations of small fish on the variable-position patch (summed for both small fish). For this comparison, I did have a directional prediction; however, because a trend in the opposite prediction is both plausible (if concentrations of territories attract intruders) and would influence my predictions, I used a two-tailed test.

When both large fish were unconfined, I was interested in the effects of the presence of neighbours and inter-patch distance on the use of the refuge, the use of feeding patches, intrusions on neighbouring patches and chases directed towards large and small fish. To compare the use of refuges and of feeding patches among treatments, I used multivariate repeated-measures analyses, with alone, near and far treatments as within-subjects effects. Because initial inspection of the data suggested that refuge use was influenced by the size of the large fish, I included mass as a covariate in the repeated-measures analysis of refuge use. For intrusion and aggression data (i.e., chases directed towards non-neighbours, chases between neighbours and escalated contests between neighbours) I compared near and far treatments with Wilcoxon signed-rank tests. Comparison with the alone treatment would not be informative. In the alone treatment, there are no neighbours present and there is only one small fish available to chase (rather than two in the unconfined treatments). Because I expected that most attempted intrusions would be unsuccessful, I defined an intrusion as the presence of a territory-holding fish on either the neighbouring patch or the section of the tank containing the neighbouring patch.

I collected data for both large fish. However, I expected that the behaviour of the two large fish in each tank would not be independent. Therefore, for tanks in which fish were of equal status, I used the means of the response variables (and of the covariate, body mass) in my analyses. Use of means did not change qualitative results or statistical significance compared with using all data points and treating each as independent. For tanks in which fish were of unequal status, using means could mask potentially interesting variation in responses between dominant and subordinate fish. Therefore, I analysed the data for dominant and subordinate fish separately, using a critical value, $\alpha=0.025$.

Results

In equal-status tanks, the large, territory-holding fish from both the fixed-position and variable-position sides of the tanks increased in mass over the experiment (change in mass of fixed-position±SE: 0.29±0.04 g; paired t-test: $t=8.0$, $df=7$, $p<0.0001$; change in mass of variable-position: 0.25±0.06 g; $t=4.5$, $df=7$, $p=0.0028$). There was no significant difference in change in mass between sides (paired t-test: $t=-0.96$, $df=7$, $p=0.37$). In unequal-status tanks, both dominant (fixed-position) and subordinate (variable-position) fish also increased in mass (fixed-position: 0.24±0.07; $t=3.4$, $df=7$, $p=0.0115$; variable-position: 0.32±0.07; $t=4.6$, $df=7$, $p=0.0025$). There was no significant difference in change in mass between sides (paired t-test: 0.60, $df=7$, $p=0.57$). The small, non-territorial fish did not grow significantly during the experiment (equal status: −0.03±0.01; $t=1.7$, $df=7$, $p=0.13$; unequal status: −0.02±0.01; $t=1.4$, $df=7$, $p=0.20$).

Neighbours confined

I predicted that fish would use neighbouring patches that were left undefended (because the neighbour was con-
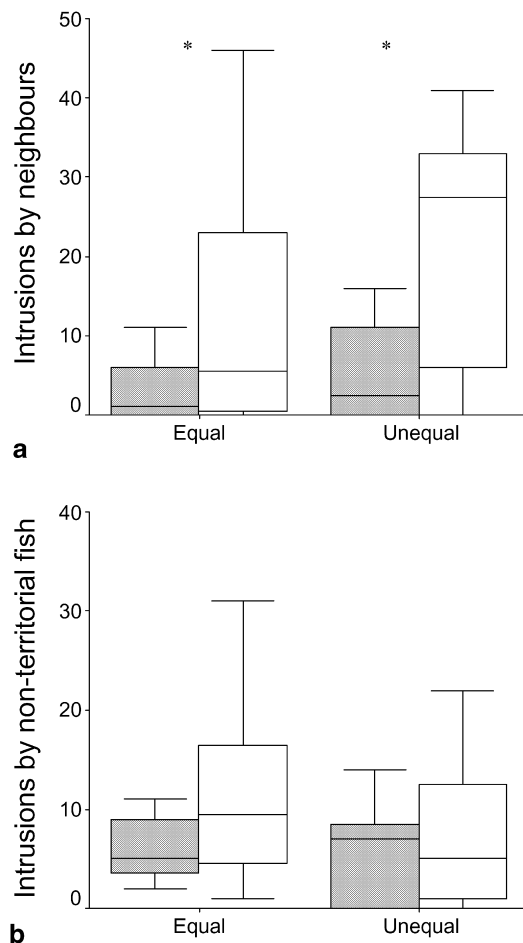
Fig. 2 Observed intrusions onto the variable-position patch by (**a**) neighbouring (fixed-position) fish and (**b**) small, non-territorial fish (summed for both small fish) when the fish normally using this patch was confined to its refuge. *Boxes* represent interquartile ranges; the *lines* across the *boxes* represent medians. *Bars* represent ranges. *Shaded boxes* represent intrusions when the variable-position patch was far from the neighbouring patch; *open boxes* represent intrusions when the neighbouring patch was near. Data are presented separately for equal-status and unequal-status tanks ($n=8$ for each). Differences within equal- or unequal status tanks that are significant are marked with an asterisk (*). Note that statistical analyses (paired t-test on ln-transformed data for **A**, Wilcoxon signed-rank test for **B**; see text for more details) were performed on paired data

fined to the refuge) more often when that patch was nearby than when it was at the far end of the tank. In tanks in which the two large fish were of equal status, the large fish from the fixed-position patch used an undefended neighbouring patch (i.e., the variable-position patch) significantly more often when this patch was near (one tailed paired t-test: $t=3.9$, df=7, $p=0.003$; Fig 2a). When the fish on the fixed-position side was dominant to that on the variable-position side, it also used the undefended neighbouring patch more often when patches were close together (one-tailed paired t-test: $t=1.9$, df=7, $p=0.048$; Fig 2a). Near and far treatments did not differ significantly in the time that fish from the fixed-position patch spent on their own patch (two-tailed paired t-tests; equal

tanks: $t=0.72$, df=7, $p=0.50$; unequal tanks: $t=1.5$, df=7, $p=0.18$).

I expected that small fish would intrude upon an undefended patch more frequently or for longer periods of time when distance to a defended patch increased, because of by-product defence by the fish at the fixed-position patch. The unconfined large fish chased small, intruding fish away from the section of the tank containing its neighbour's patch more often when that patch was near than when it was far (one-tailed Wilcoxon signed-rank test; equal tanks: $T=11.0$, $n=8$, $p=0.039$; unequal tanks: $T=11.0$, $n=8$, $p=0.039$). The overall number of chases anywhere in the tank did not differ significantly between treatments (two-tailed Wilcoxon signed-rank tests; equal tanks: $T=-4.0$, $n=8$, $p=0.58$; unequal tanks: $T=8.0$, $n=8$, $p=0.30$).

The increased number of chases at the undefended patch did not reduce the time that intruders spent at that patch. Small, intruding fish did not spend more time on the variable-position patch, measured as the number of observations, in the far treatment than in the near treatment (two-tailed paired t-tests; equal tanks: $t=1.7$, df=7, $p=0.13$; unequal tanks: $t=0.4$, df=7, $p=0.71$; Fig. 2b). Indeed, the general trend was in the opposite direction to that predicted, with small fish spending more time on this patch when it was positioned near the fixed-position patch (Fig 2b).

Neighbours unconfined

When fish were of equal status, there was a significant effect of body mass on the mean time that fish in each tank spent in the refuge (Fig. 3; repeated-measures ANCOVA between-subjects effects: $F=8.3$, df=1,6, $p=0.028$). The relationship between mass and time in the refuge was significantly influenced by treatment (repeated measures ANCOVA within-subjects effects: $F=14.4$, df=2,5, $p=0.008$; Fig. 3). I performed planned pairwise contrasts between each pair of the three repeated measures (alone, near and far), using an adjusted $\alpha=0.05/3$. There was a significant difference between near and far treatments in the relationship between body mass and time in the refuge between near and far treatments ($F=16.6$, df=1,6, $p=0.007$). Larger fish rarely used the refuge at all, so the difference between near and far treatments was greatest for smaller fish (Fig. 3). There was no difference in the slope of this relationship between fish that were alone and in the far treatment ($F=5.7$, df=1,6, $p=0.054$) or between fish that were alone and in the near treatment ($F=2.49$, df=1,6, $p=0.17$).

The time that fish of equal status spent using any patch (their own or their neighbour's) did not differ significantly among treatments (Fig. 4; $F=2.14$, df=2,6, $p=0.2$). Intrusions upon neighbouring patches were rare when both fish were unconfined, and did not differ between near and far treatments (Table 1). For these fish, distance to a neighbouring patch did not significantly influence the
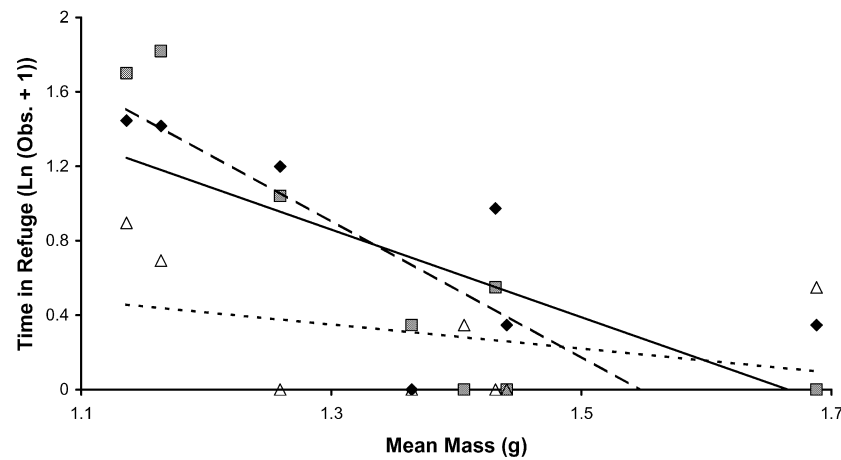
Fig. 3 The influences of body mass and the presence of and distance to neighbours on the use of refuges, from tanks in which both large fish were of equal status. Data presented are the means of refuge use and body mass for both large fish. *Markers* and *lines* represent treatments: alone (*black diamonds*, *solid line*), far (*grey squares*, *dashed line*), near (*open triangles*, *dotted line*). Slopes in the latter two treatments were significantly different

Fig. 4 Mean (±SE) time spent on both patches by large fish in the near (*dark grey bars*), far (*light grey bars*) and alone (*open bars*) treatments. For equal-status tanks, data presented are the means of both large fish (*n*=8). For unequal-status tanks dominant (fixed-position; *n*=7) and subordinate (variable-position; *n*=8) fish are presented separately
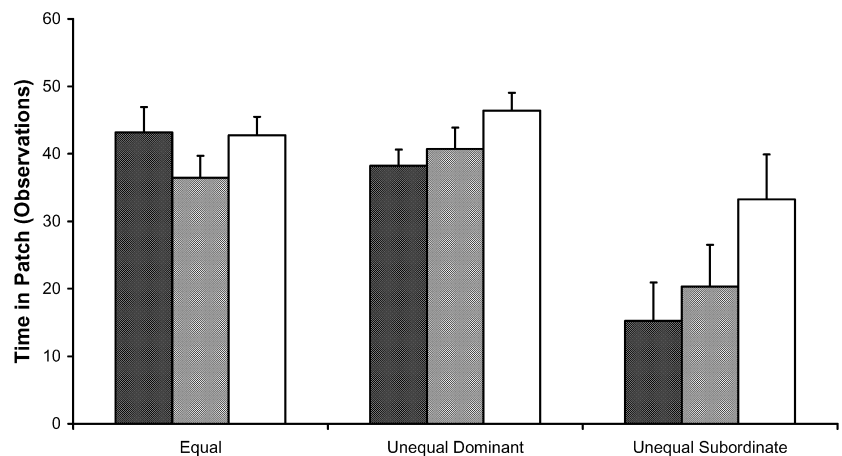
number of aggressive interactions with small, non-territorial fish or neighbouring territory-holders (Table 1).

For tanks in which fish differed in status (i.e., the fish at the fixed-position patch was dominant to that at the variable-position patch in all sections of the tank), I analysed the data separately for fixed-position-patch (dominant) and variable-position-patch (subordinate) fish. Body mass did not significantly influence between- or within-subjects comparisons of refuge use in either patch (fixed between-subjects: $F=0.04$, $df=1,6$, $p=0.84$; fixed within-subjects: $F=0.05$, $df=2, 5$, $p=0.95$; variable between-subjects: $F=2.8$, $df=1,6$, $p=0.14$; variable within-subjects: $F=2.9$, $df=2,5$, $p=0.15$). Treatment also did not significantly influence refuge use (fixed: $F=0.53$, $df=1, 6$, $p=0.61$; variable: $F=2.8$, $df=2,5$, $p=0.15$). Degrees of freedom differ between sides because I removed body mass from the final model for the fixed-position side to improve the fit of the model. Removing body mass did not improve the fit for the variable-position side, so it was retained.

The time that dominant fish spent on any patch did not differ significantly among the three treatments using the adjusted α-value of 0.025 (Fig. 4; $F=8.0$, $df=2, 5$, $p=0.028$). However, fish with a neighbouring patch nearby spent less time on any food patch than did fish that were alone (Fig. 4), although this difference was not significant at the Bonferroni adjusted critical value ($F=9.8$, $df=1, 6$, $p=0.02$). For subordinate territory-holders, there were no significant differences among treatments in time spent on food patches (Fig. 4; $F=3.5$, $df=2, 6$, $p=0.1$). The rate of intrusion onto a neighbour's patch did not differ between treatments (Table 1).

Dominant fish performed more chases of non-territorial fish when patches were close together than when they were far apart (Table 1). Interactions between subordinate and small fish and among territory holders did not differ significantly between treatments (Table 1).

Discussion

In this system, fish that were prevented from defending likely lost resources from their patch at a greater rate

Table 1 Effects of inter-patch distance on intrusions and aggression within tanks by convict cichlids (*Archocentrus nigrofasciatus*). Median values (quartile ranges) of intrusions into the section of the tank containing the neighbour's patch, observed chases by large fish directed towards smaller, non-territorial fish, chases between neighbouring large fish and observations of escalated aggression (with no clear winner) between neighbours are presented along with results of Wilcoxon signed-rank tests for matched-pairs

Type of Intrusion or aggression	Comparison	Far	Near	Far – near (within individual)	T_8	p
Intrusions into neighbour's territory	Equal	0.25 (0–2.4)	1.5 (0.5–2.4)	–0.75 (0.13–2.4)	–7	0.28
	Unequal fixed-position	6 (0–30)	18.5 (13.3–29)	12 (–11–29)	6.5[a]	0.33[a]
	Unequal variable-position	3.5 (0–10.5)	2 (0.5–3.3)	0.5 (–9–1.8)	–4	0.58
Chasing small fish	Equal	34.8 (17.4–39.8)	32.8 (23.1–59.4)	–8.0 (–23.8–9.3)	–7.0	0.38
	Unequal fixed-position	19 (17–21)	43 (32.8–59)	–27.0 (–41.0–10.0)	–14.0[a]	0.016[a]
	Unequal variable-position	14.5 (7–30.5)	30.5 (13.7–35)	–12.0 (–22.0–17.5)	–3.5	0.66
Chases between neighbours	Equal	5.5 (1.3–8.3)	3.5 (1.0–8.8)	0.0 (–1.0–3.5)	1.5	0.81
	Unequal	5.0 (1.0–20.3)	17.0 (9.8–23.3)	–3.0 (–15.0–1.5)	–13	0.07
Escalated aggression between neighbours	Equal	0.0 (0.0–1.0)	1.5 (0.3–3.8)	–0.5 (–2.8–0.8)	–6.5	0.25
	Unequal	2.0 (0.0–6.5)	1.0 (0.0–6.0)	0.0 (–4.5–4.0)	0.5	1.0

[a] n=7 for these comparisons

when neighbouring patches were nearby. When neighbours were confined, fish from the fixed-position patch spent more time at their neighbour's patch when it was near than when it was at the far end of the tank. Although I was unable to observe feeding rate, these fish foraged actively while on the variable-position patch. Thus, it is likely that the time that fixed-position fish spent at that patch was correlated with its depletion of that patch. I had expected that by-product defence from nearby territory-holders would deter potential intruders from an unguarded territory and might therefore compensate for the increased loss of resources to neighbours. However, the rate of intrusion by non-territorial fish was greater, although not significantly so, when territories were close together. If they chose to hide, territory-holders with close neighbours could expect to suffer greater losses of resources to those neighbours and other fish combined than would those with more distant neighbours.

Because of this, I predicted that fish would spend less time in their refuge when territories were close together. There was a significant interaction between body mass and the distance to a neighbour on the time that fish in equal-status tanks spent using a refuge (Fig. 3). Larger territory-holders tended not to use a refuge at all, probably because their larger body size resulted in lower perceived risk of predation (Godin 1997). As predicted, smaller territory-holders spent more time in the refuge when neighbours were distant than when they were nearby.

Interestingly, the effect of distance on theft from neighbours disappeared when both fish were unconfined (Table 1). Indeed, intrusions on the neighbouring territory were very rare when both fish could defend their patches. Nevertheless, the results are consistent with the potential for intrusion influencing time allocation by these fish.

This demonstrates that the observed rate of intrusion when territory-holders are present is a poor indicator of the intrusion pressures shaping resource defence decisions.

A possible alternative explanation for these results is a reduction in predation risk in aggregations. Animals that have close neighbours may be able to benefit through dilution of risk and increased corporate vigilance (Turner and Pitcher 1986; Lima and Dill 1990). If so, fish with close neighbours would perceive their intrinsic risk of predation to be lower and may therefore flee to their refuge less often or return more quickly. However, concentrations of prey do not necessarily decrease risk of attracting predators (Wrona and Dixon 1991). Concentrations of territories appeared to increase, not dilute, the likelihood of intrusion by non-territorial floaters in my experiment (Fig. 2b). Predators may similarly be attracted to groups of territory-holders.

Whether the anti-predator benefits of grouping can explain my results from equal-status tanks depends on the strength of these effects in the far treatment. Refuge use did not differ between fish that were alone and fish with a distant neighbour. If fish in the far treatment were still sufficiently close together to receive an anti-predation benefit, this result suggests that the observed differences between near and far treatments did not result from differences in predation risk. If fish in the far treatment were sufficiently far away from one another that they did not experience an anti-predation benefit, risk dilution or decreased costs of vigilance towards predators could explain my results from equal-status tanks. However, these effects should also have influenced the payoff to hiding in unequal-status tanks. In those tanks, fish with near neighbours spent as much time in the refuge as fish with distant

neighbours. Future experiments could tease apart the roles of reduced predation risk and increased competition for resources by allowing fish to see one another, but not steal resources from one another.

Previous studies have shown that the risk of intrusion can influence the trade-off between guarding and other activities. For example, male Seychelles warblers (*Acrocephalus sechellensis*) with many reproductive males as neighbours spent more time guarding mates and less time foraging than did males in low-density situations (Komdeur 2001). In convict cichlids, the need to guard caves, which are used both as refuges for the current brood and as future spawning sites, against conspecific intruders may explain low rates of mate-desertion by males, even when remating opportunities are high (Wisenden 1994). My results demonstrate that territory-holders also adjust avoidance of predators to the threat of and opportunities for theft from a neighbour.

My predictions were made assuming that territory-holding fish were competitively equal. However, in one-half of the tanks, this was not the case. In these tanks, there was no effect of distance to a neighbour on refuge use. The experimental design did not allow me to measure by-product defence and opportunities for theft when the dominant did not defend its patch. Only fish on the variable-position side were confined for these measurements, while dominant fish were invariably those from the fixed-position patch. This may be because fixed-position fish were never confined, so that they had more opportunity to take over the neighbour's patch. Even if distance did influence by-product defence and opportunities for theft, subordinate large fish can generally be easily evicted from any food patch, while dominant fish can use either patch with impunity. Therefore, dominant fish should not necessarily adjust their refuge use to reduce the risk that 'their' patch is intruded upon by the subordinate.

For subordinates, distance may influence theft, as dominant fish tended to use nearby undefended patches (Fig. 2a). There was no difference in by-product defence between treatments. Nevertheless, inter-patch distance did not influence refuge use for these fish. Subordinates face aggression from dominants, particularly when patches are close together. A subordinate that attempted to feed on a patch while the dominant fish was on the other was likely to be chased (personal observation). Subordinate fish may therefore attempt to avoid these costs by using food patches when dominant fish are hiding (as in willow tits (*Parus montanus*); Koivula et al. 1994). Because dominant fish do not adjust refuge use according to distance between patches, subordinates attempting to avoid dominants would also not be expected to alter their patterns of patch use according to inter-patch distance.

The results of this experiment have implications for understanding the settlement decisions of territorial animals. When the distance between neighbouring patches influences opportunity for theft, but not by-product defence, there appears to be little benefit to settling near others. Neighbours do not help in defence. Although opportunities for theft are higher when neighbours are near, increased defence appears to prevent this benefit from being realised. Fish of equal status did not differ in their combined use of both patches in all three treatments. Intrusions upon the neighbouring patch were very rare when both fish were unconfined, regardless of inter-patch distance. This increase in defence results in decreased time spent hiding from predators, which in natural systems would likely result in greater mortality.

In other species, aggregations of territories are common (Stamps 1988). Aggregation of patchy resources may impose short inter-patch distances on territorial animals, so that territory-holders have little choice but to settle near others, as was the case in this experiment. Groups may be better able to produce or attract resources than are solitary territory-holders, so that the costs of increased vigilance against intruders are outweighed by greater access to resources (e.g. on leks; Höglund and Alatalo 1995). In other systems, by-product defence or anti-predator benefits of grouping may allow individuals to avoid some of the costs of defence, vigilance and predation.

In this study, I used a simple territorial system; I attempted to keep competitive abilities of territory-holders similar, and used a rapidly depleting patch, in which the discounted future value of the territory was likely low. However, these assumptions may not be realistic for natural populations or even most laboratory populations. In larger groups and natural populations, it is unlikely that all fish would be of equal status. Also, in natural populations, territory quality is likely to gradually change over time, as resources are depleted and renew, and the future quality of the territory will be influenced by current and future decisions to hide or not by all aggregation members. To understand the decisions of fish in such groups and the payoffs for establishing a territory near those of others, it would be fruitful to use dynamic games and more natural experiments to examine how dominance status, predation risk, territory quality, by-product defence and opportunities for theft interact to influence refuge and patch use by territorial animals.

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