



# Ideal despotic distributions in convict cichlids (*Amatitlania nigrofasciata*)? Effects of predation risk and personality on habitat preference



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## ABSTRACT

Habitat structure may reduce predation risk by providing refuge from predators. However, individual behavioural differences (i.e. aggression, shyness/boldness) may also cause variation in competitive ability or tolerance of predation risk, resulting in differences in habitat preference. We manipulated habitat structure to explore the role of predation risk on foraging success, aggression and habitat use in an ideal free distribution experiment using the convict cichlid (*Amatitlania nigrofasciata*). Groups of four same-sized fish competed for food in two patches that differed in habitat complexity, with and without exposure to a predator model; all fish were then given a series of individual behavioural tests. Fish showed repeatable differences in dominance status, foraging success, aggression and habitat use over the 14-day trials. Dominants always preferred the complex habitat, while subordinates used the open habitat less after exposure to a predator model. Although an equal number of fish were found in either habitat in the absence of a predator, dominants appeared to exclude subordinates from the complex habitat, supporting an ideal despotic distribution. The individual behavioural assays predicted habitat use, but not foraging success or dominance; fish that were aggressive to a mirror were more frequently found in the open habitat during the group trials.

## 1. Introduction

The presence of physical structure often results in a decreased risk of predation (i.e. [Almany, 2004](#); [Geange and Stier, 2010](#)), decreased visibility ([Clayton, 1987](#); [Eason and Stamps, 1992](#)) and may also impede or slow movement ([Radabaugh et al., 2010](#); [Deboom and Wahl, 2013](#); [Loss et al., 2015](#)). Consequently, predator foraging rates for actively searching predators are often lower in structurally complex habitats ([Gotceitas and Colgan, 1989](#); [Warfe and Barmuta, 2004](#)), and are often preferred by prey seeking refuge ([Russo, 1987](#); [Olsson and Nyström, 2009](#)). Conversely, the opposite response occurs for prey of ambush predators ([Martin et al., 2010](#)), as the foraging success of these predators tends to increase in complex habitats ([Eklöv and Diehl, 1994](#); [Flynn and Ritz, 1999](#)). However, since prey species may also have reduced foraging success in complex habitats, habitat choice often reflects trade-offs between foraging and predator avoidance ([Werner and Hall, 1988](#); [Gotceitas, 1990](#); [Jordan et al., 1997](#); [Zamzow et al., 2010](#)). Habitat structure may also decrease the ability of dominant individuals to defend and monopolize resources ([Basquill and Grant, 1998](#); [Sundbaum and Näslund, 1998](#); [Gibb and Parr, 2010](#)), including territories ([Eason and Stamps, 1992](#)), which may result in dominants preferring open habitats when predation risk is low (i.e. [Hamilton and Dill, 2002](#);

[Höjesjö et al., 2004](#)).

Trade-offs between competition and risk may also underlie behavioural traits, such as boldness and shyness. Bold individuals take greater risks to achieve greater foraging success, while shy individuals forgo feeding for an increased chance of survival ([Gotceitas and Colgan, 1990](#)). Similarly, aggression increases both competitive success and conspicuousness to predators ([Lima and Dill, 1990](#); [Jakobsson et al., 1995](#)). However, the foraging success of aggressive or highly competitive individuals may also be modified by their relative frequency ([Giraldeau and Dubois, 2008](#)). Aggressive or competitive individuals tend to achieve greater foraging success when relatively rare, while weaker competitors may obtain greater success in the presence of many aggressive or highly competitive individuals if they adopt an alternative foraging strategy, such as sneaking food while dominants fight ([Dubois et al., 2004](#)). As predation tends to be higher in open habitats (i.e. [Nelson and Bonsdorff, 1990](#); [Hovel and Lipcius, 2001](#)), individual differences in boldness or aggression may also predict individual differences in habitat preference.

The ideal free distribution (IFD) predicts the distributions of individuals within a group, based on the distribution of resources, such as food ([Fretwell, 1972](#); [Parker and Sutherland, 1986](#)). As the IFD assumes ideal knowledge of patch quality and freedom of patch choice,

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deviations from the ideal free can indicate a loss of freedom of patch choice. Lack of choice may arise from the aggressive behaviour of conspecifics (Andren, 1990; Calsbeek and Sinervo, 2002), resulting in resource monopolization and an ideal despotic distribution (IDD; Fretwell, 1972). Alternatively, the lack of an apparent IFD may occur as a behavioural response to mitigate the risk of predation (Lima and Dill, 1990; Heithaus and Dill, 2002). Convict cichlids (*Amatitlania nigrofasciata*) can exhibit both an IFD and an IDD, depending on the defendability of resources in the environment (Grand and Grant, 1994b). In this study, we use the IFD/IDD framework to examine the role of simulated predation risk and personality on foraging success, aggression, and habitat use in the convict cichlid, a fish that exhibits aggressive behaviour when competing for food (Grand and Grant, 1994a). We predict that dominance status within each group will be determined by size and personality. Although we selected fish of similar size for each group, minor differences in body size (e.g. 1.3–5.6%) may still determine dominance status (e.g. Keeley and Grant, 1993). Personality traits like aggression and boldness, as observed during individual behaviour tests, are also associated with dominance (e.g. Colléter and Brown, 2011; David et al., 2011).

In this experiment, groups of four fish competed for food in two patches, one each in an open and structurally complex habitat, with and without prior exposure to a predator model. In the no-predator treatment, resource defence theory predicts dominant competitors will prefer the open habitat, in order to more easily defend and monopolize food, consequently driving subordinates into the complex habitat. Alternatively, the asset-protection principle (Clark, 1994) predicts that dominant competitors will prefer the complex habitat due to a behaviourally robust anti-predator strategy which commonly occurs in lab environments, whereby antipredator behaviour is generalized to situations where predators are not present (sensu Clark and Mangel, 1986), and force subordinates into the open habitat. In the predator treatments, the dominants will be less willing to engage in risky aggressive behaviour, and will likely prefer the complex habitat. In summary, we expect that deviations from an ideal free distribution will be driven either by a preference for the open habitat, to maximize foraging success, or for the complex habitat, to minimize risk, and by despotic behaviour by dominants. We tested the predictions that 1) foraging success, 2) aggression, and 3) use of the open habitat, will all decrease following exposure to a predator model, and that 4) bold, and 5) aggressive fish will prefer the open habitat.

## 2. Material and methods

In the wild, convict cichlids are generalist omnivores (Yamamoto and Tagawa, 2000) native to the freshwater lakes and streams of Central America (Wisenden, 1995). Juveniles and non-reproductive fish tend to prefer structurally complex habitats, usually woody or rocky sites which provide shelter (Conkel, 1993; Yamamoto and Tagawa, 2000). Although they do not defend feeding territories in the wild, juveniles can be easily manipulated to do so in an aquarium, depending on the defendability of the food source (Grand and Grant, 1994a).

Fish were held in three stock tanks (1 x w x h = 61.5 cm x 31.5 cm x 33.5 cm) containing dechlorinated tap water, gravel to a depth of 3 cm, an aquarium heater, plastic plants, and flowerpots, for a minimum of two weeks before being used in an experiment. Fish were held at approximately 23 °C, set on a 12:12 light/dark cycle, and were fed commercial fish flakes (Nutrafin® Max Tropical Fish Flakes). Four juvenile fish of similar body size (see below) were selected for each of 15 experimental groups (range = 0.19–3.03 g); to differentiate between group members, fish were tagged subcutaneously with a small amount of elastomer in pink, red, or green in either the cephalic, dorsal, or caudal region with an insulin syringe. No injuries or mortalities occurred as a result of the tags, while fish appeared to fully recover within a few minutes. All fish were weighed to the nearest 0.01 g at the beginning and end of the group trials, as well as after the individual

behavioural assay, and were returned to stock tanks after the completion of the experiments. Fish were individually tested following the group trials, as we did not want to risk increasing behavioural distress and possibly inducing abnormal behaviour within the groups by testing before the group trials. The primary focus of the study is on individual behaviour within a group, with the individual nested within the group as the experimental unit. To minimize our use of animals, we used a total of 40 fish; 20 were used once and 20 were used twice in the experiments for a total of 15 groups (15 × 5 = 60), but the same group of four fish were never reused. As the identity of the dominant depends on the particular dynamics within each group (Graham and Herberholz, 2009), we expect that the dominance status of individual fish may differ between groups, depending on the identities of the other group members. All reused fish were given a latency period of 8–12 weeks between trials, a time period which allowed for substantial growth and behavioural changes to occur in another species of cichlid (*Cichlasoma citrinellum*; Francis, 1990). All group members, including previously tested fish, were individually behaviourally typed the week following participation in a group trial. As developmental stage is often a more important behavioural determinant than chronological age (Noakes, 1991), and all fish remained juveniles for the duration of the experiment and did not engage in any mating behaviour, minimal, if any ontogenetic changes were expected to occur during the two to three weeks of the study period.

### 2.1. Feeding treatment

Two experimental tanks (1 x w x h = 91 × 46 × 39 cm) were set up with a gravel substrate, a heater, and an air stone, and were divided into two regions. One half of the tank was left as is (“open habitat”), while four well-spaced small plastic plants, with an approximate height and diameter of 7 × 1 cm, were placed in the right half of the tank (“complex habitat”), which also contained the heater and air bubbler. A group of four fish was placed into an experimental tank after being tagged and weighed; trials began 24 h later, and were conducted over a two week period. To determine growth, all fish were weighed again at the end of the trial.

Groups were randomly assigned to one of three treatments: 1) daily exposure to a predator model in the first week with no predator exposure in the second week, 2) daily exposure to a predator model in the second week with no predator exposure in the first week, or 3) no exposure to a predator model in either week. In the predator treatments, a wolf cichlid model (*Parachromis dovii*; 1 x w = 13 × 6 cm), a common predator of convict cichlids in the wild (Wisenden and Keenleyside, 1992), attached to a metal stick (28 cm), was moved around the entire tank by the experimenter at approximately 1 body length per second for a period of 30 s (Supplementary Fig. 1), and food was offered 15 min later.

Each week, feedings were conducted every day for five consecutive days to “train” the fish, and data were collected on the 6th and 7th days, with a total of four days of observation. Previously frozen mysis shrimp were preloaded into 3 mL syringes, one per syringe, and dropped into both habitats simultaneously every 20 s by an assistant for an 8-minute period. Fish were observed throughout the 8-minute feeding period and for 5 min afterward, for a total of 13 min. Food was present during all 13 min of observation (see below). During the observations, the identity of the fish that consumed each food item was recorded, as were all fish observed chasing or being chased. The habitat choice of each fish (i.e. open vs complex) was also noted every 30 s. Within each group, the most aggressive fish was labelled as dominant, while the remaining fish were classified as subordinates. Each treatment was replicated 5 times, for a total of 15 trials. Out of the 50 total food items provided per trial, the identity of the fish which consumed each food item was able to be determined for a mean of 39.3 ± 2.03 food items of each trial; typically this occurred shortly after the food was provided. The remaining food items were usually consumed by

unidentified fish, during unobserved foraging events. Only food items consumed by identified fish were used to determine the proportion of food consumed by each of the four fish per trial, which was subsequently used as a measure of competitive weight for each fish (sensu Grand and Dill, 1997).

## 2.2. Individual behavioural assay

Individual behavioural trials were conducted after the completion of the group trials (range = 0–3 days). Fish were netted in haphazard order from their experimental tank, and placed into one half of a small tank (1 x w x h = 30.4 × 13.4 × 20.8 cm) containing a heater and an air stone, divided lengthwise by a piece of black Plexiglas. Fish were held for 48 h before testing to reduce visual signs of behavioural distress and facilitate normal behaviour. All tests of an individual were conducted consecutively on the same day, in the same order, with approximately 15 to 30 min between each test. Fish were weighed and returned to a stock tank following the completion of the behavioural tests.

### Test 1: Time to emerge

After the acclimation period, the Plexiglas divider was raised approximately 10 cm off the floor of the tank, allowing access to the second half of the tank. The latency of the fish to swim past the divider into the other side was recorded, to a maximum of 10 min. The divider was completely removed following the test.

### Test 2: Novel food

A small pinch of crushed commercial dry cat food (Meow Mix® Original Choice) was sprinkled into the tank above the focal fish. The latency to begin feeding and the total number of bites taken were noted over a period of 10 min. Uneaten food was removed with a dipnet following the test. Fish reacted minimally, if at all, to the dipnet.

### Test 3: Mirror test

A mirror was placed against the outside wall of the test aquarium in view of the focal fish, and its behaviour was recorded for 10 min. Unlike Höjesjö et al. (2004, 2011), however, the mirror was not placed inside the tank to minimize disturbance of the fish. The initial reaction to the mirror (Supplementary Table 1), and distance and orientation relative to the mirror was noted every 10 s, as well as the number of lateral displays, chases towards the mirror, mouth wrestling attempts (Keeley and Grant, 1993), and head down displays (Sopinka et al., 2009). The mirror was removed after the completion of the test.

### Test 4: Intruder test

A conspecific visually assessed to be of the same size as the focal fish was captured from a stock tank, placed within a small transparent plastic cup (height: 10.5 cm, diameter: 7.5 cm) with a mesh cover weighed down by 2.5 cm of gravel, and slowly lowered into the test aquarium, as far as possible from the focal fish (see Bell and Stamps, 2004). The initial reaction of the focal fish (Supplementary Table 1) and its latency to approach the intruder were recorded, as well as its distance and orientation toward the intruder every 10 s. The total number of lateral and head down displays, chases, and mouth wrestling attempts were also recorded throughout the 10 min trial. The intruder was removed from the tank and measured following the test (mean length difference ± 95% C.I.: 10.29% ± 2.11%).

### Test 5: Aquatic predator model

A different predator model was used in the individual trials to avoid any possible effects of habituation to the wolf cichlid model used during the group trials. A plastic model of a larger, allopatric cichlid species, the yellow lab (*Labidochromis caeruleus*; 11 cm x 8 cm) was slowly lowered into the test aquarium, as far as possible from the focal fish. The initial response to the predator model, the latency to approach and the number of approaches of the focal fish were recorded, as was the distance and orientation relative to the predator every 10 s. After 10 min, the predator slowly approached the focal fish at a swimming speed of 1 body length per second then retreated, and the reaction was recorded (Supplementary Table 2). The predator model was removed following the completion of the test.

### Test 6: Aerial predator model

A circular piece of opaque cardboard (diameter: 16 cm) was passed back and forth over the top of the aquarium, equivalent to a swimming speed of 1 body length per second, to mimic the shadow of a predator passing overhead. The response of the focal fish (Supplementary Table 2), and any changes in behaviour were recorded.

## 2.3. Statistics

### 2.3.1. Group trials

Mixed models were constructed using the package ‘lme4’ (Bates et al., 2014) to compare the effects of the predator treatments and individual behaviour on foraging success, aggression, and habitat choice during the group trials. Three sets of models were constructed with proportion of time in the open habitat, proportion of food consumed, and number of chases as the response variables, while predator treatment, dominance status, and tag site were included as fixed effects. Fish ID, trial, observation day, and week were used as random effects, to account for the repeated measures, while ID was nested within group for the analysis, due to the structure of the data (Bates, 2010). The statistical significance of each predictor variable, and any interactions between them, were obtained from an analysis of variance of the final models using the ‘lmerTest’ package (Kuznetsova et al., 2016). Repeatabilities for individual differences in foraging success, chasing, and habitat choice were then calculated from the four days of observation using the ‘rptR’ package, which uses estimates from parametric bootstrapping to calculate confidence intervals (Stoffel et al., 2017).

Growth during the group trials was determined by the formula for specific growth rate:

$$\text{SGR} = (\log_e M_{\text{final}} - \log_e M_{\text{initial}})/t$$

with mass (M) measured in grams, and time (t) measured in days (Ricker, 1975).

### 2.3.2. Individual behavioural assay

Principal component analyses were conducted using the package ‘FactoMineR’ in R (Le et al., 2008) to reduce the behavioural measures obtained during the individual behavioural trials into composite behavioural traits. Principal components with significant eigenvalues were then selected using the ‘InPosition’ package (Beaton et al., 2014), where calculated p-values are based on permutation procedures (Peres-Neto et al., 2005). Raw variables were z-transformed prior to analysis. Retained principal components, representing composite behavioural traits, were then used as response variables in linear models. The average proportion of time spent in the open habitat, average proportion of food consumed, and average number of chases per fish were then included as predictor variables, as was dominance status, treatment order, body size, tag site, and SGR. The mean proportion of time in the open habitat, chase number, and initial weight were not normally distributed, and were log transformed prior to analysis to meet assumptions of normality.

## 3. Results

Despite the minimal size differences within the groups of fish (mean ± SD, coefficient of variation of body mass = 0.099 ± 0.043; N = 15 groups), one of the four fish emerged as the dominant competitor in each of the trials, with no co-dominants observed in any of the groups. Dominants chased conspecifics substantially more than subordinates, accounting for 47–94% (mean % ± SD: 72.8 ± 14.4%, N = 15 groups) of the total chases within the groups. Overall, dominants were not larger than subordinates within groups (Linear mixed model,  $F_{1,29} = 2.04$ ,  $P = 0.16$ ), and were only the largest fish in 5 of 15 groups. Although predator treatments were randomly assigned to the different groups, fish exposed to a predator in the second week were

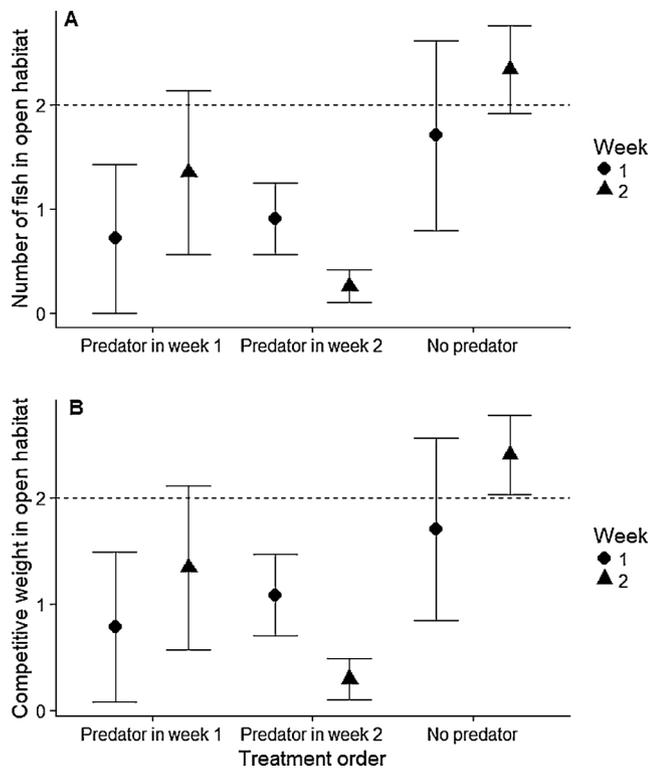


Fig. 1. Mean ( $\pm$  95% CI,  $N = 5$ ) A) number of fish, and B) competitive weight, in the open habitat during 13 min feeding trials under different predator exposure treatments. Dashed line is the ideal free prediction.

smaller than those in the other two treatments (Linear model,  $F_{2,56} = 7.50$ ,  $P = 0.001$ ; mean  $\pm$  SD weight:  $0.45 \pm 0.09$  g vs  $1.15 \pm 0.28$  g). Due to these group differences, initial body weight was added as a covariate in all analyses.

Non-parametric bootstrapped 95% C.I.'s with 1000 repetitions were calculated using the 'Hmisc' package in R (Harrell and Dupont, 2017), and displayed in the graphs which compared the behaviour of the three subordinates relative to the one dominant per group (e.g. Figs. 2–6).

### 3.1. Habitat choice

Consistent with the ideal free distribution, about two fish were found in the open habitat in the no predator treatment, whereas fewer than two fish occupied the open habitat in both predator treatments, as indicated by the 95% C.I.'s (Fig. 1A). Overall, body size (Linear mixed model,  $F_{1,240} = 0.15$ ,  $P = 0.71$ ), and tag site (Linear mixed model,  $F_{3,240} = 0.72$ ,  $P = 0.54$ ), did not affect habitat use.

There was a significant interaction between the treatment order and the presence of the predator in the number of fish in the open habitat (Linear mixed model,  $F_{1,240} = 11.36$ ,  $P = 0.00097$ ); fish in the week-two predator treatment used the open habitat less when the predator was present, relative to the other treatment groups. Overall, fewer fish used the open habitat when the predator model was present (Linear mixed model,  $F_{1,240} = 13.98$ ,  $P = 0.00025$ ; Fig. 1A).

When the total competitive weight in each habitat was considered, taking into account the portion of food consumed by each fish, the same trends were observed (Fig. 1B). In general, about half of the competitive weight was found in the open habitat in the no-predator treatment, whereas less than half of the competitive weight was found in the open in the two predator-present treatments (95% C.I.'s; Fig. 1B).

A significant interaction was also found between dominance status and the presence of the predator model (Linear mixed model,  $F_{1,240} = 11.99$ ,  $P = 0.00065$ ; Fig. 2). Dominant fish primarily used the complex habitat, whereas the subordinate fish in the no-predator

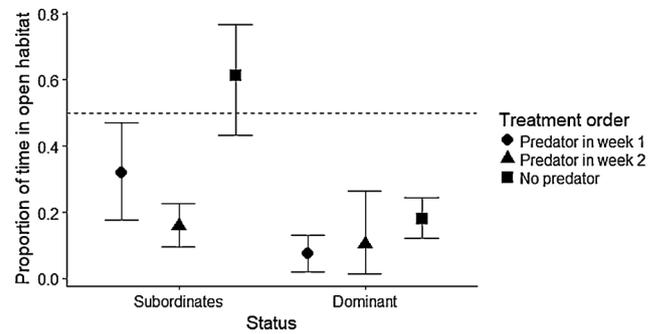


Fig. 2. Number of subordinate and dominant cichlids in the open habitat (mean  $\pm$  95% nonparametric bootstrapped CI,  $N = 5$ ) during 13 min feeding trials in both weeks under different predator exposure treatments. Dashed line is the ideal free prediction.

treatment primarily used the open habitat. Despite this interaction, dominants used the complex habitat more than did subordinates (Linear mixed model,  $F_{1,240} = 11.43$ ,  $P = 0.0015$ ; Fig. 2). Fish showed individual habitat preferences over the study (mean repeatability  $\pm$  95% C.I.:  $0.27 \pm 0.137$ ).

### 3.2. Foraging success

Dominants, as identified by higher chasing rates, consumed a greater proportion of food than subordinates in all trials (Linear mixed model,  $F_{1,240} = 9.44$ ,  $P = 0.0032$ ; Fig. 3), while the proportion of food consumed was unaffected by the predator model (Linear mixed model,  $F_{1,240} = 0.24$ ,  $P = 0.63$ ), treatment order (Linear mixed model,  $F_{2,240} = 0.04$ ,  $P = 0.96$ ), body size (Linear mixed model,  $F_{1,240} = 0.06$ ,  $P = 0.81$ ), or tag site (Linear mixed model,  $F_{3,240} = 0.57$ ,  $P = 0.64$ ). Individual differences in proportion of food consumed was significantly repeatable throughout the trials (mean repeatability  $\pm$  C.I.:  $0.40 \pm 0.194$ ).

### 3.3. Chasing

There was a significant interaction between predator treatment and dominance status on the rate of chasing (Linear mixed model,  $F_{2,240} = 11.98$ ,  $P = 0.000042$ ). The dominants in the week-two predator treatment, which were smaller, chased less than the dominants in the other two treatments (Fig. 4). Despite this interaction, dominants chased more than subordinates (Linear mixed model,  $F_{1,240} = 141.42$ ,  $P < 0.00001$ ), as did larger fish (Linear mixed model,  $F_{1,240} = 12.35$ ,  $P = 0.00084$ ). Unexpectedly, fish that were tagged on the tail tended to chase less overall (Linear mixed model,  $F_{3,240} = 2.77$ ,  $P = 0.049$ ), likely due to the slightly increased chance that these fish were subordinates (Generalized linear model,  $t_{56} = -1.82$ ,  $P = 0.068$ ). This tagging effect may have been due to chance or to the resemblance of head

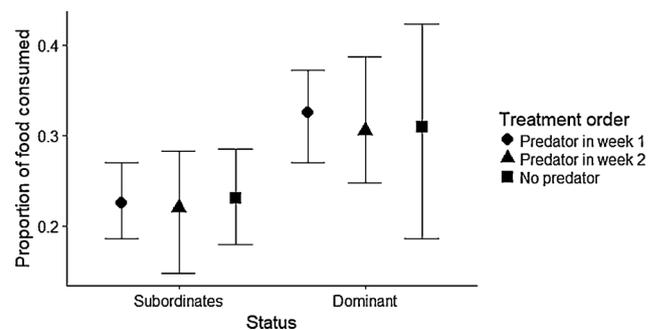


Fig. 3. Proportion (mean  $\pm$  95% nonparametric bootstrapped CI,  $N = 5$ ) of food consumed by 3 subordinate and 1 dominant cichlid during 13 min feeding trials under different predator exposure treatments.

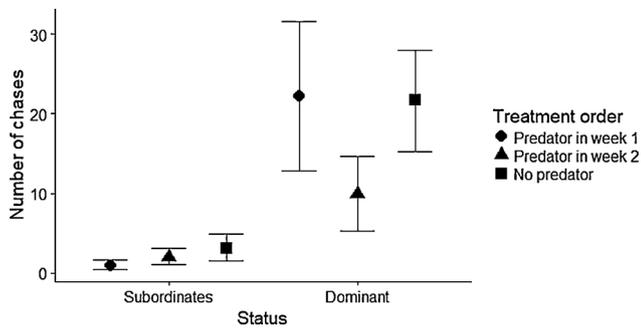


Fig. 4. Number of chases toward other fish (mean ± 95% nonparametric bootstrapped CI) by three subordinates and one dominant cichlid during 13 min feeding trials under different predator exposure treatments. (N = 5 per treatment).

and dorsal tags (but not tail tags) to dominance markings found in other species of cichlid (e.g. Denight and Ward, 1982; Radesäter and Fernö, 1979). Individual differences in chase rates were repeatable across both weeks of the study (mean repeatability ± C.I.: 0.30 ± 0.165).

3.4. Growth

There was an interaction between predator treatment and dominance status on growth rate (Linear model,  $F_{1,50} = 7.61, P = 0.022$ ; Fig. 5). The dominants in the week-two predator treatment, which were smaller, lost weight over the study (SGR mean ± SD:  $-0.00606 \pm 0.01025$ ), whereas dominants in the other treatments gained weight. However, the weight loss of the smaller dominants did not significantly differ from zero (One sample t-test,  $t_4 = -1.214, P = 0.15$ ), although the weight gain of the other dominants did (One Sample t-test,  $t_9 = 2.1351, P = 0.03076$ ). On average, subordinates gained weight over the trials, but there was no marked difference between dominants and subordinates in the no-predator and week-one predator treatments (Linear model,  $F_{1,50} = 1.08, P = 0.31$ ). Not surprisingly, larger fish grew less (Linear model,  $F_{1,50} = 10.65, P = 0.002$ ), while fish that consumed a greater proportion of food tended to grow more (Linear model,  $F_{1,50} = 2.89, P = 0.095$ ; Supplementary Fig. 2). Use of the open habitat showed a positive association with growth (Linear mixed model,  $F_{1,50} = 9.23, P = 0.0037$ ).

3.5. Individual behaviour

Three different composite behaviours emerged from a principal component analysis of the individual behavioural assays ( $p = 0.01$ ; Table 1): (PC1) aggression toward the intruder; (PC2) aggression to the mirror; and (PC3) a high feeding rate, aggression toward the mirror and intruder, and shyness to the predator. As subsequent axes are placed orthogonally in a PCA, the latter two components, PC 2 and PC 3, are

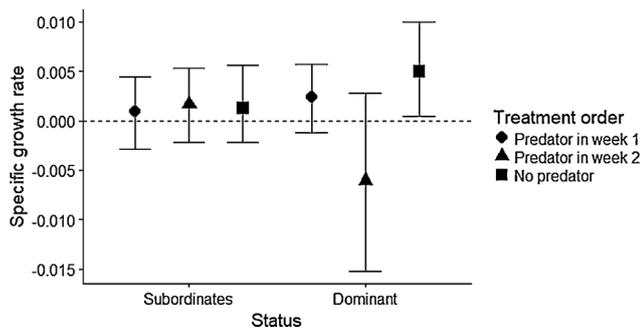


Fig. 5. Specific growth rate (mean ± 95% nonparametric bootstrapped CI) of subordinate and dominant cichlids under different predator exposure treatments (N = 5 per treatment). Dashed line is no change in body weight.

Table 1

Retained principal components from individual behavioral assays, indicating composite behavioral traits.

Test	Behavior	PC 1	PC 2	PC 3
Novel food	No. bites	-	0.118	0.878
	Mirror	-	-0.813	-0.111
Intruder	Approach latency	-	0.872	-
	< 1 body length away	-	-0.768	-
	> 2 body lengths away	0.215	-	-
	No. side displays	0.222	0.490	0.406
	No. head down displays	-0.266	0.303	0.107
	No. mouth wrestles	-	0.504	-
Aquatic Predator	Initial reaction	-	-	-0.263
	Approach latency	-0.742	0.142	-0.269
	No. approaches	0.298	-	0.413
	< 1 body length away	0.910	-	-
	> 2 body lengths away	-0.875	-	-
	No. side displays	0.832	-0.172	-0.142
	No. head down displays	0.252	-0.269	0.533
	No. charges	0.749	0.215	-
	No. mouth wrestles	0.590	-	-
	Initial reaction	0.136	-	-0.716
Cumulative proportion of variance	Approach latency	-	0.118	0.878
	No. approaches	0.305	-	0.238
	< 1 body length away	0.176	0.114	-
	> 2 body lengths away	-0.180	-0.174	-
	SS loadings	4.245	2.857	2.947
	P-value	0.01	0.01	0.01
	Proportion of variance	20.2%	13.6%	14.0%
	Cumulative proportion of variance	20.2%	33.8%	47.8%

interpreted as residuals of the first and second components, respectively (Oliveira et al., 1996). Aggressive behaviours directed toward the intruder and mirror were similar for PC 1 and PC 2, respectively. For the first two components, the fish approached quickly, spent a lot of time within one body length, and engaged in numerous side displays, and mouth wrestling attempts. In contrast, aggression in PC 3 consisted only of side and head down displays. As displays are a less risky form of aggression (Smith and Parker, 1976), that lack the energetic costs of escalated fighting (Ros et al., 2006), we characterized the displays of PC 3 as restrained aggression (Reddon et al., 2015). Hereafter, these components will be characterized as (1) intruder aggression, (2) mirror aggression, and (3) high feeding, restrained aggression and shyness. Behaviours that were equally distributed across the components, or that loaded less than 0.3 for all three components were excluded from analysis; thus the final PCA included only the behaviours that loaded differently for all three components, with a magnitude of 0.3 or greater, prior to varimax rotation. Varimax rotation was used to facilitate interpretation of the behavioural axes by minimizing the number of variables for each axis (Abdi, 2003; Table 1).

None of the three composite behaviours were strong predictors of chasing (Linear models, all  $P > 0.30$ ) or dominance status (Fig. 6). However, the smaller fish in the week-2 predator treatment emerged as slightly odd with respect to PC 3, as they showed a higher degree of feeding, restrained aggression and shyness (Fig. 6C). Individual behaviour was not affected by treatment order (Linear models, all  $P > 0.25$ ), or by the location of the tag site (Linear models, all  $P > 0.40$ ).

More intruder aggressive fish tended to be more frequently found in the open habitat (Linear model,  $F_{1,49} = 3.85, P = 0.055$ ), but did not differ in their food consumption (Linear model,  $F_{1,33} = 0.39, P = 0.53$ ) or body size (Linear mixed model,  $F_{1,33} = 0.51, P = 0.48$ ). Mirror aggression (Fig. 6b) was higher in larger fish (Linear model,  $F_{1,33} = 5.70, P = 0.021$ ), and in fish which used the open habitat more (Linear model,  $F_{1,33} = 5.32, P = 0.025$ ; Fig. 7), but was not significantly related to food consumption (Linear model,  $F_{1,33} = 0.82, P = 0.37$ ). Fish with high feeding rates that showed restrained aggression and shyness toward predators were smaller (Linear model,  $F_{1,33} = 12.69, P = 0.0008$ ), but did not differ in habitat use (Linear model,

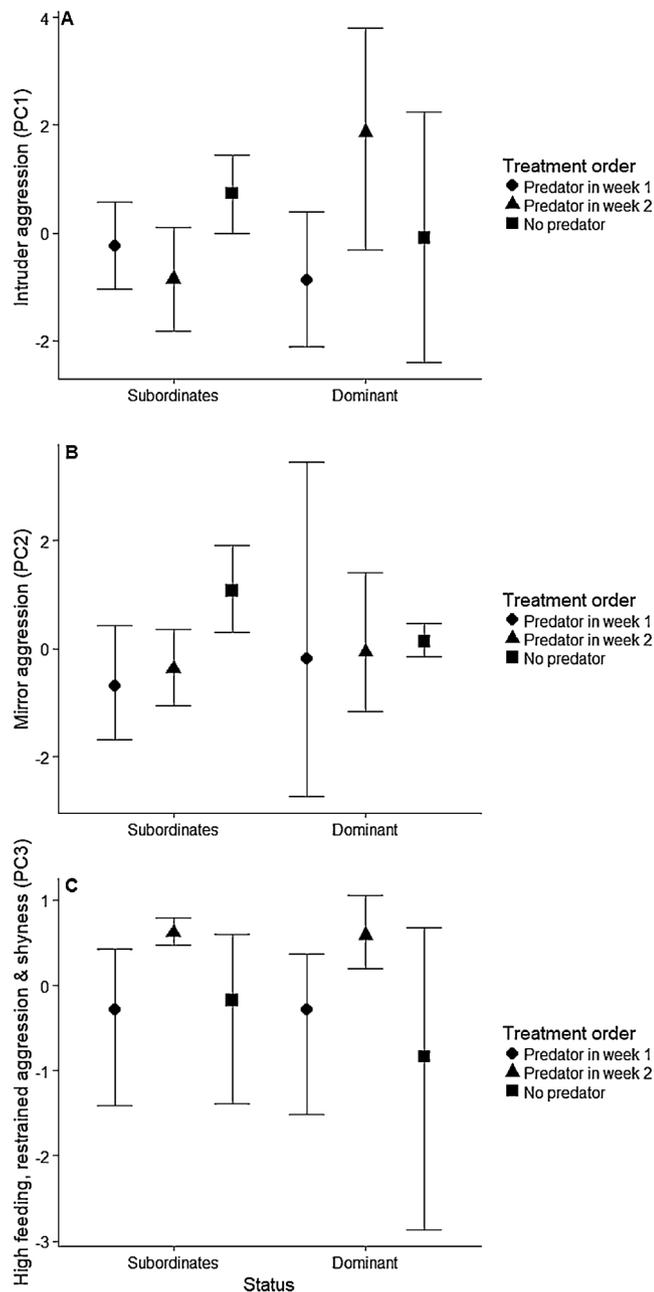


Fig. 6. Dominance status in group feeding trials across three predator exposure treatments ( $N = 5$  per treatment) in relation to three individually measured composite behavioral traits (mean  $\pm$  95% nonparametric bootstrapped CI): A) intruder aggression (PC1 scores), B) mirror aggression (PC2 scores), and C) high feeding, restrained aggression, and shyness (PC3 scores).

$F_{1,33} = 0.34$ ,  $P = 0.55$ ), or in food consumption (Linear model,  $F_{1,33} = 0.17$ ,  $P = 0.68$ ). None of the three composite behaviours was related to growth rate.

#### 4. Discussion

An apparent IFD occurred in the absence of a predator, with an equal number of fish in either habitat. However, two lines of evidence suggested otherwise. First, dominants always preferred the complex habitat, whereas subordinates altered their habitat use in the presence of a predator. Second, subordinates did not appear to gain foraging benefits from occupying the open habitats, where they likely perceived themselves to be exposed to more risk. Taken together, these data

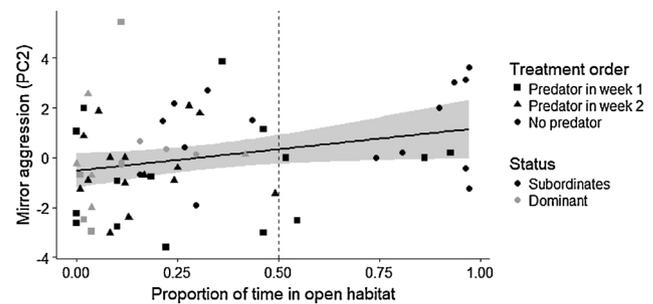


Fig. 7. Proportion of time spent in the open habitat during 13 min feeding trials under different predator exposure treatments and degree of high feeding, restrained aggression and shyness (PC 3;  $N = 5$  per treatment). Dashed line is the ideal free prediction.

suggested an IDD in the absence of a predator, where dominants excluded subordinates from the complex habitat.

In the presence of a predator, however, most fish occupied the complex habitat. Similarly, juvenile coho salmon (*Oncorhynchus kisutch*) distributed themselves according to the IFD when provided with habitats with and without cover, but more fish were found in the sheltered habitat after an increase in predation risk (Grand and Dill, 1997). This preference for complex habitats in the presence of predators is widespread in aquatic organisms, including Atlantic salmon (*Salmo salar*) parr (Huntingford et al., 1988), European perch (*Perca fluviatilis*), common roach (*Rutilus rutilus*; Brabrand and Faafeng, 1993; Persson, 1993), blacknose shiner (*Notropis heterolepis*) and bluntnose minnow (*Pimephales notatus*; MacRae and Jackson, 2001), bluegill sunfish (*Lepomis macrochirus*; Gotceitas, 1990), and eastern king prawns (*Melipotis plebejus*; Ochwada et al., 2009).

Dominant individuals always preferred the complex habitat, and also consumed more food than subordinates in all treatments. Dominants may have experienced less behavioural distress in complex habitats (Millidine et al., 2006), so they focussed their attention first on foraging and then on chasing subordinates. In contrast, subordinates may have split their attention amongst watching for predators in open habitats (Schneider, 1984; Ekman, 1987), the aggression of dominants (Rands et al., 2006), and then food (Murton et al., 1971; Smith et al., 2001). Dominants were frequently observed chasing and harassing subordinates as they foraged, while subordinates tended to become more inhibited, consuming less food following an attack.

It was not entirely clear why dominants did not grow faster than subordinates, despite their foraging advantage. Two possibilities are that dominants have a higher innate metabolic rate than subordinates (e.g. Biro and Stamps, 2010; Careau et al., 2010) or that the energetic costs of chasing subordinates (e.g. Praw and Grant, 1999) negated any potential gain from foraging. Neither explanation, however, explains why the particularly small dominants in the week-two predator treatment chased less than those in other treatments, but lost weight over the trials. We speculate that these dominants, which were smaller than the dominants in the other treatments, were unable to afford the greater energetic costs of dominance (see below) (e.g. Praw and Grant, 1999; Creel, 2001; Reid et al., 2011), which caused them to lose weight. Additionally, our experiment may not have been long enough to detect the more subtle growth differences that may have existed between the dominants and subordinates in the other two treatments.

The dominant fish in our study preferred the complex habitat, which is more consistent with the asset-protection principle rather than the resource monopolization hypothesis. It was not entirely clear why dominants avoided the open habitat, even when no predator was present. Perhaps they viewed all treatments as “dangerous” (sensu Clark and Mangel, 1986) and hence preferred the perceived safety of the complex habitat. Dominants may also have benefitted from the reduction in resting metabolic rate (RMR) that occurs in complex habitats (Millidine et al., 2006), but see (Kochhann and Val, 2017) for a counter

example. The smaller dominants, with the highest energy costs and greatest vulnerability to predators, showed the strongest preference for the safer complex habitat, further supporting risk aversion, not foraging benefits, as the main determinant of dominant habitat use (Brown and Braithwaite, 2004). Similar to our findings, mirror aggression did not predict intraspecific aggression in the mangrove rivulus (*Kryptolebias marmoratus*; Earley et al., 2000), or in two of three species of Lake Tanganyikan cichlids (Balzarini et al., 2014). Although no differences in mirror versus conspecific aggression were found in another species of cichlid (*Astatotilapia burtoni*), differences in gene expression suggested higher levels of fear when presented with a mirror (Desjardins and Fernald, 2010). Interestingly, the fish in our study that were aggressive toward a mirror, and presumably more fearful, used the open habitat more during the group trials, and were also larger, with more assets to protect (Clark, 1994). Mirrors may induce more fear because they are perceived as a novel stimulus, or alternatively, a dissociation may occur between behavioural and physiological responses toward a mirror image (Oliveira and Canário, 2011). For another species of cichlid (*Oreochromis mossambicus*), Oliveira et al. (2005) demonstrated that although male fish were aggressive toward their own mirror image, they did not exhibit the typical hormonal activity otherwise found in fighting males. Additionally, no differences in two factors that could affect aggression: motivation (Parker, 1984; Jonart et al., 2007; Arnott and Elwood, 2009) or personality (Dall et al., 2004; Réale et al., 2007), are possible with a mirror image. Finally, mirror tests may also constrain normal expressions of aggressive behaviour. For example, Arnott et al. (2011) showed that contesting convict cichlids prefer to align head-to-tail to facilitate evaluation of fighting ability and to minimize injury risk, an alignment not possible with a mirror image.

Although our mirror test did not evaluate self-recognition, many of the fish in our study reacted similarly to most fish species and behaved aggressively toward their mirror image, as if they had encountered an unknown conspecific (Brown, 2015; Hotta et al., 2018). Self-recognition in a mirror is touted as evidence for both self-awareness and high cognitive ability, both indicators of sentience, and has been shown in the great apes (e.g. *Pan troglodytes*) and dolphins (*Tursiops truncatus*; Reiss and Marino, 2001), elephants (*Elephas maximus*; Plotnik et al., 2006), and the magpie (*Pica pica*; Prior et al., 2008). However, being unable to recognize oneself in a mirror does not mean that an animal is not sentient (Brown, 2015). For fish, self-recognition may occur via other sensory cues, such as olfaction (Thünken et al., 2009), while a high cognitive ability is also demonstrated through complex behaviours like parental care, cooperation within social groups, nest building, and tool use (Brown, 2015).

## 5. Conclusions

In summary, some surprising results emerged from the habitat choice experiment: 1) foraging success and chase rate were not affected by predation risk, whereas; 2) dominants always preferred the complex habitat; and, 3) use of the open habitat decreased following exposure to a predator model, but only for subordinates. Fish also showed evidence of personality, with significant and repeatable individual differences in foraging, chasing, and habitat use.

The individual behavioural assays provided some insight into the habitat choice experiment. Surprisingly, dominance status was not predicted by the behavioural assays. There is often a strong relationship between the behaviour measured during individual assays and in social settings (Herborn et al., 2010; Lichtenstein et al., 2017), but not always (Réale et al., 2000; Adriaenssens and Johnsson, 2010). Interestingly, aggression toward a mirror, a conspecific, and restrained aggression were each on different behavioural axes, appearing to be distinct behaviours. The dominants in the week-two predator trials, which were slightly odd in terms of chase rate and growth rate, were also odd in behaviour, showing higher levels of feeding, restrained aggression and shyness, behaving similarly to the smaller subordinates when alone.

Perhaps these less-typical dominants were subject to greater difficulties to maintain their status, and hence lost more weight compared to other dominants and subordinates. Mirror aggression was the best predictor for use of the open habitat, while dominants were not identifiable in the individual assays, possibly due to greater behavioural differences between the group and individual trials. Shy individuals, like the smaller fish in the week two predator treatment, may have been more consistent in their behaviour due to a lower degree of plasticity (Frost et al., 2007); additionally, fish which used the open habitat may have suffered loser effects, while dominants did not gain winner effects (Dugatkin and Earley, 2004). Although habitat choice was not affected by body size in our study, smaller fish were less aggressive and bold when alone than larger fish.

In summary, dominance status determined habitat use and foraging rate, but not growth rate. Subordinate fish did not gain foraging benefits from using the open habitat, but appeared to be excluded from the complex habitat by the dominants, indicating an ideal despotic distribution. We suggest that dominants used the complex habitat to avoid predation and mitigate the increased physiological costs associated with dominance. These costs were illustrated by the smallest dominants in our study, which were unable to buffer these costs and lost weight over the study despite showing similar rates of food consumption and lower rates of chasing.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.beproc.2018.12.002>.

## References

- Abdi, H., 2003. Factor Rotations in Factor Analyses. Encyclopedia for Research Methods for the Social Sciences. Sage, Thousand Oaks, CA.
- Adriaenssens, B., Johnsson, J.I., 2010. Shy trout grow faster: exploring links between personality and fitness-related traits in the wild. *Behav. Ecol.* 22, 135–143. <https://doi.org/10.1093/beheco/arq185>.
- Almany, G.R., 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* 106, 275–284. <https://doi.org/10.1111/j.0030-1299.2004.13193.x>.
- Andren, H., 1990. Despotic distribution, unequal reproductive success, and population regulation in the jay *Garrulus glandarius* L. *Ecology* 71, 1796–1803. <https://doi.org/10.2307/1937587>.
- Arnott, G., Elwood, R., 2009. Probing aggressive motivation in a cichlid fish. *Biol. Lett.* 762–764. <https://doi.org/10.1098/rsbl.2009.0526>.
- Arnott, G., Ashton, C., Elwood, R.W., 2011. Lateralization of lateral displays in convict cichlids. *Biol. Lett.* 7, 683–685.
- Balzarini, V., Taborsky, M., Wanner, S., Koch, F., Frommen, J.G., 2014. Mirror, mirror on the wall: the predictive value of mirror tests for measuring aggression in fish. *Behav. Ecol. Sociobiol. (Print)* 68, 871–878. <https://doi.org/10.1007/s00265-014-1698-7>.
- Basquill, S.P., Grant, J.W., 1998. An increase in habitat complexity reduces aggression and monopolization of food by zebra fish (*Danio rerio*). *Can. J. Zool.* 76, 770–772. <https://doi.org/10.1139/z97-232>.
- Bates, D.M., 2010. *lme4: Mixed-effects Modeling With R*. Springer, Madison, Wisconsin.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-7.

- Beaton, D., Fatt, C.R.C., Abdi, H., 2014. An Exposition of multivariate analysis with the singular value decomposition in R. *Comput. Commun. Stat. Case Stud. Data Anal. Appl.* 72, 176–189.
- Bell, A.M., Stamps, J.A., 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Anim. Behav.* 68, 1339–1348. <https://doi.org/10.1016/j.anbehav.2004.05.007>.
- Biro, P.A., Stamps, J.A., 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends Ecol. Evol. (Amst.)* 25, 653–659. <https://doi.org/10.1016/j.tree.2010.08.003>.
- Brabrand, Å., Faafeng, B., 1993. Habitat shift in roach (*Rutilus rutilus*) induced by pikeperch (*Stizostedion lucioperca*) introduction: predation risk versus pelagic behaviour. *Oecologia* 95, 38–46. <https://doi.org/10.1007/BF00649504>.
- Brown, C., 2015. Fish intelligence, sentience and ethics. *Anim. Cogn.* 18, 1–17.
- Brown, C., Braithwaite, V.A., 2004. Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcopi*. *Anim. Behav.* 68, 1325–1329.
- Calsbeek, R., Sinervo, B., 2002. An experimental test of the ideal despotic distribution. *J. Anim. Ecol.* 71, 513–523. <https://doi.org/10.1046/j.1365-2656.2002.00619.x>.
- Careau, V., Réale, D., Humphries, M.M., Thomas, D.W., 2010. The pace of life under artificial selection: personality, energy expenditure, and longevity are correlated in domestic dogs. *Am. Nat.* 175, 753–758. <https://doi.org/10.1086/652435>.
- Clark, C.W., 1994. Antipredator behavior and the asset-protection principle. *Behav. Ecol.* 5, 159–170.
- Clark, C.W., Mangel, M., 1986. The evolutionary advantages of group foraging. *Theor. Popul. Biol.* 30, 45–75.
- Clayton, D.A., 1987. Why mudskippers build walls. *Behaviour* 102, 185–195. <https://doi.org/10.1163/156853986X00117>.
- Colléter, M., Brown, C., 2011. Personality traits predict hierarchy rank in male rainbowfish social groups. *Anim. Behav.* 81, 1231–1237.
- Conkel, D., 1993. *Cichlids of North and Central America*. T.F.H. Publications, Inc, USA.
- Creel, S., 2001. Social dominance and stress hormones. *Trends Ecol. Evol. (Amst.)* 16, 491–497. [https://doi.org/10.1016/S0169-5347\(01\)02227-3](https://doi.org/10.1016/S0169-5347(01)02227-3).
- Dall, S.R., Houston, A.I., McNamara, J.M., 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* 7, 734–739. <https://doi.org/10.1111/j.1461-0248.2004.00618.x>.
- David, M., Auclair, Y., Cézilly, F., 2011. Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Anim. Behav.* 81, 219–224. <https://doi.org/10.1016/j.anbehav.2010.10.008>.
- DeBoom, C.S., Wahl, D.H., 2013. Effects of coarse woody habitat complexity on predator–prey interactions of four freshwater fish species. *Trans. Am. Fish. Soc.* 142, 1602–1614. <https://doi.org/10.1080/00028487.2013.820219>.
- Denight, M.L., Ward, J.A., 1982. Relationship of chin spot size to dominance in the black-chinned mouthbrooding cichlid fish (*Sarotherodon melanothron*). *Anim. Behav.* 30, 1099–1104.
- Desjardins, J.K., Fernald, R.D., 2010. What do fish make of mirror images? *Biol. Lett.* 6, 744–747. <https://doi.org/10.1098/rsbl.2010.0247>.
- Dubois, F., Giraldeau, L.A., Hamilton, I.M., Grant, J.W., Lefebvre, L., 2004. Distraction sneakers decrease the expected level of aggression within groups: a game-theoretic model. *Am. Nat.* 164, E32–E45.
- Dugatkin, L.A., Earley, R.L., 2004. Individual recognition, dominance hierarchies and winner and loser effects. *Proc. R. Soc. Lond., B, Biol. Sci.* 271, 1537–1540.
- Earley, R.L., Hsu, Y., Wolf, L.L., 2000. The use of standard aggression testing methods to predict combat behaviour and contest outcome in *Rivulus marmoratus* dyads (Teleostei: Cyprinodontidae). *Ethology* 106, 743–761. <https://doi.org/10.1046/j.1439-0310.2000.00586.x>.
- Eason, P.K., Stamps, J.A., 1992. The effect of visibility on territory size and shape. *Behav. Ecol.* 3, 166–172. <https://doi.org/10.1093/beheco/3.2.166>.
- Eklöv, P., Diehl, S., 1994. Piscivore efficiency and refuging prey: the importance of predator search mode. *Oecologia* 98, 344–353.
- Ekman, J., 1987. Exposure and time use in willow tit flocks: the cost of subordination. *Anim. Behav.* 35, 445–452. [https://doi.org/10.1016/S0003-3472\(87\)80269-5](https://doi.org/10.1016/S0003-3472(87)80269-5).
- Flynn, A.J., Ritz, D.A., 1999. Effect of habitat complexity and predatory style on the capture success of fish feeding on aggregated prey. *J. Mar. Biol. Assoc. U.K.* 79, 487–494.
- Francis, R.C., 1990. Temperament in a fish: a longitudinal study of the development of individual differences in aggression and social rank in the Midas cichlid. *Ethology* 86, 311–325.
- Fretwell, S.D., 1972. *Populations in a Seasonal Environment*, No. Five. Princeton University Press, Princeton, New Jersey.
- Frost, A.J., Winrow-Giffen, A., Ashley, P.J., Sneddon, L.U., 2007. Plasticity in animal personality traits: does prior experience alter the degree of boldness? *Proc. R. Soc. Lond., B, Biol. Sci.* 274, 333–339.
- Geange, S.W., Stier, A.C., 2010. Priority effects and habitat complexity affect the strength of competition. *Oecologia* 163, 111–118. <https://doi.org/10.1007/s00442-009-1554-z>.
- Gibb, H., Parr, C.L., 2010. How does habitat complexity affect ant foraging success? A test using functional measures on three continents. *Oecologia* 164, 1061–1073. <https://doi.org/10.1007/s00442-010-1703-4>.
- Giraldeau, L.A., Dubois, F., 2008. Social foraging and the study of exploitative behavior. *Adv. Stud. Behav.* 38, 59–104.
- Gotceitas, V., 1990. Foraging and predator avoidance: a test of a patch choice model with juvenile bluegill sunfish. *Oecologia* 83, 346–351. <https://doi.org/10.1007/BF00317558>.
- Gotceitas, V., Colgan, P., 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. *Oecologia* 80, 158–166. <https://doi.org/10.1007/BF00380145>.
- Gotceitas, V., Colgan, P., 1990. The effects of prey availability and predation risk on habitat selection by juvenile bluegill sunfish. *Copeia* 1990, 409–417. <https://doi.org/10.2307/1446346>.
- Graham, M.E., Herberholz, J., 2009. Stability of dominance relationships in crayfish depends on social context. *Anim. Behav.* 77, 195–199.
- Grand, T.C., Dill, L.M., 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. *Behav. Ecol.* 8, 437–447.
- Grand, T.C., Grant, J.W.A., 1994a. Spatial predictability of food influences its monopolization and defence by juvenile convict cichlids. *Anim. Behav.* 47, 91–100.
- Grand, T.C., Grant, J.W.A., 1994b. Spatial predictability of resources and the ideal free distribution in convict cichlids, *Cichlasoma nigrofasciatum*. *Anim. Behav.* 48, 909–919.
- Hamilton, I.M., Dill, L.M., 2002. Monopolization of food by zebrafish (*Danio rerio*) increases in risky habitats. *Can. J. Zool.* 80, 2164–2169. <https://doi.org/10.1139/z02-199>.
- Harrell, F.E. Jr, Dupont, C., 2017. Hmisc: Harrell Miscellaneous. R package version 4.0-3.
- Heithaus, M.R., Dill, L.M., 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83, 480–491. [https://doi.org/10.1890/0012-9658\(2002\)083](https://doi.org/10.1890/0012-9658(2002)083).
- Herborn, K.A., Macleod, R., Miles, W.T., Schofield, A.N., Alexander, L., Arnold, K.E., 2010. Personality in captivity reflects personality in the wild. *Anim. Behav.* 79, 835–843. <https://doi.org/10.1016/j.anbehav.2009.12.026>.
- Höjesjö, J., Johnsson, J., Bohlin, T., 2004. Habitat complexity reduces the growth of aggressive and dominant brown trout (*Salmo trutta*) relative to subordinates. *Behav. Ecol. Sociobiol. (Print)* 56, 286–289. <https://doi.org/10.1007/s00265-004-0784-7>.
- Höjesjö, J., Adriaenssens, B., Bohlin, T., Jönsson, C., Hellström, I., Johnsson, J.J., 2011. Behavioural syndromes in juvenile brown trout (*Salmo trutta*); life history, family variation and performance in the wild. *Behav. Ecol. Sociobiol. (Print)* 65, 1801–1810.
- Hotta, T., Komiya, S., Kohda, M., 2018. A social cichlid fish failed to pass the mark test. *Anim. Cogn.* 21, 127–136.
- Hovel, K.A., Lipcius, R.N., 2001. Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. *Ecology* 82, 1814–1829. [https://doi.org/10.1890/0012-9658\(2001\)082](https://doi.org/10.1890/0012-9658(2001)082).
- Huntingford, F.A., Metcalfe, N.B., Thorpe, J.E., 1988. Choice of feeding station in Atlantic salmon, *Salmo salar*, parr: effects of predation risk, season and life history strategy. *J. Fish Biol.* 33, 917–924. <https://doi.org/10.1111/j.1095-8649.1988.tb05540.x>.
- Jakobsson, S., Brick, O., Kullberg, C., 1995. Escalated fighting behaviour incurs increased predation risk. *Anim. Behav.* 49, 235–239.
- Jonart, L.M., Hill, G.E., Badyaev, A.V., 2007. Fighting ability and motivation: determinants of dominance and contest strategies in females of a passerine bird. *Anim. Behav.* 74, 1675–1681. <https://doi.org/10.1016/j.anbehav.2007.03.012>.
- Jordan, F., Bartolini, M., Nelson, C., Patterson, P.E., Soulen, H.L., 1997. Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 208, 45–56. [https://doi.org/10.1016/S0022-0981\(96\)02656-1](https://doi.org/10.1016/S0022-0981(96)02656-1).
- Keeley, E.R., Grant, J.W., 1993. Visual information, resource value, and sequential assessment in convict cichlid (*Cichlasoma nigrofasciatum*) contests. *Behav. Ecol.* 4, 345–349. <https://doi.org/10.1093/beheco/4.4.345>.
- Kochmann, D., Val, A.L., 2017. Social hierarchy and resting metabolic rate in the dwarf cichlid *Apistogramma agassizii*: the role of habitat enrichment. *Hydrobiologia* 789, 123–131. <https://doi.org/10.1007/s10750-016-2806-7>.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2016. lmerTest: Tests in Linear Mixed Effects Models. R Package Version 2. pp. 0–33. <https://CRAN.R-project.org/package=lmerTest>.
- Le, S., Josse, J., Huisson, F., 2008. FactoMineR: An R Package for Multivariate Analysis. *J. Stat. Softw.* 25, 1–18. <https://doi.org/10.18637/jss.v025.i01>.
- Lichtenstein, J.L., Wright, C.M., Luscskie, L.P., Montgomery, G.A., Pinter-Wollman, N., Pruitt, J.N., 2017. Participation in cooperative prey capture and the benefits gained from it are associated with individual personality. *Curr. Zool.* 63, 561–567. <https://doi.org/10.1093/cz/zow097>.
- Lima, S.L., Dill, L.M., 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640.
- Loss, C.M., Binder, L.B., Muccini, E., Martins, W.C., de Oliveira, P.A., Vandresen-Filho, S., Prediger, R.D., Tasca, C.I., Zimmer, E.R., Costa-Schmidt, L.E., de Oliveira, D.L., 2015. Influence of environmental enrichment vs. time-of-day on behavioral repertoire of male albino Swiss mice. *Neurobiol. Learn. Mem.* 125, 63–72. <https://doi.org/10.1016/j.nlm.2015.07.016>.
- MacRae, P.S.D., Jackson, D.A., 2001. The influence of smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages. *Can. J. Fish. Aquat. Sci.* 58, 342–351. <https://doi.org/10.1139/cjfas-58-2-342>.
- Martin, C.W., Fodrie, F.J., Heck, K.L., Mattila, J., 2010. Differential habitat use and antipredator response of juvenile roach (*Rutilus rutilus*) to olfactory and visual cues from multiple predators. *Oecologia* 162, 893–902. <https://doi.org/10.1007/s00442-010-1564-x>.
- Millidine, K.J., Armstrong, J.D., Metcalfe, N.B., 2006. Presence of shelter reduces maintenance metabolism of juvenile salmon. *Funct. Ecol.* 20, 839–845. <https://doi.org/10.1111/j.1365-2435.2006.01166.xwahl>.
- Murton, R.K., Isaacson, A.J., Westwood, N.J., 1971. The significance of gregarious feeding behaviour and adrenal stress in a population of wood pigeons *Columba palumbus*. *J. Zool.* 165, 53–84. <https://doi.org/10.1111/j.1469-7998.1971.tb02176.x>.
- Nelson, W.G., Bonsdorff, E., 1990. Fish predation and habitat complexity: are complexity thresholds real? *J. Exp. Mar. Biol. Ecol.* 141, 183–194. [https://doi.org/10.1016/0022-0981\(90\)90223-Y](https://doi.org/10.1016/0022-0981(90)90223-Y).
- Noakes, D.L.G., 1991. Ontogeny of behaviour in cichlids. In: Keenleyside, H.A. (Ed.), *Cichlid Fishes: Behavior, Ecology and Evolution*, pp. 209–224. Chapman & Hall, London.

- Ochwada, F., Loneragan, N.R., Gray, C.A., Suthers, I.M., Taylor, M.D., 2009. Complexity affects habitat preference and predation mortality in postlarval *Penaeus plebejus*: implications for stock enhancement. *Mar. Ecol. Prog. Ser.* 380, 161–171. <https://doi.org/10.3354/meps07936>.
- Oliveira, R.F., Canário, A.V., 2011. Nemo through the looking-glass: a commentary on Desjardins & Fernald. *Biol. Lett.* 7, 487–488.
- Oliveira, L.F., Simpson, D.M., Nadal, J., 1996. Calculation of area of stabilometric signals using principal component analysis. *Physiol. Meas.* 17, 305.
- Oliveira, R.F., Carneiro, L.A., Canário, A.V., 2005. Behavioural endocrinology: no hormonal response in tied fights. *Nature* 437, 207.
- Olsson, K., Nyström, P., 2009. Non-interactive effects of habitat complexity and adult crayfish on survival and growth of juvenile crayfish (*Pacifastacus leniusculus*). *Freshwater Biol.* 54, 35–46.
- Parker, G.A., 1984. Evolutionarily stable strategies. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology: an Evolutionary Approach*, 2nd ed. Blackwell Scientific, Oxford, pp. 30–61.
- Parker, G.A., Sutherland, W.J., 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Anim. Behav.* 34, 1222–1242. [https://doi.org/10.1016/S0003-3472\(86\)80182-8](https://doi.org/10.1016/S0003-3472(86)80182-8).
- Peres-Neto, P., Jackson, D.A., Somers, K.M., 2005. How many principal components? Stopping rules for determining the number of non-trivial axes revisited. *Comput. Stat. Data Anal.* 49, 974–997. <https://doi.org/10.1016/j.csda.2004.06.015>.
- Persson, L., 1993. Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. *Oikos* 68, 12–22. <https://doi.org/10.2307/3545304>.
- Plotnik, J.M., De Waal, F.B., Reiss, D., 2006. Self-recognition in an asian elephant. *Proc. Natl. Acad. Sci. U.S.A.* 103, 17053–17057.
- Praw, J.C., Grant, J.W., 1999. Optimal territory size in the convict cichlid. *Behaviour* 136, 1347–1363. <https://doi.org/10.1163/156853999500767>.
- Prior, H., Schwarz, A., Güntürkün, O., 2008. Mirror-induced behavior in the magpie (*Pica pica*): evidence of self-recognition. *PLoS Biol.* 6, e202.
- Radabaugh, N.B., Bauer, W.F., Brown, M.L., 2010. A Comparison of Seasonal Movement Patterns of Yellow Perch in Simple and Complex Lake Basins. *N. Am. J. Fish. Manage.* 30, 179–190. <https://doi.org/10.1577/M08-243.1>.
- Radesäter, T., Fernö, A., 1979. On the function of the ‘eye-spots’ in agonistic behaviour in the fire-mouth cichlid (*Cichlasoma meeki*). *Behav. Processes* 4, 5–13.
- Rands, S.A., Pettifor, R.A., Rowcliffe, J.M., Cowlshaw, G., 2006. Social foraging and dominance relationships: the effects of socially mediated interference. *Behav. Ecol. Sociobiol.* (Print) 60, 572. <https://doi.org/10.1007/s00265-006-0202-4> <https://doi.org/10.1098/rstb.2010.0208>.
- Réale, D., Gallant, B.Y., Leblanc, M., Festa-Bianchet, M., 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Anim. Behav.* 60, 589–597. <https://doi.org/10.1006/anbe.2000.1530>.
- Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J., 2007. Integrating animal temperament within ecology and evolution. *Biol. Rev.* 82, 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>.
- Reddon, A.R., O'Connor, C.M., Marsh-Rollo, S.E., Balshine, S., Gozdowska, M., Kulczykowska, E., 2015. Brain nonapeptide levels are related to social status and affiliative behaviour in a cooperatively breeding cichlid fish. *R. Soc. Open Sci.* <https://doi.org/10.1098/rsos.140072>. 140072.
- Reid, D., Armstrong, J.D., Metcalfe, N.B., 2011. Estimated standard metabolic rate interacts with territory quality and density to determine the growth rates of juvenile Atlantic salmon. *Funct. Ecol.* 25, 1360–1367. <https://doi.org/10.1111/j.1365-2435.2011.01894.x>.
- Reiss, D., Marino, L., 2001. Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. *Proc. Natl. Acad. Sci. U. S. A.* 98, 5937–5942.
- Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. *B. Fish. Res. Board Can.* 19, 1–382.
- Ros, A.F., Becker, K., Oliveira, R.F., 2006. Aggressive behaviour and energy metabolism in a cichlid fish, *Oreochromis mossambicus*. *Physiol. Behav.* 89, 164–170.
- Russo, A.R., 1987. Role of habitat complexity in mediating predation by the gray damselfish *Abudefduf sordidus* on epiphytal amphipods. *Mar. Ecol. Prog. Ser.* 36, 101–105.
- Schneider, K.J., 1984. Dominance, predation, and optimal foraging in white-throated sparrow flocks. *Ecology* 65, 1820–1827. <https://doi.org/10.2307/1937778>.
- Smith, J.M., Parker, G.A., 1976. The logic of asymmetric contests. *Anim. Behav.* 24, 159–175.
- Smith, R.D., Ruxton, G.D., Cresswell, W., 2001. Dominance and feeding interference in small groups of blackbirds. *Behav. Ecol.* 12, 475–481. <https://doi.org/10.1093/beheco/12.4.475>.
- Sopinka, N.M., Fitzpatrick, J.L., Desjardins, J.K., Stiver, K.A., Marsh-Rollo, S.E., Balshine, S., 2009. Liver size reveals social status in the African cichlid *Neolamprologus pulcher*. *J. Fish Biol.* 75, 1–16.
- Stoffel, M.A., Nakagawa, S., Schielzeth, H., 2017. rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.* 8, 1639–1644. <https://doi.org/10.1111/2041-210X.12797>.
- Sundbaum, K., Näslund, I., 1998. Effects of woody debris on the growth and behaviour of brown trout in experimental stream channels. *Can. J. Zool.* 76, 56–61. <https://doi.org/10.1139/z97-174>.
- Thünken, T., Waltschky, N., Bakker, T., Kullmann, H., 2009. Olfactory self-recognition in a cichlid fish. *Anim. Cogn.* 12, 717–724.
- Warfe, D.M., Barmuta, L.A., 2004. Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia* 141, 171–178. <https://doi.org/10.1007/s00442-004-1644-x>.
- Werner, E.E., Hall, D.J., 1988. Ontogenetic habitat shifts in bluegill: the foraging-rate predation risk trade-off. *Ecology* 69, 1352–1366.
- Wisenden, B.D., 1995. Reproductive behaviour of free-ranging convict cichlids, *Cichlasoma nigrofasciatum*. *Environ. Biol. Fish.* 43, 121–134.
- Wisenden, B.D., Keenleyside, M.H., 1992. Intraspecific brood adoption in convict cichlids: a mutual benefit. *Behav. Ecol. Sociobiol.* (Print) 31, 263–269. <https://doi.org/10.1007/BF00171681>.
- Yamamoto, M.N., Tagawa, A.W., 2000. *Hawai'i's Native and Exotic Freshwater Animals*. Mutual Publishing, Honolulu, Hawaii.
- Zamzow, J.P., Amsler, C.D., McClintock, J.B., Baker, B.J., 2010. Habitat choice and predator avoidance by Antarctic amphipods: the roles of algal chemistry and morphology. *Mar. Ecol. Prog. Ser.* 400, 155–163. <https://doi.org/10.3354/meps08399>.