Habitat Complexity and Behaviour: Personality, Habitat Selection and Territoriality

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Abstract

Habitat complexity and behaviour: personality, habitat selection and territoriality

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Structurally complex habitats support high species diversity and promote ecosystem health and stability, however anthropogenic activity is causing natural forms of complexity to rapidly diminish. At the population level, reductions in complexity negatively affect densities of territorial species, as increased visual distance increases the territory size of individuals. Individual behaviour, including aggression, activity and boldness, is also altered by complexity, due to plastic behavioural responses to complexity, habitat selection by particular personality types, or both processes occurring simultaneously. This thesis explores the behavioural effects of habitat complexity in four chapters. The first chapter, a laboratory experiment based on the ideal free distribution, observes how convict cichlids (*Amatitlania nigrofasciata*) trade-off the higher foraging success obtainable in open habitats with the greater safety provided in complex habitats under overt predation threat. Dominants always preferred the complex habitat, forming ideal despotic distributions, while subordinates altered their habitat use in response to predation. The second chapter also employs the ideal free distribution to assess how convict cichlids within a dominance hierarchy trade-off between food monopolization and safety in the absence of a predator. Dominants again formed ideal despotic distributions in the complex habitat, while dominants with lower energetic states more strongly preferred the complex habitat. For both laboratory experiments, personality did not predict habitat preference. The third chapter, a field study with juvenile Atlantic salmon (*Salmo salar*), tested whether stream restorations that increase habitat complexity will also select for particular personality traits, and we again found that complexity did not favour any particular personality types. A broader range perspective regarding the effects of habitat complexity on behaviour was addressed in the fourth chapter via a meta-analysis on a wide range of territorial and non-territorial taxa. Territoriality modified the effects of complexity on behaviour, likely due to the strong reliance of territorial species on visual cues. Taken together, all four chapters demonstrate the high context dependency of the effects of complexity on behaviour. Nevertheless, whether or not an individual is territorial emerged as an important predictor of how habitat complexity is likely to affect its behaviour.

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Contributions of Authors

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General Introduction

Complex habitats often support a rich biodiversity of species. MacArthur & MacArthur (1961) were one of the first to describe this relationship, noting that warbler species diversity increased in a forest habitat along with increasing foliage height diversity, as each warbler species occupied a different layer of foliage. More generally, more species are able to coexist due to the higher number of potential habitats, or potential niches, found in complex habitats (Willis et al. 2005; Matias et al. 2010; Taniguchi et al. 2003). As a result, structurally complex habitats, like coral reefs (Graham & Nash 2013; Gratwicke & Speight 2006) and tropical rainforests (Schwarzkopf & Rylands 1989; Williams et al. 2002), are also characterized by high species diversity. Interestingly, there is some evidence that structurally complex habitats not only support high species diversity, but also facilitate its creation: polymorphisms in bacteria were favoured and evolved faster in complex habitats, leading to greater evolutionary diversity (Korona et al. 1994; Price et al. 2011).

Habitat complexity is rapidly diminishing in a wide range of natural habitats due to anthropogenic effects. For example, in terrestrial systems, land use is often characterized by excessive logging and the use of fire, often resulting in the fragmentation and desertification of tropical forests (e.g. Nepstad et al. 1999; Wang et al. 2004). Similar overharvesting occurs in aquatic systems, where the loss of apex predators can trigger the transformation of kelp forests into algae-dominated ecosytems (Steneck et al. 2002; Leinaas & Christie 1996), or excessive trawling devastates the complexity of ocean floor habitats (Althaus et al. 2009; Watling & Norse 1998). Additionally, the loss of habitat complexity may amplify and facilitate the establishment and impacts of invasive species (Brown & Gurevitch 2004; Hobbs & Huenneke 1992; MacDougall & Turkington 2005), while invaders themselves may enable further reductions of biotic structure (e.g. Liebhold et al. 1995; Lozano et al. 2001; Mack & D'Antonio 1998; Poland

& McCullough 2006). Although these scenarios are all characterized by drastic losses of structural diversity, more subtle human-mediated environmental modifications, like selective logging (Johns 1988), crop monocultures (Benton et al. 2003), and the channelization of streams (Shankman 1996; Lau et al. 2006), also result in more uniform physical habitats with decreased quantities of abiotic and biotic structural complexity. Indeed, the loss of physical structure is frequently a characteristic of human mediated environmental activity.

The loss of physical structure in natural habitats is troubling, as habitat complexity has many positive impacts on the health and stability of ecosystems. Physically complex habitats are characterized by the presence of refugia, which may keep predators or larger conspecifics from accessing some portion of the habitat, resulting in weaker and more indirect species interactions and higher overall stability (Thébault & Fontaine 2010). Thus, habitat complexity tends to weaken and decouple predator-prey interactions, which then increases community persistence and ecosystem stability (Kovalenko et al. 2017), leading to more resilient ecosystems with fewer extinction cascades (Fischer & Lindenmayer 2007). Additionally, communities in complex habitats show greater resistance to anthropogenic nutrient inputs, due to more efficient energy flow (Brookes et al. 2005), and are physically protected during natural disturbances (e.g. MacKenzie & Cormier 2011; Pearsons et al. 1992). Habitat structure may also regulate water flow (Lenihan 1999) or light levels (Eriksson et al. 2006), factors which may also influence the fitness of a given species.

Many conservation efforts focus their efforts on retaining or restoring the complexity of natural habitats. For example, the presence of hedges and strips of wildflowers form a crucial component of the reintroduction success of the grey partridge (*Perdix perdix*; Buner et al. 2005). More generally, a wide range of bird species benefit from revegetation, or the planting of native trees and shrubs in formerly depleted habitats (Munro et al. 2010). Additionally, sustainable farming practices ensure that habitat complexity is present at a range of spatial scales, in order to increase wildlife biodiversity in farmlands (Benton et al. 2003), while coexistence with wildlife is promoted by patches of grasses and shrubs of various heights and densities within the rangelands of domestic cattle (Fuhlendorf & Engle 2001). Similarly, in aquatic systems, conservation of fisheries is often achieved through the restoration of aquatic habitats (Muotka et al. 2002; Smart & Dick 1999; Turner et al. 1999); improvements in fish spawning success occur when fine sediment is replaced with a more complex substrate, composed of cobble and gravel (Barlaup 2008; Manny et al. 2010), while the construction of artificial reefs helps to revive degenerating coral reef habitat (Clark & Edwards 1999; Rilov & Benayahu 1998). As conservation efforts are often constrained by limited resources, it is essential to predict how a target species or community will respond to changes in habitat complexity, in order to ensure the desired result.

Loss of habitat complexity is also frequently accompanied by reductions in resources, such as food, shelter, or potential territories (e.g. Halaj et al. 2000; Lande 1988; Turner et al. 1999). According to the ideal free distribution (IFD), organisms will settle across patches in direct proportion to resource abundance (Fretwell 1972); consequently, reductions in resources will alter the distribution of populations, resulting in lower population densities in more open habitats. In addition to providing resources, complex habitats increase the survival of prey by providing refuge from predators (Briand & Cohen 1987), harsh environmental conditions (Friedlander et al. 2003), aggressive (Baird et al. 2006; Chaloupková et al. 2007) or predatory conspecifics (Langellotto & Denno 2004), and anthropogenic effects (Garden et al. 2007; Lake et al. 2007). However, although complex habitats are generally protective habitats for prey targeted by actively searching predators (Boesch & Turner 1984; Nagelkerken et al. 2000), this is not always the case for the prey of ambush predators (e.g. Eklöv & Diehl 1994; Finke & Denno 2002; Flynn & Ritz 1999).

Densities of territorial species are also particularly affected by habitat complexity. As territorial behaviour is affected by visibility, territorial defense becomes more costly and difficult in complex habitats (Breau & Grant 2002; Gray et al. 2000). Consequently, losses of habitat complexity result in lower densities for territorial species (Dolinsek et al. 2007a; Venter et al. 2008; but see Imre et al. 2002), due to the larger territories formed in open habitats (Eason & Stamps 1992; Imre et al. 2002). Foraging behaviour is likewise affected by habitat complexity. Although complex habitats may provide more food (Laegdsgaard & Johnson 2001; Venter et al. 2008), they can reduce foraging and negatively affect resource monopolization, thus making competitive dominance more difficult to achieve (Basquill & Grant 1998; Höjesjö et al. 2004).

In addition to affecting territorial and foraging behaviour, habitat complexity also affects individual behaviour, particularly boldness, aggression, and activity. This may occur in two distinct ways. Individuals can modify their behaviour accordingly while in open and complex habitats (e.g. Basquill & Grant 1998; Clayton 1987) - thus displaying plastic behavioural responses to complexity. Alternatively, individuals that show consistent differences in behavioural traits, or personality (Réale et al. 2010), may select habitats that facilitate expression of their particular behavioural traits (e.g. Wilson et al. 1993). Additionally, both of these processes may occur simultaneously (e.g. Dingemanse et al. 2010). Losses of habitat complexity may also affect the distribution of personalities, by favouring individuals with particular personality traits, like boldness (e.g. Wilson et al. 1993) and aggression (e.g. Danley 2011), that are associated with open habitats.

In this thesis, I explore the effect of habitat complexity on individual behaviour in four chapters. In the first chapter, I conducted a laboratory experiment based on the ideal free distribution to observe habitat selection, or how individuals trade-off the higher foraging success obtainable in open habitats with the greater safety of the complex habitat under overt predation threat. Groups of four same size convict cichlids were exposed to a predator model, then selected either an open or complex habitat while competing for food. For the second chapter, the ideal free distribution was again used to explore habitat selection, by observing how unequal competitors in a dominance hierarchy trade-off food monopolization and safety in the absence of a predator. Open and complex habitats were directly compared by allowing groups of six cichlids of four distinct size categories to compete for food in each habitat separately, before being allowed to choose between the two habitats. In chapter three, I conducted a field study with juvenile Atlantic salmon to test whether stream restorations that increase habitat complexity will also select for particular personality traits. Finally, the fourth chapter, a meta-analysis, moves beyond fish for a broader perspective on the general effects of habitat complexity on behaviour. This chapter quantifies and summarizes the effects of a variety of forms of habitat complexity on the territory size, density, foraging activity, survival and behaviour of a wide range of territorial and non-territorial invertebrates, fish, reptiles, birds and mammals. In all four chapters, I considered whether personality, or consistent behavioural differences (Réale et al. 2007), played a role in how animals responded to habitat structure. In short, this thesis explores how personality and territoriality affect habitat selection, and modify the effects of habitat complexity on behaviour.

Chapter 1. Ideal despotic distributions in convict cichlids (*Amatitlania nigrofasciata*)? Effects of predation risk and personality on habitat preference

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, consistent with an ideal despotic distribution. The individual behavioural assays predicted habitat use, but not foraging success or dominance; shyer fish with more restrained aggression were more frequently found in the open habitat during the group trials.

Keywords: dominance; habitat complexity; ideal free; ideal despotic; personality; predation

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 are often lower in complex habitats (Gotceitas and Colgan, 1989; Warfe and Barmuta, 2004), and are often preferred by prey seeking refuge (Russo, 1987; Olsson and Nyström, 2009). 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), which may result in dominants preferring open habitats when predation risk is low (i.e. Hamilton and Dill, 2002; Höjesjö et al., 2004).

Similar to the effects of trade-offs between foraging and predator avoidance on habitat selection, trade-offs between competition and risk may also underlie behavioural traits, such as boldness and shyness. Bolder individuals take greater risks to achieve greater foraging success, while shyer individuals forgo feeding for an increased chance of survival (Gotceitas and Colgan, 1990). Neophobia, or aversion and fear toward novel objects (Coleman and Mellgren, 1994), reflects a similar balance between competitive success and antipredator vigilance (Jones and Godin, 2010), while aggression increases competitive success and conspicuousness to predators (Lima and Dill, 1990; Jakobsson et al., 1995). As predation tends to be higher in open habitats (i.e. Nelson and Bonsdorff, 1990; Hovel and Lipcius, 2001), individual differences in boldness, exploration or aggression may also predict individual differences in habitat preference.

The ideal free distribution (IFD) predicts the distributions of individuals across patches, 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, 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 can exhibit either an IFD or 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). Groups of four fish competed for food in two patches, one each in an open and 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 to minimize their risk of predation (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) bolder, and 5) more aggressive fish will prefer the open habitat.

2. Material and methods

Fish were held in three stock tanks (l 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 ($N = 60$; 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. 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. To minimize our use of animals, about half of the fish were used twice, but the same group of four fish were never reused.

2.1. Feeding treatment

Two experimental tanks (l x w x h = 91x 46 x 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 x 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; trials were conducted over a two week period.

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

Feedings were conducted every day for five consecutive days to "train" the fish, and data were collected on the 6th and 7th days. Previously frozen mysis shrimp were preloaded into 3 mL syringes, and dropped into both habitats simultaneously every 20 seconds for an 8-minute period. Fish were observed throughout the 8-minute feeding period and for 5 minutes afterward, for a total of 13 minutes. 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 seconds. Each treatment was replicated 5 times, for a total of 15 trials. The identity of the successful forager was determined for a mean of 39.3 ± 2.03 food items consumed per trial, out of the 50 food items provided per trial; typically this occurred shortly after the food was provided. Proportion of food consumed within each trial was subsequently used as a measure of competitive weight for each fish (sensu Grand and Dill, 1997); these values were then multiplied by 4 to account for the four fish present in each group.

2.2. Individual behavioural assay

Individual behavioural trials were conducted after the completion of the group trials. Fish were netted in random order from their experimental tank, and placed into one half of a small tank (l x w x h = 30.4 x 13.4 x 20.8 cm) containing a heater and air pump, divided lengthwise by a piece of black Plexiglas. Fish were held for 48 hours 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, with approximately 15 to 30 minutes 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 minutes. 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), which differed from the flake food fed in the stock tanks in chemical composition, granule size, and colour, 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 minutes. 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 (l x w: 14 x 14 cm) was placed against the outside wall of the test aquarium in view of the focal fish, and its behaviour was recorded for 10 minutes. 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 1.1), and distance and orientation relative to the mirror was noted every 10 seconds, 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 1.1) and its latency to approach the intruder were recorded, as well as its distance and orientation toward the intruder every 10 seconds. The total number of lateral and head down displays, chases, and mouth wrestling attempts were also recorded throughout the 10 minute trial. The intruder was removed from the tank and measured following the test (mean length difference, 95% C.I.'s [LCI, UCI]: 10.29% [8.18%, 12.40%]).

Test 5: Aquatic predator model

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 seconds. After 10 minutes, 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 1.2). The predator model was removed following the test's completion.

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 1.2), 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 week were included as fixed effects. Fish ID, trial, and observation day were used as random effects, to account for the repeated measures. Residuals for all three models were normally distributed in diagnostic normal q-q plots. Likelihood ratio tests using the package 'lmtest' (Zeileis and Hothorn, 2002) were then used to determine the significance of interactions between fixed effects, by comparing mixed models with an otherwise identical mixed model which lacked the interaction term, while the statistical significance of the fixed effects was obtained from an analysis of variance of the final models. Repeatabilities for individual differences in foraging success, chasing, being chased and habitat choice were calculated from the four days of observation during the group trials 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:

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

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 number of behavioural measures obtained during the individual behavioural trials into composite behavioural traits, and to identify any correlated behavioural traits, which often correspond to behavioural syndromes (Sih et al., 2004). 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). 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 fixed effects, as was dominance status, treatment order, and SGR.

3. Results

Despite the minimal size differences within the groups of fish (mean ± SD, CV 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. The dominant fish accounted for 47 to 94% (mean % ± SD: 72.8 ± 14.4%, $N = 15$ groups) of the total aggression within the groups. Overall, dominants were not larger than subordinates (Paired *t*-test, t_{14}=-0.18, P=0.86), 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 smaller than those in the other two treatments (Linear mixed model, $t_{2,57}$=-3.61, P=0.001; mean ± SD weight: 0.45 ± 0.09 g vs 1.15 ± 0.28 g). Due to these group differences, initial body weight was added as a covariate in all analyses.

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 (Figure 1.1A). Overall, body size did not affect habitat use (Linear mixed model, $F_{1,240}$=0.92, P=0.35).

As expected, there was a significant interaction between the two predator-present treatments and week in the number of fish in the open habitat (Likelihood ratio test, X^2=12.36, P=0.00044); not surprisingly, fish in the week-two predator treatment used the open habitat less during the second week, whereas those in the other treatment showed the opposite trend. Overall, fewer fish used the open habitat when the predator model was present (Linear mixed model, $F_{1,240}$=15.53, P=0.00011; Figure 1.1A).

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 also observed (Figure 1.1B). 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; Figure 1.1B).

A significant interaction was also found between dominance status and the presence of the predator model (Likelihood ratio test, X^2_1=11.75, P=0.00061; Figure 1.2). Dominant fish primarily used the complex habitat, whereas the subordinate fish in the no-predator treatment primarily used the open habitat. Despite this interaction, dominants used the complex habitat more than did subordinates (Linear mixed model, $F_{1,240}$=240, P=0.00034; Figure 1.2). Fish showed individual habitat preferences over the study (mean repeatability, 95% C.I.'s [LCI, UCI]: 0.29 [0.15, 0.43]).

3.2. Foraging success

Dominants, as identified by higher chase rates, consumed a greater proportion of food than subordinates in all trials (Linear mixed model, $F_{1, 240}$=7.92, P=0.0066; Figure 1.3), while the proportion of food consumed was unaffected by the predator model (Linear mixed model, $F_{1,240}$=0.24, P=0.62), week (Linear mixed model, $F_{1,240}$=0.16, P=0.69), or body size (Linear mixed model, $F_{1, 240}$=0.02, P=0.88). Individual differences in proportion of food consumed was significantly repeatable throughout the trials (mean repeatability, 95% C.I.'s [LCI, UCI]: 0.38 [0.20, 0.56]).

3.3. Aggression

There was a significant three-way interaction between predator treatment, dominance status, and week on the rate of chasing (Figure 1.4A; Likelihood ratio test, X^2_1=12.99, P=0.00031). Based on the confidence intervals, dominants chased more in the second week when not exposed to the predator model (Figure 1.4A). There was also a two-way interaction between dominance status and treatment order (Figure 1.4B; Likelihood ratio test, X^2_2=17.33, P=0.00017); the dominants in the week-two predator treatment, which were smaller, chased less than the dominants in the other two treatments (Figure 1.4B). Despite these interactions, dominants chased more than subordinates (Linear mixed model, $F_{1,240}$=134.73, P<0.00001), as did larger fish (Linear mixed model, $F_{1,240}$=11.92, P=0.0032). Individual differences in chase rate were repeatable across both weeks of the study (mean repeatability, 95% C.I.'s [LCI, UCI]: 0.34 [0.18, 0.50]).

3.4. Growth

There was an interaction between predator treatment and dominance status on growth rate (Likelihood ratio test, X^2_2=8.78, P=0.012; Figure 1.5). The dominants in the week-two predator treatment, which were smaller, lost weight over the study (SGR mean ± SD: -0.00606 ± 0.01025), whereas dominants in the other treatments gained weight. 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, $F_{1,51}$=1.34, P=0.25). Not surprisingly, fish that consumed a greater proportion of food grew more (Linear model, $F_{1,51}$=4.09, P=0.048; Supplementary Figure 1.1), while larger fish grew less (Linear model, $F_{1,51}$=5.38, P=0.024). Use of the open habitat showed a positive yet nonsignificant association with growth (Linear mixed model, $F_{1,51}$=3.26, P=0.077).

3.5. Individual behaviour

Three different composite behaviours emerged from a principal component analysis of the individual behavioural assays (p=0.01; Table 1.1): (PC1) aggression toward the intruder with boldness toward the predator model; (PC2) aggression to the mirror and shyness toward the predator; and (PC3) aggression toward the intruder and shyness to the predator. Aggressive behaviours directed toward the intruder and mirror were similar for PC 1 and PC 2, respectively. These fish approached quickly, spent a lot of time within one body length, and engaged in numerous side displays and mouth wrestling attempts. In contrast, intruder aggression in PC 3 consisted only of head down displays, characteristic of more restrained aggression (Reddon et al., 2015). Hereafter, these components, or behavioural syndromes (Sih et al. 2004), will be characterized as (1) intruder aggression and boldness, (2) mirror aggression and shyness, and (3) 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 (Table 1.1).

None of the three composite behaviours were strong predictors of dominance status (Figure 1.6). However, the smaller dominants in the week-2 predator treatment emerged as slightly odd with respect to PC 3, as they showed a higher degree of restrained aggression and shyness than the other dominants (Figure 1.6C). Ignoring this treatment, dominants showed less restrained intruder aggression and shyness than subordinates. When the smaller fish from the week two predator treatment were excluded from analysis, PC 3 became negatively associated with dominance (Linear model, $F_{1,33}$=4.19, P=0.049), revealing that these smaller dominants behaved similarly to subordinates when alone.

Bolder, more intruder aggressive fish were larger (Linear model, $F_{1,33}$=5.59, P=0.024), but did not differ in their food consumption (Linear model, $F_{1,33}$=0.01, P=0.90) or habitat use (Linear mixed model, $F_{1,33}$=0.78, P=0.38). Mirror aggression and shyness (Figure 1.6b) was not significantly related to body size (Linear model, $F_{1,33}$=3.48, P=0.071), food consumption (Linear model, $F_{1,33}$=1.29, P=0.26) or habitat use (Linear model, $F_{1,33}$=0.01, P=0.91). Fish that showed restrained aggression toward intruders and shyness toward predators were more frequently found in the open habitat (Linear model, $F_{1,33}$=11.05, P=0.0022; Figure 1.7), but did not differ in body size (Linear model, $F_{1,33}$=0.11, P=0.74), or in food consumption (Linear model, $F_{1,33}$=1.63, P=0.21). 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 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), perch (*Perca fluviatilis*), roach (*Rutilus rutilus*; Brabrand and Faafeng, 1993; Persson, 1993), blacknose shiner (*Notropis heterolepis*) and bluntnose minnow (*Pimephales notatus*; MacRae and Jackson, 2001), sunfish (*Lepomis macrochirus*; Gotceitas, 1990), and prawns (*Penaeus 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 felt relatively safe 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).

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 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 increased their metabolic rate and caused them to lose weight.

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 behavioural distress and resting metabolic rate (RMR) that occurs in complex habitats (Millidine et al., 2006), but see (Kochhann and Val, 2017) for a counter example.

Similar to our findings, mirror aggression did not predict intraspecific aggression in the mangrove rivulus (*Rivulus 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). These findings are consistent with our own; fish that were aggressive toward a mirror were also shyer towards predators, suggesting more fear. Mirrors may be induce more fear because they are perceived as a novel stimulus. 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. More research is needed to fully elucidate the differences and similarities between aggression directed toward a mirror and a conspecific.

4.1. 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, aggression 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 high levels of restrained aggression and shyness, resembling subordinates more than dominants. 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. Interestingly, this same trait was the best predictor or the use of the open habitat, further supporting an IDD.

In contrast to the dominant's strong preference for the complex habitat, fish that showed restrained aggression and shyness when alone were more frequently found in the open habitat. This may indicate behavioural compensation for the higher degree of predation risk characteristic of most open habitats. For example, marine gastropods (*Gibbula cineraria*, *G. umbilicalis*, *Osilinus lineata*, *Littorina littorea*), with more vulnerable shells were less bold toward predators than less vulnerable individuals (Cotton et al., 2004). Similarly, male field crickets (*Gryllus integer*), with longer mating songs, were more cautious toward predators than crickets with shorter songs (Hedrick, 2000); while smaller sunfish (*Lepomis macrochirus*) selected vegetated habitats in the presence of a predator (*Micropterus salmoides*; Werner et al., 1983). 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 benefit 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 behavioural distress. 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.

Figure Legends

Figure 1.1. Mean (95% C.I.'s, *N*=5) A) number of fish, and B) competitive weight, in the open habitat during 13 minute feeding trials under different predator exposure treatments. Dashed line is the ideal free prediction.

Figure 1.2. Number of subordinate and dominant cichlids in the open habitat (mean, 95% C.I.'s, *N*=5) during 13 minute feeding trials in both weeks under different predator exposure treatments. Dashed line is the ideal free prediction.

Figure 1.3. Proportion (mean, 95% C.I.'s, *N*=5) of food consumed by 3 subordinate and 1 dominant cichlid during 13 minute feeding trials under different predator exposure treatments

Figure 1.4. Number of chases toward other fish (mean, 95% C.I.'s) by three subordinates and one dominant cichlid during 13 minute feeding trials under different predator exposure treatments (*N*=5 per treatment)

Figure 1.5. Specific growth rate (mean, 95% C.I.'s) of subordinate and dominant cichlids under different predator exposure treatments (*N*=5 per treatment). Dashed line is no change in body weight.

Figure 1.6. Dominance in group feeding trials across three predator exposure treatments (*N*=5 per treatment) in relation to three individually measured composite behavioral traits A) intruder aggression and boldness (PC1), B) mirror aggression and shyness (PC2), and C) restrained intruder aggression and shyness (PC3).

Figure 1.7. Proportion of time spent in the open habitat during 13 minute feeding trials under different predator exposure treatments and degree of restrained intruder aggression and shyness (PC 3; *N*=5 per treatment). Dashed line is the ideal free prediction.

Table 1.1

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

Test	Behavior	PC 1	PC 2	PC 3
Novel food	No. bites	0.291	**0.509**	**0.644**
Mirror	Approach latency	-0.087	**-0.718**	0.237
	< 1 body length away	0.046	**0.706**	-0.319
	> 2 body lengths away	0.142	**-0.621**	0.380
	No. side displays	0.177	**0.559**	0.200
	No. head down displays	-0.387	0.356	0.095
	No. mouth wrestles	0.257	**0.513**	-0.300
Intruder	Initial reaction	0.111	-0.342	-0.166
	Approach latency	**-0.794**	0.232	-0.246
	No. approaches	**0.529**	-0.016	0.319
	< 1 body length away	**0.881**	-0.170	-0.076
	> 2 body lengths away	**-0.874**	0.228	-0.008
	No. side displays	**0.700**	-0.377	-0.106
	No. head down displays	0.233	-0.057	**0.623**
	No. charges	**0.630**	0.008	-0.085
	No. mouth wrestles	**0.744**	0.062	-0.258
Aquatic	Initial reaction	-0.029	**-0.521**	**-0.532**
Predator	Approach latency	0.291	**0.509**	**0.644**

No. approaches	**0.471**	0.005	0.116
< 1 body length away	**0.560**	0.314	**-0.442**
> 2 body lengths away	**-0.600**	-0.359	**0.415**
Eigenvalue	5.298	3.520	2.603
P-value	0.01	0.01	0.01
Proportion of variance	25.23%	16.76%	12.40%
Cumulative proportion of variance	25.23%	41.99%	54.39%

Components larger than 0.4 in absolute value represent behaviors characteristic of a particular composite behavioural trait, and are indicated in bold.

Figure 1.1

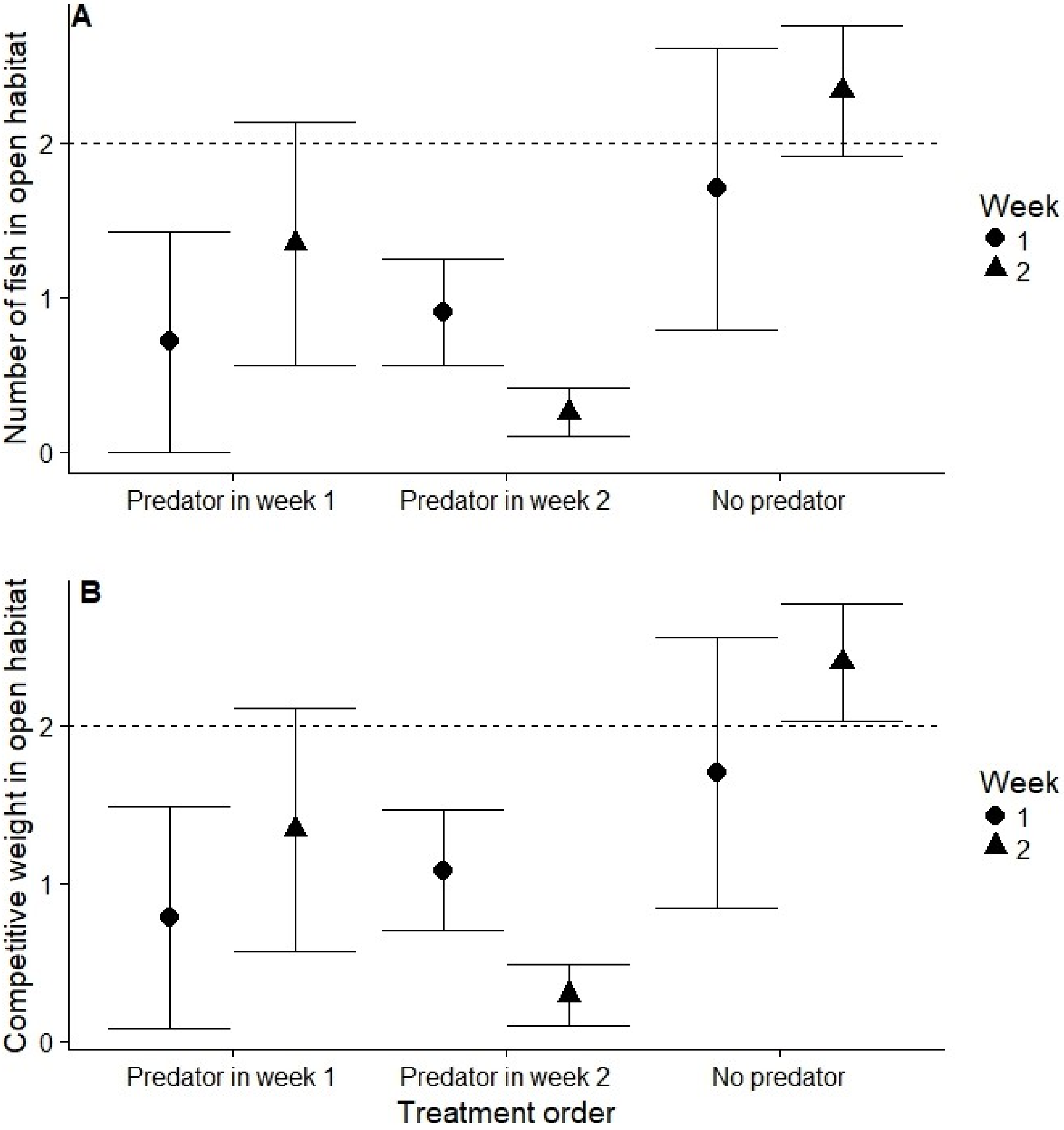

A
Number of fish in open habitat
0
1
2
Predator in week 1
Predator in week 2
No predator
Week
● 1
▲ 2
B
Competitive weight in open habitat
0
1
2
Predator in week 1
Predator in week 2
No predator
Treatment order
Week
● 1
▲ 2

Figure 1.2

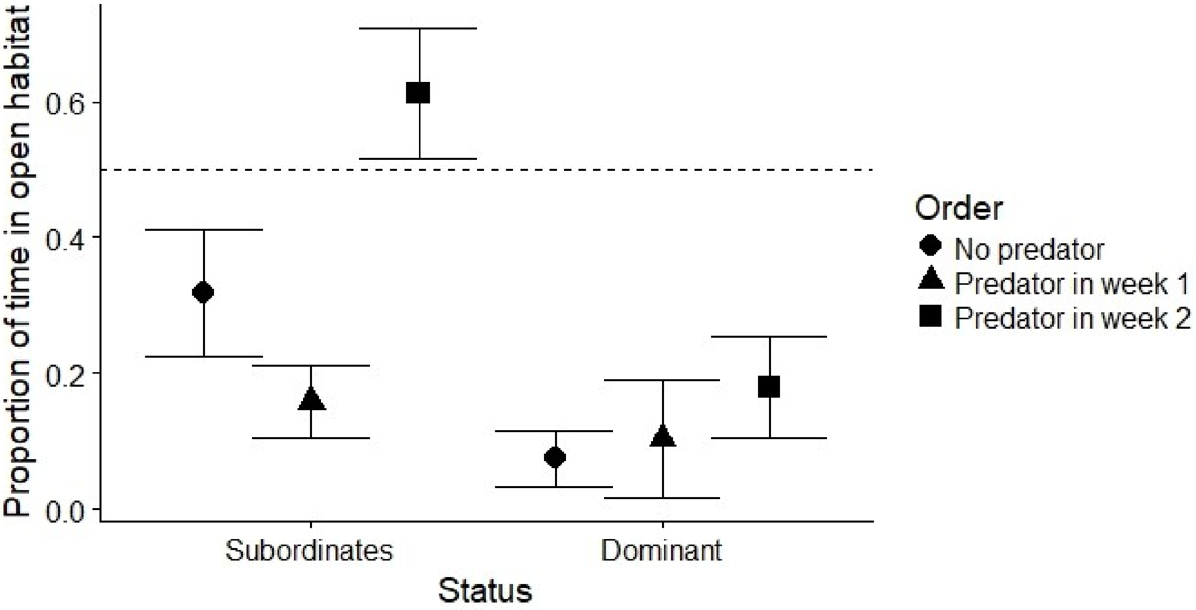

Proportion of time in open habitat
0.6
0.4
0.2
0.0
Subordinates
Dominant
Status
Order
● No predator
▲ Predator in week 1
■ Predator in week 2

Figure 1.3

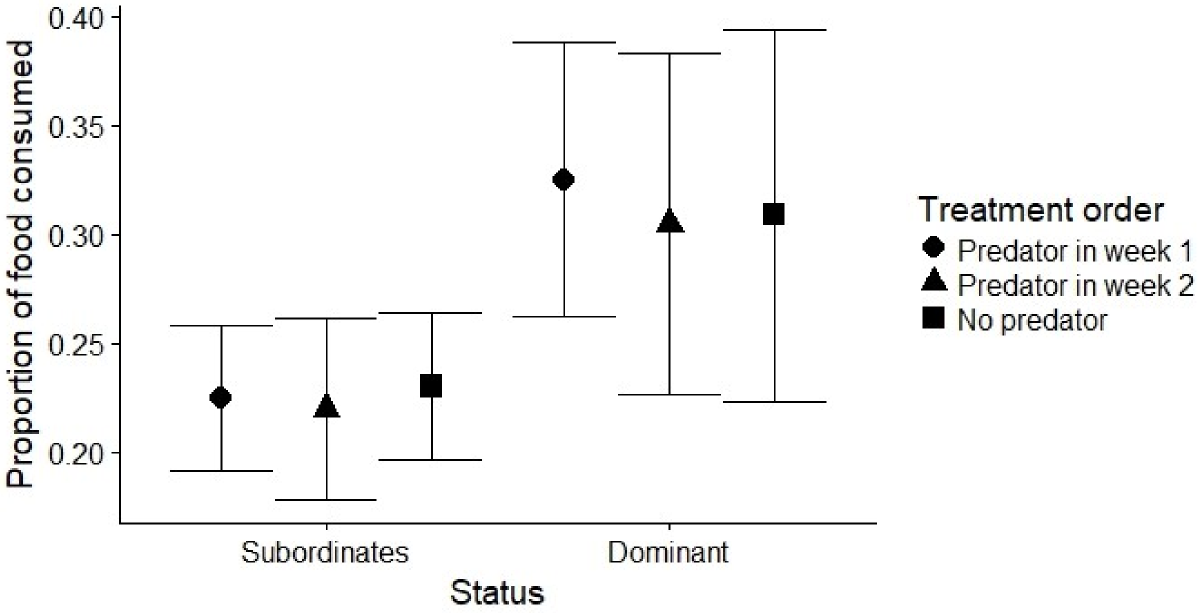

0.40
0.35
0.30
0.25
0.20
Proportion of food consumed
Subordinates
Dominant
Status
Treatment order
● Predator in week 1
▲ Predator in week 2
■ No predator

Figure 1.4

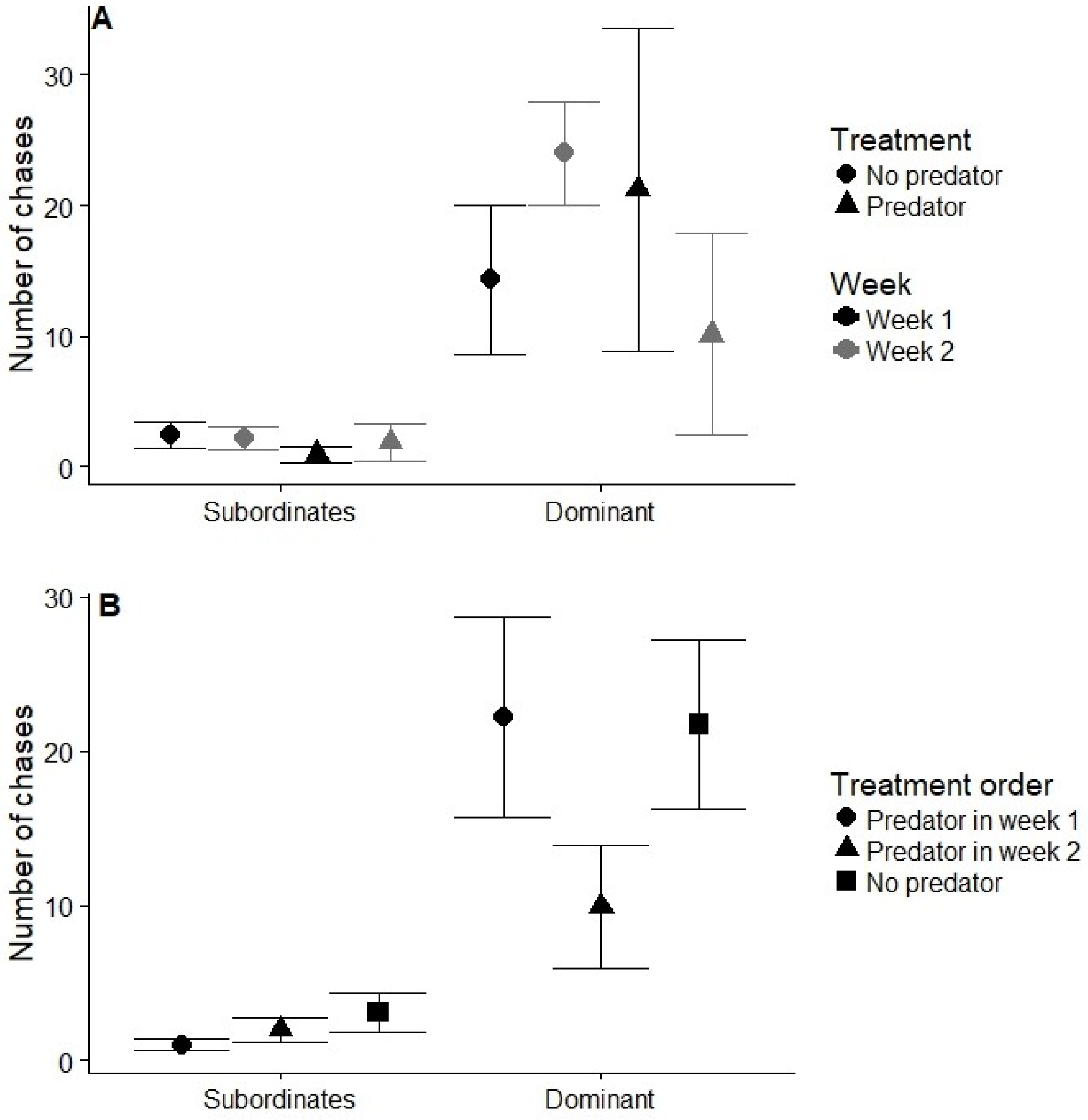

A
Number of chases
0
10
20
30
Subordinates
Dominant
Treatment
● No predator
▲ Predator
Week
● Week 1
● Week 2
B
Number of chases
0
10
20
30
Subordinates
Dominant
Treatment order
● Predator in week 1
▲ Predator in week 2
■ No predator

Figure 1.5

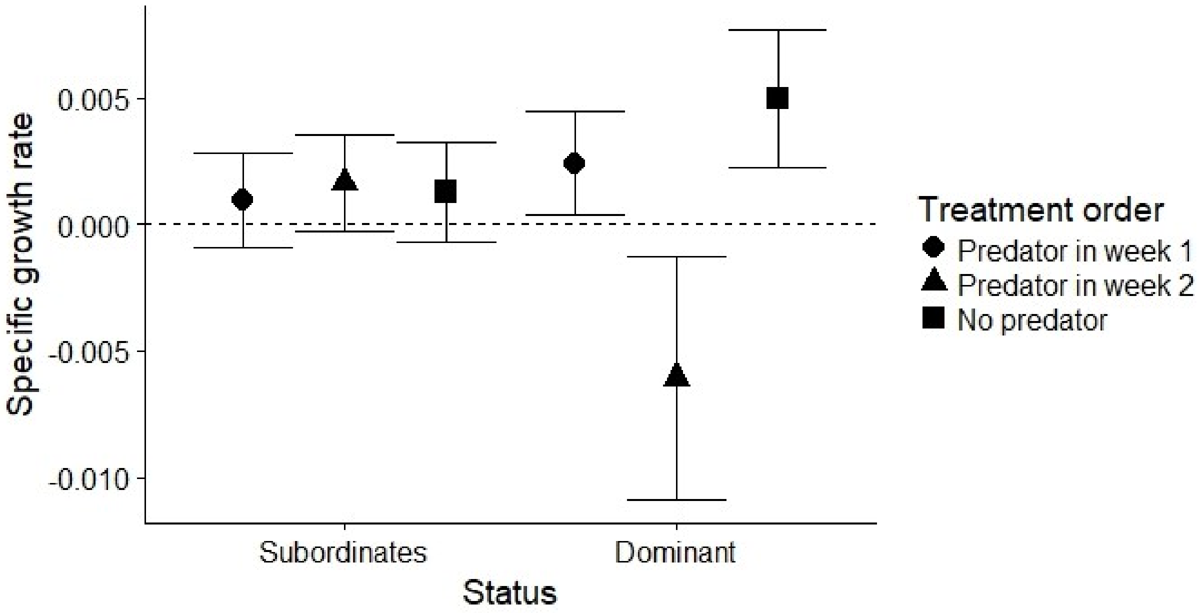

Specific growth rate
0.005
0.000
-0.005
-0.010
Subordinates
Dominant
Status
Treatment order
● Predator in week 1
▲ Predator in week 2
■ No predator

Figure 1.6

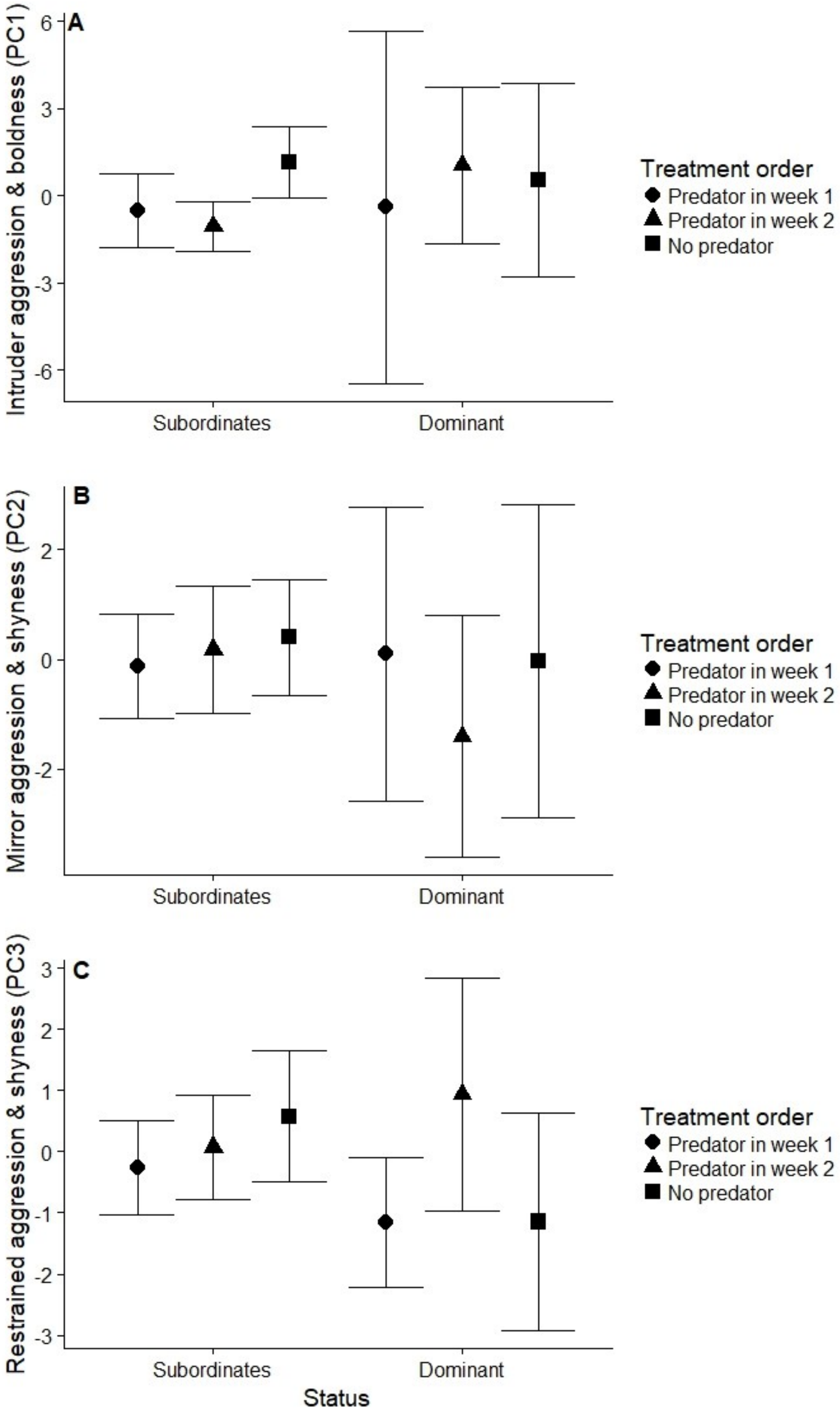
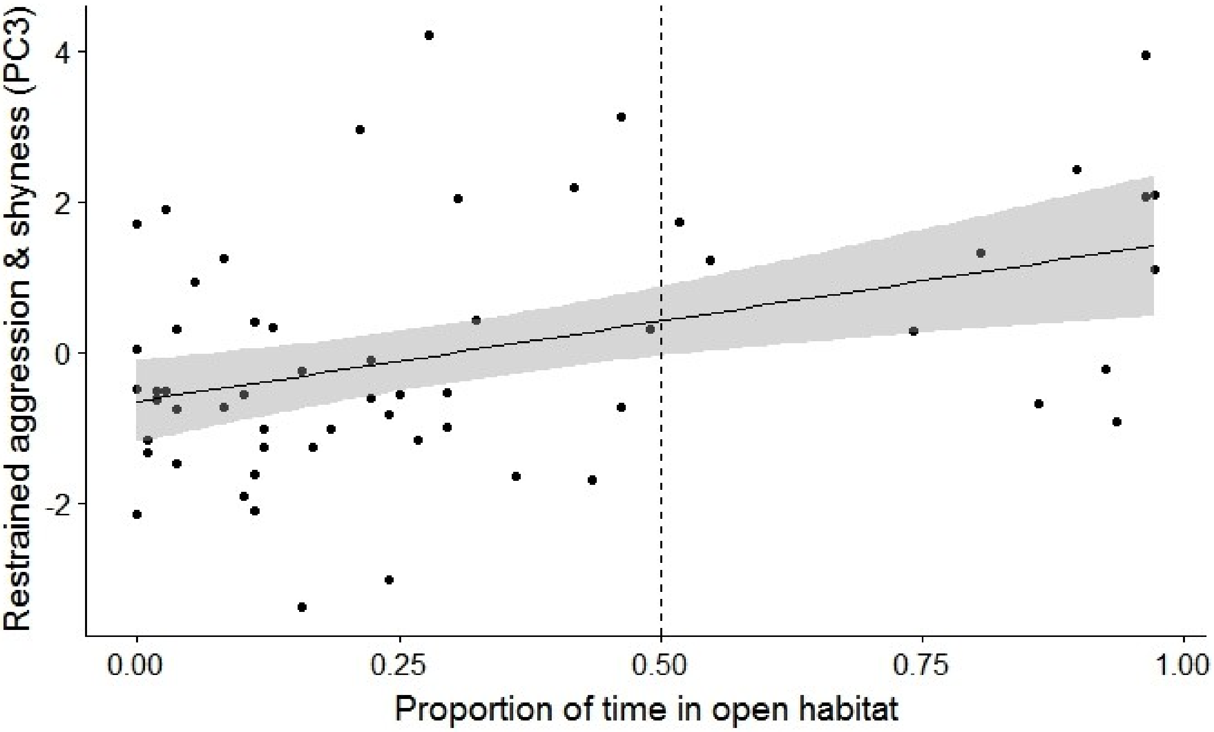

A
Intruder aggression & boldness (PC1)
6
3
0
-3
-6
Subordinates
Dominant
Treatment order
● Predator in week 1
▲ Predator in week 2
■ No predator
B
Mirror aggression & shyness (PC2)
2
0
-2
Subordinates
Dominant
Treatment order
● Predator in week 1
▲ Predator in week 2
■ No predator
C
Restrained aggression & shyness (PC3)
3
2
1
0
-1
-2
-3
Subordinates
Dominant
Status
Treatment order
● Predator in week 1
▲ Predator in week 2
■ No predator

Figure 1.7


Restrained aggression & shyness (PC3)
4
2
0
-2
0.00
0.25
0.50
0.75
1.00
Proportion of time in open habitat

Supplementary Figure Legends

Supplementary Figure 1.1: Proportion of food consumed and specific growth rate for all fish under different predator exposure treatments (r^2=0.057; n=60).

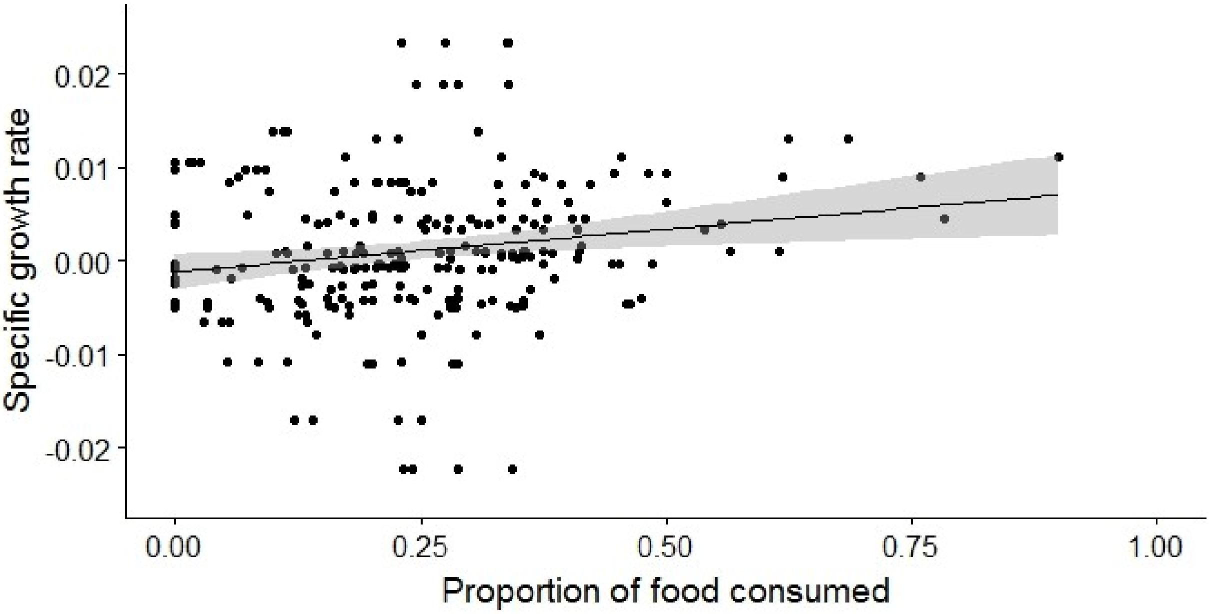
Supplementary Table 1.1: Numeric values assigned to the initial response of convict cichlids to a mirror, a conspecific intruder, and an aquatic predator model.

Score	**Behaviour**
2	Swam toward, approached
1	Oriented toward
0	Neutral or no response
-1	Oriented away
-2	Swam away, hid

Supplementary Table 1.2: Numeric values assigned to the response of convict cichlids to the approach of an aquatic or aerial predator model.

Score	**Behaviour**
4	Frightened darting
3	Move > 1 bl
2	Move <1 bl
1	Increase in fanning
0	No change in behaviour

Supplementary Figure 1.1



Chapter 2. Effects of habitat complexity, dominance and personality on habitat selection: ideal despotic cichlids

ABSTRACT

Habitat structure can impede visibility and movement, resulting in lower resource monopolization and aggression. Consequently, dominants and more aggressive individuals may prefer open habitats to maximize resource gain, or conversely, they may prefer complex habitats, along with shyer individuals, to minimize predation risk. We explored the role of dominance on foraging, aggression and habitat choice using convict cichlids (*Amatitlania nigrofasciata*) in a two-patch ideal free distribution experiment. Groups of six fish of four distinct sizes competed for shrimp in single-patch trials in both an open and complex habitat; half the groups experienced each habitat type first. Following these single-patch trials, each group chose between habitat types in a two-patch trial; each fish then underwent an individual behavioural assessment using a battery of "personality" tests. In the single-patch trials, the largest fish chased more in the complex habitat, while individual fish differed in foraging, chasing, and habitat use, with repeatabilities of 0.51, 0.33 and 0.76. In the two-patch trials, dominants preferred and defended the complex habitat, with more than half the fish and competitive weight in the open habitat. Dominants also chased morewhen the open habitat was encountered first, negatively affecting the growth of the other fish. Despite their preference for the complex habitat, dominant fish were the boldest individuals, when tested alone, while the second largest fish were shyer, and smaller, subordinate fish were inconsistently aggressive. Smaller dominants and those that foraged less in the open preferred the complex habitat, suggesting both risk and energetic state affect habitat preference in dominant convict cichlids.

Keywords: *Amatitlania nigrofasciata*, convict cichlid, dominant, habitat choice, habitat complexity, ideal despotic, ideal free

The primary advantage of dominance is the priority of access to resources (Kaufmann, 1983). Although contested resources may vary across species, they primarily include food (e.g. Maclean & Metcalfe, 2001; Wittig & Boesch, 2003), mates (Cowlishaw & Dunbar 1991; Hutchings et al., 1999), or shelter (Shulman, 1985; Usio et al., 2001), while space may substitute for these in territorial species (Johnsson et al., 1999; Rowland 1989; Thiessen et al., 1971). However, the factors which make a particular habitat valuable, such as structural complexity, may vary for individuals differing in dominance status. The presence of physical complexity within a habitat can impede visibility (Clayton, 1987; Eason & Stamps, 1992), or movement (Deboom & Wahl, 2013; Loss et al., 2015; Radabaugh et al., 2010); as a result, resource monopolization (e.g. Basquill & Grant, 1998) and aggressive behaviour are often lower in complex than open habitats (Batzina & Karakatsouli, 2014; Chaloupkova et al., 2007; Corkum & Cronin, 2004; Danley, 2011; Ninomiya & Sato, 2009). Consequently, more aggressive competitors may experience increased competitive success in open habitats, but smaller, less competitive individuals are more often found in habitats with more habitat complexity (Gibb & Parr, 2010; Höjesjö et al., 2004).

The distribution of individuals within a given habitat can be predicted from the distribution of their resources, such as food, using the ideal free distribution (IFD; Fretwell, 1972; Parker & Sutherland, 1986). The IFD assumes that if individuals have ideal knowledge of resource quality, and the freedom to switch patches, then they will be distributed in direct proportion to their resources. Deviations from the ideal free can indicate a lack of information, such as difficulty in evaluating patch quality (e.g. Abrahams, 1986), or the presence of aggressive behaviour (Andren, 1990; Calsbeek & Sinervo, 2002; Murray et al., 2007), which may prevent some individuals from entering a particular patch, called ideal despotic distributions (IDD). IDDs are characterized by aggression and resource monopolization by one or more dominant individuals, with lower competitive success for the remaining group members (Fretwell, 1972). Despotic distributions have been observed in mammals (Messier et al., 1990; Murray et al., 2007), birds (Andren, 1990; Møller, 1995; Zimmerman et al., 2003), lizards (Calsbeek & Sinervo, 2002), and fish (Hakoyama & Iguchi, 2001; Purchase & Hutchings, 2008).

Body size is often an accurate predictor of both competitive success and dominance rank, often called resource holding potential (Parker, 1974; French & Smith, 2005; Hughes, 1992; Whiteman & Coté, 2004). Larger individuals are often more aggressive, bolder and successful at monopolizing resources, such as food or mates (Colléter & Brown, 2011; Stamps, 2007). However, size is not always a reliable predictor of social dominance, and may be a consequence, rather than a cause, of relative competitive ability (e.g. Huntingford et al., 1990). Individual differences in behaviour, or personality (Réale et al., 2007), such as aggression or shyness/boldness, may underlie variation in competitive ability or habitat preference that is not accounted for by body size (Colléter & Brown, 2011; Wolf & Weissing, 2012). Additionally, differences in body condition, or state (e.g. Hazlett et al., 1975), and the subjective value of a resource (Hurd, 2006), often underlie differences in aggression.

Although dominance can be predicted by relative size and personality differences, personality is normally assessed individually, in an artificial setting (e.g. Dingemanse et al., 2010; Réale et al., 2007; van Oers et al., 2008). Consequently, laboratory tests of dominance or aggression can be poor predictors of social dominance or aggression in more natural scenarios (e.g. Adriaenssens & Johnsson, 2010; Martin & Réale, 2008). Additionally, individual behaviour tested in the absence of conspecifics may not accurately reflect behaviour observed within a group, as individuals may alter their behaviour depending on social context and interactions with conspecifics (Bergmüller & Taborsky, 2010), especially for aggression, which can be a reciprocal behaviour whose escalation and duration is dependent on the recipient's response (Wilson et al., 2009). Thus, an individual's relative level of aggression (e.g. Arnold & Taborsky, 2010), or shyness/boldness (e.g. van Oers et al., 2004) may change based on the behaviour or personality of the other members of the group.

In this study, we investigated the roles of dominance status, personality and habitat complexity on the foraging success, aggression and habitat use, in the convict cichlid, *Amatitlania nigrofasciata*. Convict cichlids are ideal for this study because they exhibit size-based dominance hierarchies (Weir & Grant, 2004) and both an IFD and IDD, depending on the defendability of the resource (Grand & Grant, 1994a, b). Groups of six fish, differing widely in body size, competed for food in a single patch experiment in both an open and complex habitat to quantify their competitive weight (sensu Parker & Sutherland, 1986) in each habitat. Fish were then given access to both habitats simultaneously, with dominants able to choose their preferred habitat. We tested the following predictions. According to resource defence theory, in the one-patch trials, dominants are predicted to be (1) more aggressive and (2) monopolize a greater share of the food in the open versus the complex habitat (Baird et al., 2006; Basquill & Grant, 1998; Höjesjö et al., 2004). When allowed to choose their habitat in the two-patch trials, dominants should (3) choose the habitat in which they are most competitive, presumably the open habitat. Alternatively, dominants may be more cautious than smaller subordinates in an open habitat, because of a higher perceived risk of predation to protect their accumulated assets (sensu Clark, 1994). According to the asset protection principle, which predicts that cautious behaviour will increase along with accumulated assets (Clark, 1994), dominants may be (4) less aggressive in open habitats, causing any differences in predicted resource monopolization between habitats to diminish or even reverse (Church & Grant, submitted). In the two-patch treatment, we also tested (5) whether the fish conformed to an IFD, an equal number of fish or competitive weights in both habitats or to an IDD, too few fish or competitive weights in the habitat chosen by the dominant. In addition to the feeding trials, we quantified the behaviour of all individuals in a battery of "personality tests" to test whether (6) personality traits predicted dominance status, or the use of open vs complex habitats.

METHODS

Fish were held in stock tanks (61.5 x 31.5 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. Tanks were maintained at approximately 23° Celsius, set on a 12:12 light/dark cycle, and fish were fed commercial fish flakes (Nutrafin® Max Tropical Fish Flakes). Experimental groups ($N = 9$) were selected based on relative body size (see below), and fish were tagged subcutaneously with small amounts of pink, red or green elastomer in the cephalic, dorsal or caudal region to differentiate between group members. 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 (see below). Fish were returned to stock tanks after the completion of the experiments. No individuals were used more than twice, and groups were never repeated.

Feeding Experiment

Each experimental group consisted of six fish that belonged to four easily distinguishable size categories: one Large ($X \pm$ SD: 4.10 g ± 1.75), one Medium ($X \pm$ SD: 2.25 g ± 1.06), one Small ($X \pm$ SD: 1.38 g ± 0.77), and three Extra Small fish ($X \pm$ SD: 0.52 g ± 0.27; $N = 9$ groups).

The coefficient of variation (SD / X) was used to quantify the unevenness of size within the groups. Size differences were substantial within the groups (X ± SD, CV body mass: 1.40 ± 0.64, $N = 9$), but minimal among the three Extra Small fish in each group (X ± SD, CV body mass: 0.0048 ± 0.0048).

Two experimental tanks (l x w x h = 91 x 46 x 40 cm) were each set up with gravel to a depth of 3cm, an undergravel filter and a heater. Three of the four sides were covered with black plastic to minimize disturbance of the fish, while the front (91 cm) of each tank was left uncovered to allow for observations. Tanks were divided in half lengthwise by a mesh divider, which prevented fish from moving into the other side of the tank but allowed water to flow through. Following Basquill and Grant (1998), one of the sides was randomly chosen as the complex habitat by adding four equally spaced plastic plants approximately 24 cm in height, in addition to the filter and heater, while the other half of the tank was left as the open habitat. The initial habitat treatment for each group was randomly selected. Groups were moved into the other side of the tank following two consecutive days of data collection (i.e. feeding trials) in the initial habitat. After fish were observed in both habitats, the divider was removed, which enabled fish to choose between the two habitats. Hence, each group of six fish was subjected to three treatments: complex; open; and, a choice of both.

A large sheet of clear Plexiglas (l x w = 91 x 46 cm) was placed on top of the experimental tank during the feeding trials. The Plexiglas was divided into 4 adjacent sections (22.75 cm long), and the two outermost sections were further subdivided into 6 sections (l x w = 11.4 x 15.3 cm). A small hole (0.5 cm) was drilled in the centre of each subsection, and funnels were placed into each of the six holes to create the feeding patches. Individual mysis shrimp were preloaded into 3 mL syringes, then dropped into one of the six holes, randomly chosen by rolling a six-sided die. In the open and complex habitats, fish were fed every 20 seconds for a total of 46 shrimp in 15 minutes, then observed for 5 minutes afterward for a total of 20 minutes. After the partition was removed and fish were granted access to both habitats, the same total number of shrimp ($N = 46$) were placed into both habitats simultaneously; one shrimp randomly appeared via one hole in each of the two habitats every 20s. Feeding trials in both habitats lasted for a period of 7 minutes and 40 seconds, and fish were observed for an additional 5 minutes, for a total of 13 minutes. Feeding trials were given for at least five consecutive days before data collection, or until all fish participated in a minimum of two consecutive feedings. During observations, the number of prey items consumed by each fish was recorded, and was subsequently used as a measure of competitive weight (sensu Grand & Dill, 1997). Each competitive weight was then multiplied by 6 to account for the number of fish in each group. The identity of any fish that initiated or elicited a chase, defined as a unidirectional burst of movement towards a conspecific (Weir & Grant, 2004), was also noted, as was the habitat of each fish (open or complex) every 30 seconds after the removal of the partition.

Individual Behavioural Assay

Following (Church & Grant, submitted), individual behavioural trials were conducted after the completion of the group trials. Fish ($N = 53$ of 54 fish; one jumped out of its tank) were netted in random order from their experimental tank, and placed into one half of a small tank (l x w x h = 30.4 x 13.4 x 20.8 cm), containing a heater and air pump, and initially divided in half lengthwise by a piece of black Plexiglas. Fish were held for a period of 48 hours before testing began to reduce any visual signs of behavioural distress. All tests were conducted consecutively on the same day, with approximately 15 and 30 minutes between each test. Following the completion of the behavioural tests, fish were weighed and returned to one of the stock tanks.

Test 1: Emergence Time

After the acclimation period, the Plexiglas divider was raised off the floor of the tank (approximately 10 cm), 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 minutes. Following the test, the divider was completely removed.

Test 2: Novel Food

A small quantity of crushed commercial dry cat food (Meow Mix® Original Choice) was sprinkled into the tank from above; this novel food differed from the fish flakes fed in the stock tanks in chemical composition, granule size, and colour. Fish were observed for a period of 10 minutes, and the latency to begin feeding and the total number of bites taken were noted. Following the test, uneaten food was removed with a dipnet. Fish reacted minimally, if at all, to the dipnet.

Test 3: Mirror Test

A mirror (l x w: 14 x 14 cm) was placed against the outside wall of the test aquarium in view of the focal fish, and its behaviour was recorded for 10 minutes, following Höjesjö et al. (2004, 2011); however the mirror was not placed within the water column to minimize disturbance of the fish. The initial reaction to the mirror (Supplementary Table 2.1) was noted, as well as the distance and orientation relative to the mirror every 10 seconds, and the number of side and head down displays, chases towards the mirror, and mouth wrestling attempts (Keeley & Grant, 1993; Sopinka et al., 2009). The mirror was removed after the completion of the test.

Test 4: Intruder Test

A conspecific visually assessed to be approximately 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 and 2.5 cm of gravel, and slowly lowered into the test aquarium, as far as possible from the focal fish (sensu Bell & Stamps, 2004). The initial reaction of the focal fish (Supplementary Table 2.1) and its latency to approach the intruder were recorded, as well as its distance and orientation toward the intruder every 10 seconds. The total number of side and head down displays, chases, and mouth wrestling attempts (Keeley & Grant, 1993; Sopinka et al., 2009) were also recorded throughout the 10 minute trial. The intruder was removed from the tank and measured (mean length difference, 95% C.I.'s [LCI, UCI]: 7.66% [5.91%, 9.42%]) after the test.

Test 5: Aquatic Predator Model

A plastic model of a larger cichlid species, the yellow lab (*Labidochromis caeruleus*; length x height: 11x 8 cm), a common predator of convict cichlids in the wild, 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 seconds. After 10 minutes, the predator slowly approached the focal fish at a speed of 1 body length per second and retreated, and the reaction was recorded (Supplementary Table 2.1). 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 slowly passed back and forth over the top of the aquarium at a steady pace, 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, and any changes in behaviour, were recorded (Supplementary Table 2.2).

Statistics

Group Trials

Mixed models were constructed with the 'lme4' package (Bates et al., 2014) to compare the effects of relative body size and habitat on foraging success, aggression and habitat choice. Three sets of models were constructed for proportion of food consumed, number of chases, and proportion of time spent in the open habitat as the response variables. Habitat complexity, habitat order, and size category were included as fixed effects, while fish ID, trial number and observation day were used as random effects, to account for the repeated measures. Residuals for all three models were normally distributed in diagnostic normal q-q plots. Models were reduced through backwards stepwise elimination of nonsignificant fixed effects using analysis of variance ($\alpha > 0.05$). Likelihood ratio tests using the package 'lmtest' (Zeileis & Hothorn, 2002) were then run to determine the significance of interactions, by comparing otherwise identical mixed models with and without the interaction term, while the significance of the fixed effects was assessed via an analysis of variance for each final model; Tukey tests were subsequently conducted using the 'multcomp' package (Hothorn et al., 2008). Repeatability of individual differences and associated confidence intervals were then calculated using the 'rptR' package, which generates confidence intervals from parametric bootstrapping (Stoffel et al., 2017), for foraging success, chasing, and habitat choice observed on four days during the group trials.

The coefficient of variation (SD / X) was also used to quantify the monopolization of food and uneveness of aggression within groups in both the complex and open habitat. Growth throughout the trials was calculated using the formula for specific growth rate:

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

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

Individual Behavioral Assay

Principal component analyses were conducted using the package 'FactoMineR' in R (Le et al., 2008) to reduce the all the behavioural measures obtained during the individual behavioural assay 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). Variables were Z-transformed prior to analysis. Retained principal components, representing composite behavioral 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 for each fish were included as fixed effects, as were habitat order, size category, and SGR. The statistical significance of the fixed effects was again attained from an analysis of variance for each model. All statistical analysis were conducted in R (R Core Team 2015).

RESULTS

All fish began participating immediately in the feeding trials in the single-patch, complex treatment and in the two-patch choice treatment. Consequently, groups of fish spent a total of seven days in both of these treatments. However, the Large fish took longer to participate in the single-patch open treatment, and as a result, groups of fish spent twice as much time in this treatment ($\bar{X}$ ± SD days: 13.7 days ± 2.5 days). In contrast to others, the Large fish initially appeared more inhibited during the training phase in the open treatment, by remaining stationary, swimming less and residing in the periphery of the tank.

One-Patch Treatments

Foraging success in the one-patch treatments was affected by a three way interaction between size, habitat and habitat order (Linear mixed model, $F_{3,216} = 3.82$, $P = 0.011$). When groups were exposed to the open habitat first, Large fish consumed a smaller proportion of food in the open habitat, while Medium fish consumed less food in the complex habitat (Fig. 2.1a, insert). For all other treatment combinations, habitat x order were not significant (Linear mixed models: all P-values > 0.10), nor were size category x habitat (Linear mixed models: all P-values > 0.10). Contrary to both hypotheses, resource monopolization, as measured by the CV of food eaten within groups, did not differ significantly between habitats (CV, $\bar{X}$, 95% C.I.'s [LCI, UCI]: complex = 0.807 [0.691, 0.923]; open = 0.705 [0.588, 0.822]; Linear mixed model, $F_{1,36} = 3.71$, $P = 0.065$), nor was it affected by treatment order (Linear mixed model, $F_{1,36} = 2.86$, $P = 0.13$). Larger fish consumed more food (Linear mixed model, $F_{3,216} = 12.01$, $P < 0.00001$; Fig. 2.1a); on average, the Large fish consumed 33% of the food. Fish showed individual differences in foraging success during the four observed feeding trials (repeatability, $\bar{X}$, 95% C.I.'s [LCI, UCI]: 0.512 [0.349, 0.675]).

Chase rate was affected by an interaction between size category and treatment order (Linear mixed model, $F_{3,216} = 3.81$, $P = 0.015$); large fish chased more frequently when the open habitat was given first (Fig. 2.2a, insert). Chase rate was also affected by an interaction between size category and treatment (Linear mixed model, $F_{3,216} = 14.50$, $P < 0.00001$); Large fish chased more in the complex than in the open habitat (Tukey's post-hoc test, $z = -6.26$, $P < 0.00001$; Fig. 2.2a), which was consistent with the asset protection rather than the resource monopolization hypothesis. No differences in chasing occurred between habitats for the other size categories (Linear mixed models, all $P > 0.20$; Fig. 2.2a). Chasing was also more variable within the group in the complex than the open habitat, as indicated by a higher CV of chasing (CV, *X,* 95% C.I.'s [LCI, UCI]: complex = 1.47 [1.27, 1.67], open = 1.13 [0.97, 1.29]; Linear mixed model, $F_{1,36} = 18.16$, $P = 0.00023$), but was not affected by treatment order (Linear mixed model, $F_{1,36} = 2.76$, $P = 0.14$). Chasing differed among the size categories (Linear mixed model, $F_{3,216} = 45.55$, $P < 0.00001$) with more chases from larger fish (Fig. 2.2a). Chase rate was repeatable for individual fish during the four observed feeding trials (repeatability, *X,* 95% C.I.'s [LCI, UCI]: 0.332 [0.081, 0.583]).

Two-Patch Treatment

The monopolization of food was higher in the two-patch than in the one-patch trials (Linear mixed model, $F_{1,54} = 14.66$, $P = 0.0004$; Fig. 2.1a). This increase in monopolization was due to the Large fish, whose foraging success increased in the two-patch treatment (Tukey's post-hoc test, $z = -3.53$, $P = 0.011$), while the foraging success of the Small fish decreased (Tukey's post-hoc test, $z = 3.71$, $P = 0.0058$). Surprisingly, chasing showed the opposite pattern; chase rate was lower (Linear mixed model, $F_{1,324} = 30.05$, $P < 0.00001$; Fig. 2.2B), and less variable within groups in the two- versus the one-patch trials (Linear mixed model, $F_{1,54} = 102.38$, $P < 0.00001$). This reduction in chasing was due primarily to the Large (Tukey's post-hoc test, $z = -6.95$, $P < 0.00001$) and Medium fish (Tukey's post-hoc test, $z = -3.93$, $P = 0.0024$), which chased less in the two-patch treatment.

Habitat use was affected by size category (Linear mixed model, $F_{3,108} = 3.80$, $P = 0.015$); Large fish were found most often in the complex habitat, Medium fish were equally distributed in both habitats, but Small and Extra Small fish were most often in the open habitat (Fig. 2.3). Consistent with an ideal despotic distribution, more fish than expected (*X,* 95% C.I.'s [LCI, UCI]: 3.70 [3.39, 4.01]) were found in the open relative to the complex habitat. Furthermore, based on the average competitive weights from the one-patch experiments, more competitive weight than expected was also found in the open than in the complex habitat (*X,* 95% C.I.'s [LCI, UCI]: 3.38 [3.19, 3.57]). Use of the open habitat was not affected by habitat order (Linear mixed model, $F_{1,108} = 0.65$, $P = 0.43$), and was highly repeatable for individual fish across the two days of observations (repeatability, *X,* 95% C.I.'s [LCI, UCI]: 0.76 [0.55, 0.97]). A strong negative relationship was found between the habitat choice of the two largest fish across all observations (Pearson's $r_7 = -0.893$, $P < 0.00001$); when the Large fish was in the complex habitat, the Medium fish was found in the open habitat, and vice versa (Fig. 2.4).

While dominant fish spent more time in the complex habitat, there was also marked variability in habitat use. Of the nine Large fish, five spent >90% of the time in the complex habitat, two spent ~50% of the time in each habitat, and two spent more than 80% in the open habitat. Despite this variability in habitat preference, most Large fish foraged equally well in the two one-patch treatments (Pearson's $r_7 = 0.73$, $P = 0.026$; Fig. 2.5), including the four fish that spent most of their time in the open habitat. However, there were two notable exceptions who foraged much more poorly in the open than in the complex habitats; both fish also spent more than 90% of their time in the complex, their preferred foraging habitat. These two fish also chased relatively less in the open habitat; their ratio of chases in the complex/open habitat was 2.5 and 2.67, respectively, compared to the mean ratio of 1.58 (C.I.'s [LCI, UCI]: [1.00, 2.16]). Furthermore, fish that used the open habitat more were larger (Linear mixed model, $F_{1,18} = 9.03$, $P = 0.014$; Supp. Fig. 2.1) and fed more successfully in the open habitat (Linear mixed model, $F_{1,18} = 5.48$, $P = 0.032$).

Growth

Growth rate was affected by treatment order (Linear model, $F_{1,54} = 10.68$, $P = 0.0021$; Fig. 2.7), but not body size (Linear model, $F_{1,54} = 1.39$, $P = 0.26$; Fig. 2.6). There was essentially no net growth for all size categories that experienced the open habitat first. However, the Small and Extra-small fish that experienced the complex habitat first grew over the course of the trials. Surprisingly, growth rate was not affected by the proportion of food consumed (Linear model, $F_{1,46} = 0.67$, $P = 0.42$), number of chases (Linear model, $F_{1,46} = 0.19$, $P = 0.67$) or habitat use (Linear model, $F_{1,46} = 0.06$, $P = 0.81$).

Individual Behaviour

A principal component analysis of the individual behavioural assays for all fish revealed five distinct behavioural axes (All P-values < 0.01; Table 2.2). The first component trait, named "Aggression and Boldness", combined aggressive behaviour toward the mirror and intruder, and boldness toward the predator model. The second component trait, "Inconsistent Aggression", combined nonaggressive behaviour toward the mirror with aggression toward the intruder. The third trait, "Food Motivation and Boldness", combined a short latency to feed with lots of bites, aggression toward the mirror, and boldness toward the predator. The fourth trait, "Low

Exploration", combined a long latency to emerge with aggression toward the intruder. Finally, the fifth trait, "Shyness", combined inconsistent behaviour toward the intruder with shyness toward the predator model.

Inconsistent aggression (Linear mixed model, $F_{3,53} = 14.14$, $P = 0.0027$) and shyness (Linear mixed model, $F_{3,53} = 11.61$, $P = 0.0089$) differed among size categories. Small fish were the most inconsistently aggressive while Large and Medium fish were the least (Figure 2.7A), whereas shyness was lowest in the Large fish and highest in the Medium fish (Figure 2.7B). Inconsistent aggression was also associated with less chasing in the group trials (Linear mixed model, $F_{1,53} = 5.87$, $P = 0.019$) and less food consumption (Linear mixed model, $F_{1,53} = 3.89$, $P = 0.048$). No other differences in food consumption, use of the open habitat, habitat order, or growth rate were found for any of the traits.

DISCUSSION

As expected, competitive success and frequency of aggression were strongly size dependent. Larger fish had higher competitive weights and rates of chasing, and were never chased by a smaller fish. Contrary to the predictions of resource defence theory, but consistent with the asset protection hypothesis, food monopolization and aggression were not higher in the open habitat in the one-patch treatments. Larger fish seemed more inhibited in their behaviour when initially encountering the open habitat, and often took a week or more to begin participating in the feeding trials, in contrast to the smaller fish which began feeding immediately. Although the greater energy reserves of larger fish enabled them to refrain from foraging with minimal cost, this option is often not possible for smaller fish with meager energy reserves (e.g. Rands et al., 2003). The reticent behaviour of the largest fish suggests that they consider the open habitat as inherently more risky or stressful than the complex habitat, which supports the asset protection principle - larger individuals will protect their assets rather than engage in risky behaviour (Clark, 1994). However, this reticent behaviour of dominants was not due to being inherently shyer, as they scored high for boldness in individual assays. Dominant fish appear to be more comfortable exerting their dominance when in a complex habitat; perhaps using the antipredator effect of habitat complexity to compensate for the increased risk of detection inherent to aggressive behaviour (Jakobsson et al., 1995; Kelly & Godin, 2001). Similarly, in sized matched groups, dominant, but not subordinate, convict cichlids also preferred complex habitats regardless of predation risk (Church & Grant, submitted).

On average, the largest fish showed a clear preference for the complex habitat and aggressively guarded it from conspecifics in the two-patch treatment. Consequently, ideal despotic distributions occurred, with more fish and more competitive weight found in the open habitat. As suggested above, the increased chasing by dominants in complex habitats may have resulted from the perceived safety of the complex habitats lowering the costs of aggression, or that complex habitats are more valuable than open habitats, and worth defending (Brown et al., 2006; Elwood et al., 1998; Mohamad et al., 2010). Dominant behaviour was also affected by the order habitats were encountered. When the open habitat was first, the dominant fish consumed less food in the open habitat, chased less initially, but had higher overall levels of chasing throughout the group trials. Dominants that began in the complex habitat appeared comfortable exerting their dominance straightaway, while the dominants that began in the open habitat were initially inhibited but subsequently chased more, perhaps to establish and assert their dominance. The higher overall rates of chasing in the groups experiencing open treatments first may have caused the growth rates for all fish to decrease.

Overall, these results suggest that the habitat preference of dominant convict cichlids is driven more by concerns about asset protection than by resource monopolization. Most dominants preferred the complex habitat for the greater apparent safety without paying much in terms of a foraging cost. However, the four dominants that spent the most time in the open habitat tended to be larger and had higher foraging success in the open. Taken together, these results were somewhat contradictory; although dominants engaged in asset protection overall, smaller dominants with less assets to protect preferred the less risky complex habitat, whereas larger dominants with greater assets preferred the riskier open habitat. As larger dominants and those with greater foraging success in the open likely experience less energetic uncertainty than smaller, less competitive dominants, these findings suggest that dominant convict cichlids with fewer energy reserves tend to seek complex habitats, possibly to reduce the behavioural distress they experience in open habitats. Although the group trials support asset protection overall, they also suggest that variability in dominant habitat choice may also be affected by energetic state. As the large body size of the dominant fish in the present study likely buffered against detectable changes in weight due to behavioural distress during the duration of the study (Church & Grant, submitted), habitat choice trials of a longer duration or that utilize more subtle measures of energetic state will be necessary to test this interpretation directly.

Throughout the group trials, individual fish showed repeatable behavioural differences in foraging, chasing, and use of the open habitat, with repeatabilities in the one-patch trials of 0.51, 0.33 and 0.76, respectively. Although behaviour observed during the individual behavioural assays was not related to chasing, or habitat choice, behaviour differed consistently across the four size categories. Fish in the two smallest size categories showed high aggression toward intruders but not toward the mirror, while boldness in the absence of aggression was high for dominants, but low for the second largest fish. Although smaller fish were less aggressive overall, fish in the two smallest size categories were more inconsistently aggressive, and were only aggressive toward the conspecific intruder and not toward the mirror. For these smaller size categories, aggression toward a conspecific intruder does not appear to be related to aggression toward a mirror. Smaller residents, like focal fish during the individual behavioural assay, may be more likely to attack intruders first, demonstrating a Napoleon complex (Just & Morris, 2003), as intruders are more likely to flee a resident than to fight (Svensson et al., 2012). Consequently, as our personality assay demonstrates, intruder tests may not accurately test conspecific aggression in subordinate convict cichlids.

IDDs and IFDs may only occur when a resource is economically defendable or not, respectively (e.g. Grand & Grant, 1994b). Similarly, an IDD was also found in black bears (*Ursus americanus*), where larger males were able to restrict the access of females and smaller males from preferred food sites (Beckmann & Berger, 2003). Similar IDDs over defendable resources have also been found in brook trout (*Salvelinus fontinalis*; Purchase & Hutchings, 2008; but see Girard et al., 2004), muskrat (*Ondatra zibethicus*; Messier et al., 1990), lizards (*Uta stansburiana*; Calsbeek & Sinervo, 2002), gulls (*Larus cachinnans*; Bosch & Sol, 1998), condors (*Vultur gryphus*; Donázar et al., 1999), and oystercatchers (*Haematopus ostralegus*, Ens & Goss-Custard, 1984). In contrast, for species not actively defending resources, including the non-territorial juveniles of another species of cichlid (*Aequidens portalegrensis*; Tregenza & Thompson, 1998), and two species of minnow (*Semotilus atromaculatus*, *Rhinichthys atratulus*; Fraser & Sise, 1980), the predictions for the IFD were met. Accordingly, within a flock of ducks in which a minority engaged in resource defense, a combination of distributions with both despotic and ideal free elements occurred (*Anas platyrhynchos* L.; Harper, 1982). Our study contributes to this literature by showing that the aggressive behaviour of dominant fish was inhibited in the open habitat, suggesting that risky habitats may inhibit the formation of IDDs. In addition to requiring defendable resources, we suggest that dominants may only feel comfortable exerting their despotism in a relatively safe, complex habitat.

Table 2.1: Retained principal components from individual behavioural assays of fish in the group feeding trials (*N* = 53 fish).

Test	**Behaviour**	**PC 1**	**PC 2**	**PC 3**	**PC 4**	**PC 5**
Novel food	Latency to emerge	0.097	-0.174	0.043	**0.712**	0.146
	Latency to eat	-0.331	0.037	**-0.628**	-0.150	-0.079
	Num. bites	0.298	-0.215	**0.632**	-0.012	0.305
Mirror	Initial reaction	0.253	-0.076	-0.137	**0.597**	0.387
	Approach latency	**-0.530**	**0.426**	-0.073	0.263	-0.364
	< 1 body length away	0.326	**-0.676**	-0.172	-0.361	0.366
	> 2 body lengths away	-0.290	**0.653**	0.218	0.395	-0.317
	Num. side displays	**0.674**	-0.106	-0.143	-0.165	-0.051
	Num. charges	0.175	-0.309	0.374	-0.318	-0.029
	Num. mouth wrestles	**0.599**	-0.391	-0.238	**0.411**	0.146
Intruder	Initial reaction	-0.028	0.165	0.149	0.314	**0.650**
	Approach latency	**-0.604**	**-0.467**	-0.377	0.011	-0.012
	Num. approaches	**0.441**	-0.162	**0.501**	0.017	**-0.422**
	< 1 body length away	**0.591**	**0.606**	-0.211	-0.246	0.129
	> 2 body lengths away	**-0.711**	**-0.525**	0.023	0.137	-0.093
	Num. side displays	**0.463**	**0.521**	-0.029	-0.175	0.198
	Num. head down displays	0.216	-0.034	**0.756**	-0.020	-0.003
	Num. charges	0.193	0.371	-0.032	-0.051	-0.020
	Num. mouth wrestles	0.290	**0.589**	-0.085	-0.043	0.145

Predator	Initial reaction	0.210	0.186	**-0.452**	0.151	0.270
	Approach latency	**0.798**	0.059	0.101	0.203	0.157
	Num. approaches	**0.676**	-0.048	-0.137	0.133	-0.086
	< 1 body length away	**0.620**	-0.308	-0.211	0.287	**-0.504**
	> 2 body lengths away	**-0.689**	0.258	0.258	-0.210	0.382
	Reaction to approach	0.117	-0.027	0.268	0.387	0.001
	Reaction to aerial	**0.423**	0.253	0.028	0.135	-0.126
	Eigenvalue	5.573	3.345	2.570	2.129	1.869
	***P*-value**	0.01	0.01	0.01	0.01	0.01
	Proportion of variance	21.43%	12.87%	9.88%	8.19%	7.19%
	Cumulative proportion of variance	21.43%	34.30%	44.18%	52.37%	59.56%

[1] Coefficients larger than 0.4 in absolute value represent behaviours characteristic of a particular composite behavioural trait, and are indicated in bold.

[2] PC 1: “Aggression & Boldness”, PC 2: “Inconsistent Aggression”, PC 3: “Food Motivation & Boldness”, PC 4: “Low Exploration”, PC 5: “Shyness”

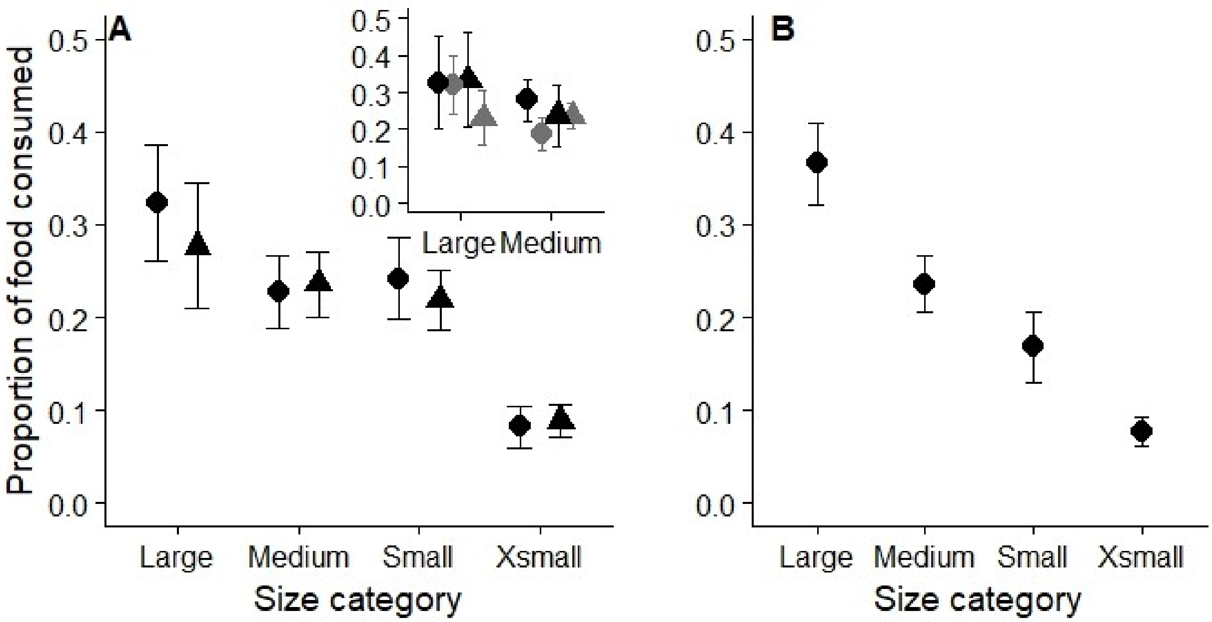


Figure 2.1: Mean (*X*, 95% C.I.'s, *N* = 9) effect of size category and habitat on the proportion of food consumed by groups of six fish during a) one-patch and b) two-patch feeding trials in complex and open habitats. Insert illustrates the three-way interaction between body size, treatment order and habitat on foraging success in both treatments. (legend: ● = complex habitat, ▲= open habitat, black = complex habitat first, grey = open habitat first)

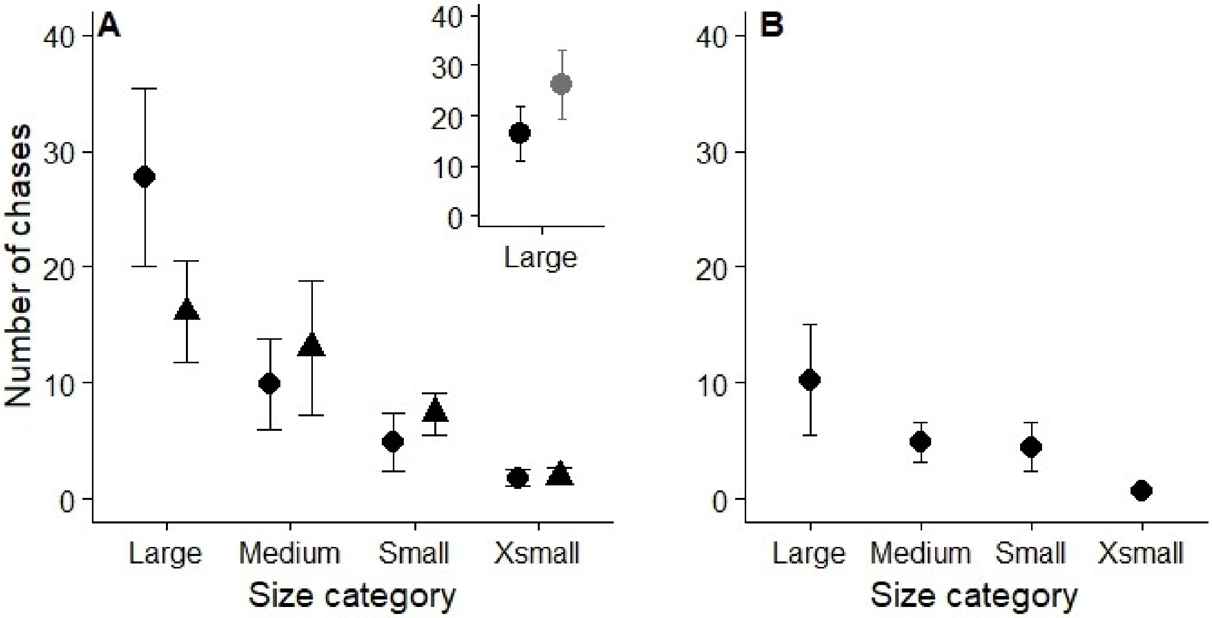


Figure 2.2: Mean (*X*, 95% C.I.'s, *N* = 9) effect of size category on chasing in groups of six fish during a) one-patch and b) two-patch feeding trials in complex and open habitats. Insert illustrates the interaction between body size and treatment order on chasing in both treatments. (legend: ● = complex habitat, ▲ = open habitat, black = complex habitat first, grey = open habitat first)

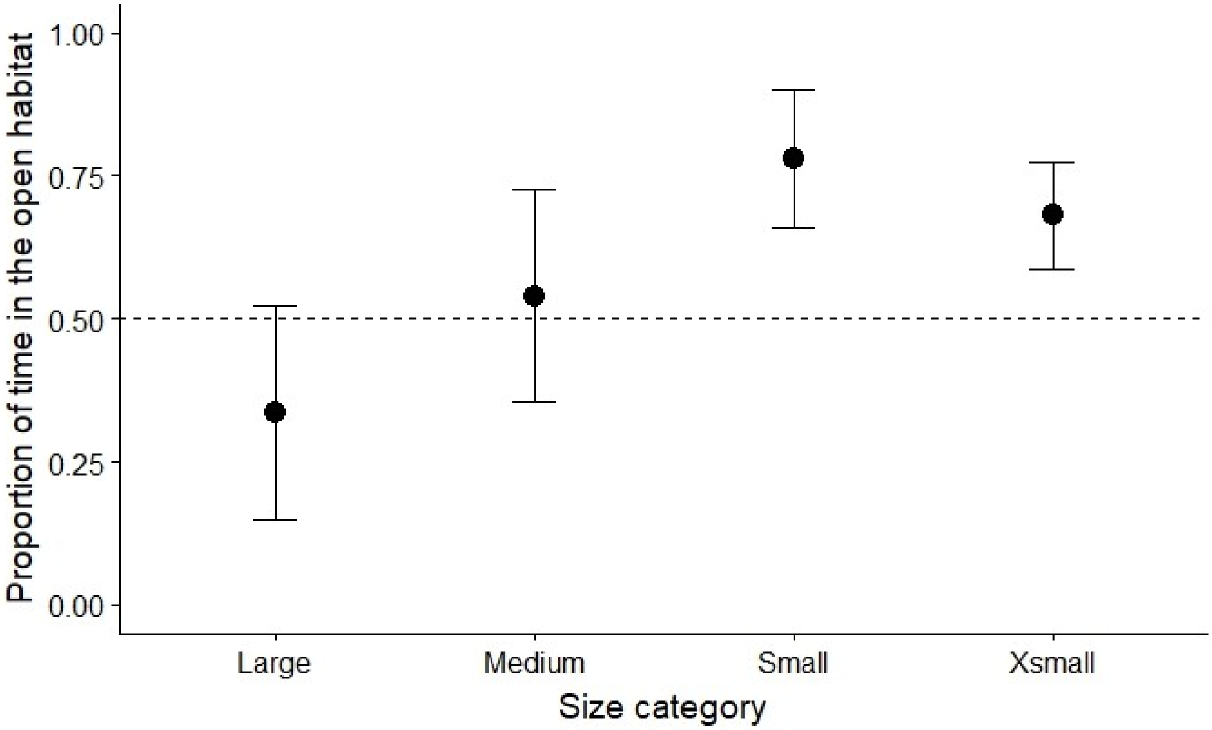


Figure 2.3: Proportion of time (*X*, 95% C.I.'s, *N* = 9) spent in the open habitat by each size category, for groups of six fish of four different sizes during food trials in the complex and open habitat in the two-patch experiment. Dashed line shows the ideal free prediction.

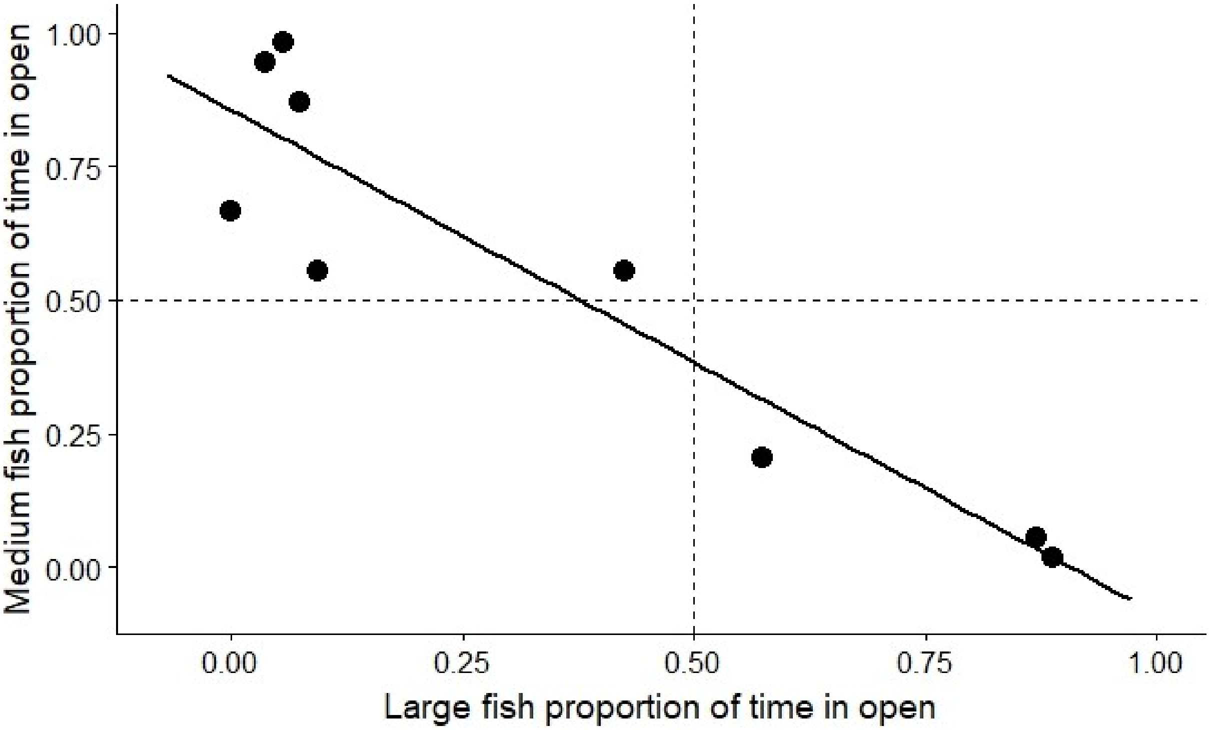


Figure 2.4: Proportion of time spent in the open habitat by the two largest fish (*N* = 9 trials) during two days of observation in the two-patch treatment. Fish were given food and access to both a complex and an open habitat. Dashed lines show the ideal free prediction.

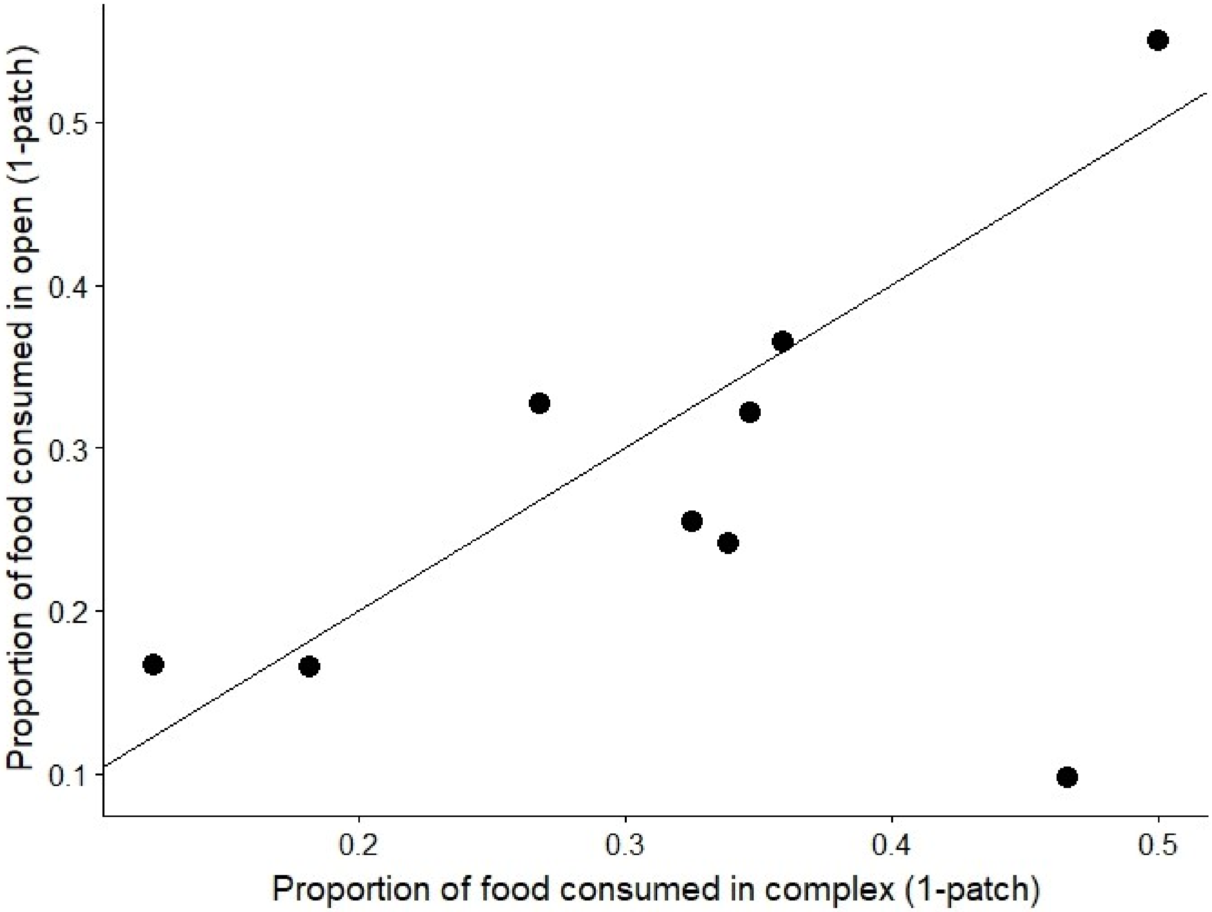


Figure 2.5: Proportion of food consumed by the Large fish in the open and complex habitat during two days of observations in the one-patch treatments (*N* = 9 fish). Line shows equal foraging success in both habitats during the one-patch treatments.

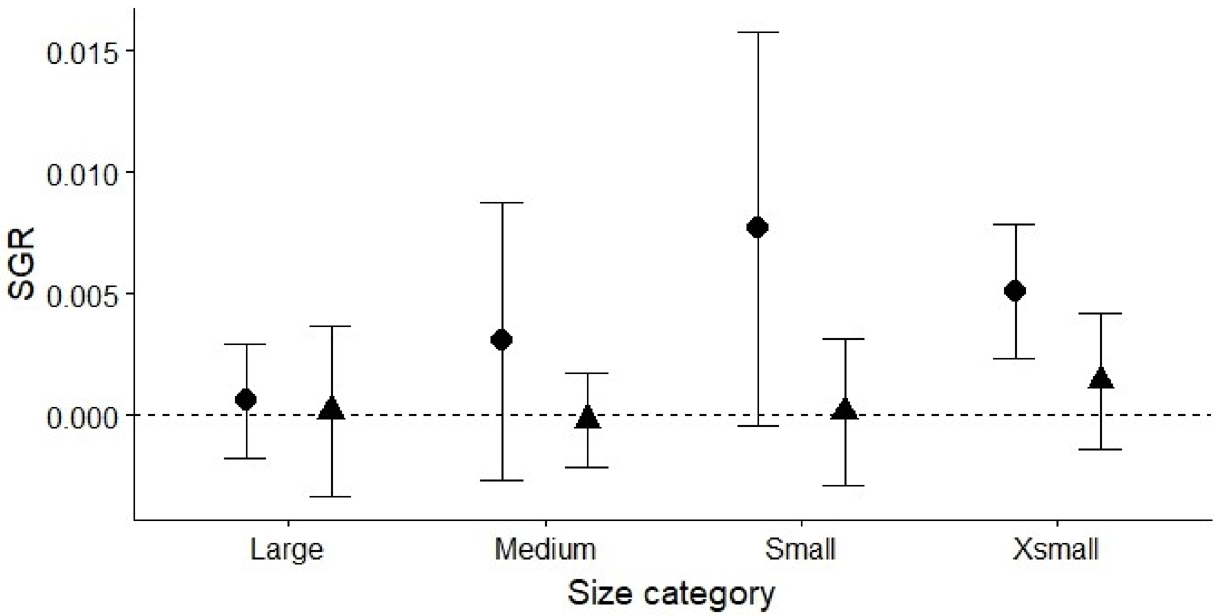


Figure 2.6: SGR (*X*, 95% C.I.'s, *N* = 9) for each size category in groups of six fish given access to an open and complex habitat in a different order in the one-patch treatments. Dashed line shows 0. (legend: ●=complex habitat first, ▲=open habitat first)

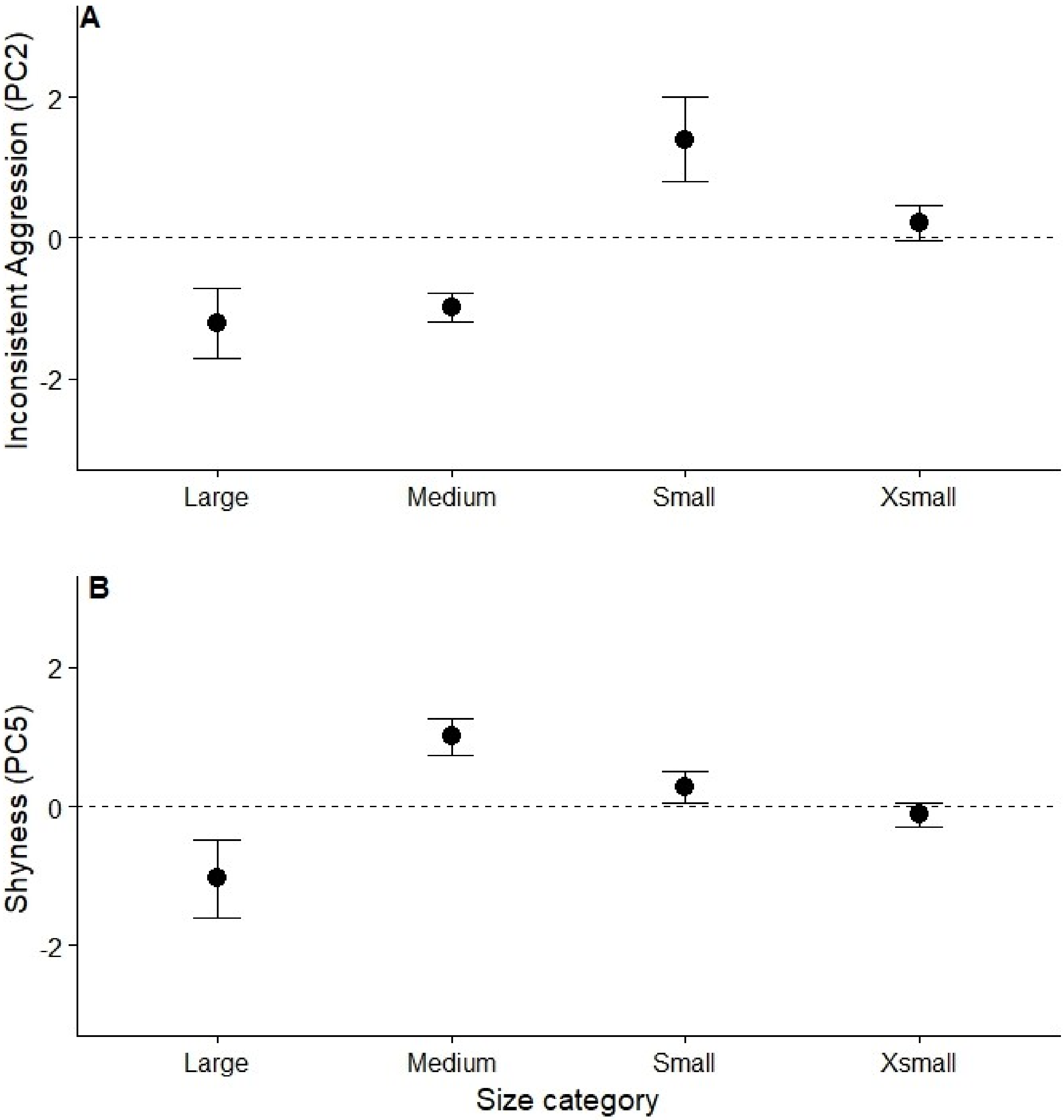


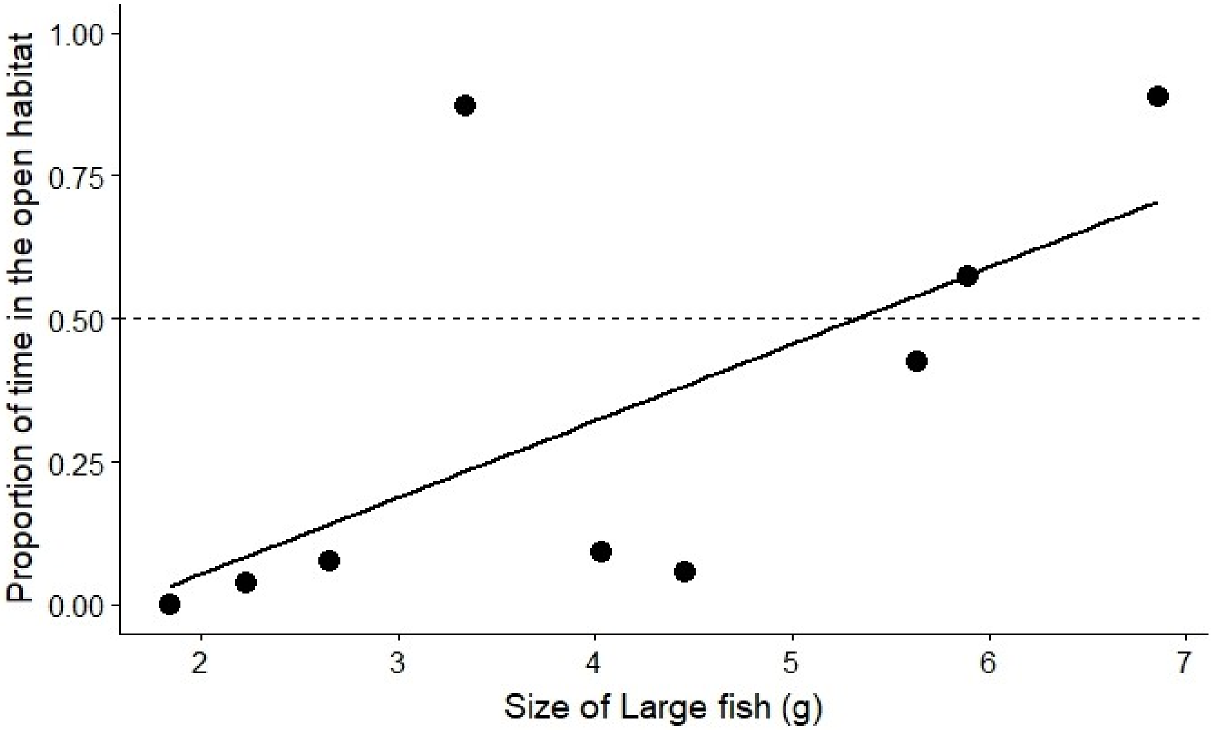
Figure 2.7: Degree of A) Inconsistent Aggression (PC 2 scores), and B) Shyness (PC 5 scores), from the individual behavioural assay, from each of four size categories. Dashed line shows 0.

Supplementary Table 2.1: Numeric values assigned to the initial response of convict cichlids to a mirror, a conspecific intruder, and an aquatic predator model.

Score	**Behaviour**
2	Swam toward, approached
1	Oriented toward
0	Neutral or no response
-1	Oriented away
-2	Swam away, hid

Supplementary Table 2.2: Numeric values assigned to the response of convict cichlids to the approach of an aquatic or aerial predator model.

Score	**Behaviour**
4	Frantic swimming
3	Move > 1 bl
2	Move <1 bl
1	Increase in fanning
0	No change in behaviour



Supplementary Figure 2.1: Initial body size of the Large fish and proportion of time spent in the open habitat during the two-patch experiment. Dashed line shows the ideal free prediction.

Chapter 3. Does increasing habitat complexity favour particular personality types of juvenile Atlantic salmon, *Salmo salar*?

ABSTRACT

The costs and benefits of a particular behavioural trait, such as boldness or aggression, may vary depending on the physical environment. We tested whether the common practice of adding physical structure (i.e. boulders) to streams to increase salmonid density has behavioural consequences, as open habitats are predicted to favour individuals that are more bold and aggressive. Wild young-of-the-year Atlantic salmon were captured from habitats of varying physical complexity and placed in to semi-natural stream enclosures for 11 days while their behaviour was observed and tested in both open and structurally complex environments. We found evidence for personality, or consistent individual behavioural differences across contexts, for avoidance and site attachment, with repeatabilities of 0.287 and 0.206, respectively, but not for activity or frequency of aggression. Fish were significantly more active and aggressive in the open habitats, and more site-attached in the complex habitats. Active and aggressive fish also grew more in the wild, while site-attached fish grew less in the wild, but more in the enclosures. However, contrary to our expectation, the complexity of the original habitat was not a significant predictor of personality. Our results suggest stream restorations involving increasing habitat complexity will alter the behaviour of young-of-the-year Atlantic salmon, but will not favour any particular personality types.

Keywords: Atlantic salmon, boulders, habitat complexity, personality, stream restoration

Complex habitats differ from open habitats by providing physical structure that can be used as refuge from the physical environment, competitors and predators (Höjesjö et al., 2004; Millidine et al., 2006), thus altering the costs and benefits of different behaviour patterns. Aggressive behaviour (Adams, 2001; Grant, 1993) is less effective in complex habitats where physical structure reduces visual contact between competitors and decreases the success of resource defence and monopolization (Basquill & Grant, 1998; Eason & Stamps, 1992). Consequently, overall levels of aggression tend to be lower in structured habitats (Höjesjö et al., 2004) in a variety of territorial species such as birds (Burger, 1974), lizards (Eason & Stamps, 1992) and fish (Danley, 2011; Imre et al., 2002). Similarly, in open habitats, bold behaviour is often rewarded through preferential access to food (Ward et al., 2004) or mating opportunities (Myhre et al., 2013), but may also increase encounter rate with predators (Grabowski, 2004; Wong, 2013). Physical structure may also obstruct movement or increase activity costs (Brownsmith, 1977; Schooley et al., 1996); accordingly, fish (Enefalk & Bergman, 2016; Radabaugh et al., 2010), primates (Jaman & Huffman, 2008) and ants (Crist & Wiens, 1994) show higher activity levels in open relative to complex habitats (but see Cenni et al., 2010). Variation in habitat complexity may also help maintain behavioural diversity within a population, by inducing spatial variation in selection pressures that facilitate the coexistence of different behavioural strategies (Brockmark et al., 2007; Höjesjö et al., 2004).

Although certain behaviours may be more effective in a particular habitat, behaviour is not infinitely plastic and can be limited by physiological, cognitive or sensory constraints (e.g. Hazlett, 1995; Johnson & Sih, 2007). Indeed, individuals often behave consistently over time or across different contexts, exhibiting personality (Réale et al., 2007). Although widespread, personality reflects a limit to plasticity, or behavioural adaptability to the environment, and may constrain optimal behaviour in certain situations (Conrad et al., 2011). Plasticity can also be its own quantifiable personality trait that varies among individuals, reflecting a trade-off between adaptability and consistency (e.g. Briffa et al., 2008). Differences in personality may also correspond to differences in life history strategy (Réale et al., 2009); accordingly, faster growth and higher fecundities are found in more aggressive, bold and active individuals across a broad range of taxa (Biro & Stamps, 2008). Differences in personality may also result in differences in habitat choice, whereby individuals with different personality traits are 'sorted' into different habitats (e.g. Duckworth, 2006; Hensley et al., 2012).

Salmonids are an excellent model system for investigating how habitat complexity may affect personality. Juvenile salmonids have personalities when observed in the laboratory (Adriaenssens & Johnsson, 2011; Höjesjö et al., 2004), and their territorial behaviour is affected by habitat structure. Physical structure is thought to increase the costs of territory defence (Eason & Stamps, 1992), causing the rate of aggression to decrease (Höjesjö et al., 2004) and territory size to shrink (Venter et al., 2008), so that complex habitats can support higher densities (Dolinsek et al., 2007a; Kalleberg, 1958). In addition, many salmonid populations that have been negatively affected by human activities are the focus of current substantive conservation efforts (Parrish et al., 1998). Salmonid restoration projects often focus on adding physical structure to the stream environment (Nislow et al., 1999), including boulders, weirs and large woody debris to create a more heterogeneous physical environment (Whiteway et al., 2010). The costs of these restoration projects range from a few thousand to a few hundred thousand dollars per project, with the majority of restorations resulting in short-term increases in salmonid abundance (Whiteway et al., 2010). However, the effect of stream restoration projects on the behaviour of the target fish has not been widely assessed (but see Enefalk & Bergman, 2016). This study will be the first, to our knowledge, to determine whether increasing habitat complexity favours particular behavioural phenotypes in the population.

In this study, we explore the relationship between habitat complexity and behaviour in young-of-the-year (YOY) Atlantic salmon, *Salmo salar*. YOY salmon were captured from habitats with varying degrees of physical complexity and placed into seminatural stream enclosures, where their behaviour was observed and tested in both an open and complex habitat. We determined whether (1) personality exists in YOY Atlantic salmon, when measured in a seminatural setting, by quantifying four aspects of personality: neophobia, aggression, shyness/boldness and activity. Body size and growth during the trial were used as correlates of fitness. If habitat sorting by personality occurs, then we would expect to see personality types, evident through individual behavioural differences observed within the enclosures, to differ in the habitat complexity of the site of capture. Specifically, we tested the predictions that (2) fish captured from open habitats would be more aggressive, bold and active than those from complex habitats. Independent of habitat of capture, we also tested the predictions that (3) fish would have higher rates of aggression, boldness and activity in the open enclosure habitat than in the complex enclosure habitat. Finally, we tested the predictions that growth rate would be higher for fish that were (4) captured from open habitats and (5) were more aggressive, bold and active.

METHODS

Enclosures

The study was conducted in Catamaran Brook, a third-order tributary of the Little Southwest Miramichi River located in Northumberland County, New Brunswick (46°53'N, 66°06'W). This pristine habitat serves as a nursery stream for a naturally reproducing population of wild salmon

(Dolinsek et al., 2007a). We used the lower 2 km of Catamaran Brook to capture fish for the experiment and to set up stream enclosures.

YOY salmon were captured with dip-nets while snorkelling in sites of varying habitat complexity. While we could not capture every fish that was encountered, our success rate was similar in both habitats. Hence, any bias in personality caused by our sampling method was likely similar in both habitats. All sites of capture were marked with a small numbered cobble, and fish were placed individually into covered plastic bins (35.6 × 20.3 × 11.7 cm) on the side of the stream. Water within the bins was refreshed at regular intervals to maintain a constant temperature. Our measure of habitat complexity at the site of capture was the mean visual distance measured in eight cardinal directions (N, NE, E, SE, S, SW, W, NW) to a maximum of 100 cm, with the upstream direction selected as North. Water depth was also measured at each of these locations.

All fish were weighed to the nearest 0.01 g, and fork length measured to the nearest 0.5 mm (mean ±SD: weight: 0.79 ± 0.42 g; length: 3.83 ± 0.59 cm). Fish were then tagged subcutaneously with elastomer in one of three colours (pink, orange, green) in one of three different body regions (upper-dorsal, mid-dorsal, caudal), such that each fish's tag was visible from above. Fish were given approximately 1 h to recover from tagging in the bins before being released into the enclosures.

A total of six enclosures (4 × 1 × 1 m) were used at a given time with six fish per enclosure, a population density typical in high-density regions in the stream (Imre et al., 2005). Substrate for each enclosure consisted of gravel (<5 cm in diameter), small cobbles (5–7 cm in diameter) and boulders (~20 cm in diameter) obtained from the surrounding stream bed. Each enclosure was randomly chosen to initially have either an open or complex habitat. For both treatments (hereafter habitats), gravel and small cobbles were added to the bottom of the enclosures. Boulders were added at a density of 6 per m^2 to the complex habitats (Dolinsek et al., 2007a; Dolinsek et al., 2007b), for a total of 24 well-spaced boulders within each complex enclosure.

Groups of six fish were added to each enclosure. The original design was to capture fish from extreme habitats (i.e. open versus complex) and place three fish from each habitat into each enclosure. However, due to the low densities of YOY (K. D. W. Church, personal observation), we captured fish from a variety of habitats (see Results) and placed them into the enclosures in the approximate order of capture (see Results), to minimize the time fish spent in the covered bins. The six enclosures were used three times with different salmon, for a total of 18 replicates over the period of July to August 2015. The shallow depth (mean ±SD: 19.4 ± 8.4 cm, $N = 18$) in the enclosures allowed the fish to be clearly seen when viewed from above. Nylon cords were strung between the support posts at the corners of each enclosure to determine the x,y coordinates of all possible locations within the enclosure. Enclosures were open on top, leaving the fish exposed to some of their natural predators, including fishing spiders (*Dolomedes triton*) and kingfishers (*Megaceryle alcyon*), although aquatic predators, such as brook trout, *Salvelinus fontinalis*, were excluded. Personality tests were conducted daily on all visible fish, excluding acclimation periods and days with inclement weather.

Fish were given 48 h to acclimate to the enclosures before observations began. After all visible fish were observed (see below) on two separate occasions within the initial treatment, a period that ranged from 3 to 5 days depending on the weather and visibility, the habitats were switched. Large boulders were removed from the complex habitats and added to the open habitats, while the fish remained in the enclosures. Fish were given 24 h to acclimate to their new habitat before observations recommenced. After all visible fish were observed twice in the second habitat, all fish were removed from the enclosures, and reweighed and remeasured before being released. Most trials were 11 days in duration, to give fish approximately equal time in each treatment; however, several trials were extended by a few days due to inclement weather (mean ±SD = 11.2 ± 0.6 days, range 11–14 days).

Our study was approved by the Concordia University Animal Research Ethics Committee (protocol number 30000246) in accordance with the guidelines of the Canadian Council on Animal Care and the ASAB/ABS Guidelines for the use of animals in research.

Behavioural Observations

Fish within the enclosures were observed from above, while either standing or sitting next to the enclosure, depending on visibility. A focal fish was randomly chosen from any visible fish with discernible tags, which ranged from one to five fish at any given time, and then individually observed for a period of 10 min. The location, and position changes, or movement, were noted, as well as the location and duration of any hiding behaviour, when the focal fish ceased to be visible to the observer. While the fish was hidden, the enclosure was scanned at frequent intervals to record the location and time of emergence. The initial location of the focal fish and all further changes in location were recorded to the nearest 5 cm using the *x,y* axes along the perimeter of the enclosures. After the completion of the observation, the observer would continue testing the same fish (see below) until it disappeared, at which point another focal fish would be selected and observed.

Following the observation, three ‘personality tests’ were conducted for each focal fish. Fish were presented with a novel object, a mirror simulating the approach of a conspecific, and two predator models (a brook trout and a fishing spider), as described below. Observations and personality tests were conducted on a total of 30 fish in both the open and complex habitats: 24 fish were observed and tested twice in each habitat; three fish were observed and tested three times in the open habitat and twice in the complex habitat; and, an additional three fish were observed twice in the open habitat and once in the complex habitat. Our sample size of 30 individuals is sufficient for calculating behavioural repeatability across contexts with a statistical power of 80% (Dingemanse & Dochtermann, 2013). The identity of the fish chasing or being chased was noted throughout the observation and test period and was used to quantify aggression. Chases were defined as a unidirectional burst of movement of one fish towards another, and no differentiation was made between fish with open and closed mouths (Weir et al., 2004). Water temperature and the mean of three measures of surface velocity per enclosure were also noted for each day of behavioural testing.

Personality tests

(1) A novel object in the form of a 7 cm long rubber worm was attached to a 30 cm metal stick. The initial location of the focal fish was noted, then the worm was introduced into the water about seven body lengths lateral to the focal fish and approached at a speed of approximately one body length per second. The closest distance of the novel object to the focal fish before it fled, the flight initiation distance (FID), was recorded, as was the latency to emerge from hiding and the location of emergence. Distance fled was calculated as the distance between the original and emergence locations. Fish were observed for a 10 min period, or until they returned to their original location. Multiple worms in distinct colours and body shapes were used to ensure novelty with repeated tests.

(2) A mirror 7 cm in diameter with a handle 15 cm in length was slowly introduced from the side, similar to Höjesjö et al. (2004, 2011). The mirror was introduced approximately seven

body lengths lateral to the focal fish, at an angle that allowed the focal fish to observe its approaching reflection at an approximate speed of one body length per second. The original location of the focal fish, the FID between the mirror and the fish, the latency to emerge to a maximum of 10 min and the emergence location were again recorded.

(3) Life-sized models of two common aquatic predators of YOY salmon were introduced sequentially to the focal fish: a brook trout (Symons, 1974) and a fishing spider (Nyffeler & Pusey, 2014). The predator models were placed approximately seven body lengths lateral to the focal fish, angled diagonally, and approached from the side at an approximate speed of one body length per second. The original location of the fish, the FID between the fish and predator models, the latency to emerge within a 10 min period and the emergence location were recorded for both models.

Our intention was to test for three distinct personality traits: neophobia, aggression and boldness. However, fish did not inspect the novel object or behave aggressively towards the mirror, indicating a more generalized neophobic response (see Results). Highly aggressive, bold and non-neophobic fish are predicted to chase other fish frequently, rarely hide, have a low FID and short flight distance, and quickly return after exposure to the novel object, the mirror and the predator models. In contrast, nonaggressive, shy and neophobic fish are predicted to be chased and to hide frequently, and to show a high FID, large flight distance and long return latency in response to the novel object, mirror and predator models.

Statistics

A single principal component analysis (PCA) was used on a correlation matrix of the behaviours from all assays with the package ‘FactoMineR’ (Le et al., 2008) to reduce the number of behavioural variables and to ascertain the relationships between them, in order to identify any correlated behavioural traits, or potential behavioural syndromes (Sih et al. 2004). The statistical significance of all principal components was then determined using the 'InPosition' package in R (Beaton et al., 2014), which uses permutation procedures (Peres-Neto et al., 2005). Significant principal components were then used in mixed models as the response variable. The PCA was completed with both raw and standardized data (i.e. *z* score), with identical results.

Maximum likelihood mixed models were constructed with the package 'lme4' (Bates et al., 2014) and used to test the predictions that the habitat complexity of the site of capture and the enclosure would affect personality and plasticity. Initial models had seven fixed factors: date, water temperature, openness and depth of capture site, enclosure treatment, mean velocity and observation number (1–4) to account for possible habituation (Martin & Réale, 2008), and two random factors: individual ID and enclosure ID. All continuous fixed effects were standardized via *z* transformations. Backwards stepwise multiple regression with analysis of variance likelihood ratio tests were used to determine variable retention ($\alpha = 0.05$) for all fixed effects. Retained fixed effects were then used in two nested candidate models with different random effects: model 1 only accounted for the effect of the enclosures, while model 2 accounted for both an enclosure effect as well as individual differences. The existence of personality was then verified by comparing the two candidate models using likelihood ratio tests with the 'lmtest' package (Zeileis & Hothorn, 2002). Final models were then used to calculate best linear unbiased predictors (BLUPs) for the intercepts of the random effects, which were subsequently used as individual behavioural profiles. BLUPs are the preferred method when calculating standard values for individual morphological or behavioural traits measured repeatedly over time (Martin & Pelletier, 2011).

Repeatability, or the degree of behavioural variation due to individual differences, was calculated for each composite behavioural trait from each final mixed model using the formula for the intraclass correlation coefficient:

$$r = s\mathrm{A}^2/s^2 + s\mathrm{A}^2$$

with $s\mathrm{A}^2$ representing variance among individuals, and s^2 representing the residuals, or variance within individuals (Falconer & Mackay, 1996). Confidence intervals for the repeatabilities were obtained from parametric bootstrapping estimates using the 'rprR' package (Stoffel et al., 2017).

Growth during the trial was calculated using the formula for specific growth rate (SGR):

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

with mass (M) measured in grams, and time (t) measured in days (Ricker, 1975). Specific growth rate and body size are both reliable fitness proxies linked to survival in juvenile Atlantic salmon, especially overwinter survival (Gardiner & Geddes, 1980; Perez & Munch, 2010). Fish consume energy stores and lose weight over the winter (Egglishaw & Shackley, 1977), so that smaller fish, or those that grow more slowly, have a reduced capacity for energy storage and suffer higher mortality (Gardiner & Geddes, 1980). For fish that do survive their first winter, slower growth and lower energy stores may also lead to a delay in the time until smolting or maturity; however, these body size and growth differences would not yet be discernible in the fish we used in our study (Metcalfe et al., 1988).

SGR was used as a correlate of fitness during the trial, while residuals of initial body weight and date (to correct for the effect of date on body size) were used as a correlate of fitness in the wild. Generalized linear models were constructed with fitness correlates as the response variables, and the BLUPs for each behavioural trait were included as fixed effects. Final models were again reduced using backwards stepwise multiple regression, with analysis of variance likelihood ratio tests. All statistical analysis were performed in R (R Core Team, 2015).

RESULTS

Habitat Complexity

The 108 fish used in this study were captured from habitats that varied in mean visual distance from 10.9 to 100 cm (mean ±SE = 55.3 ± 18.4 cm, $N = 108$; Fig. 3.1a). To assess personality, we observed 30 of these 108 fish in both habitats in the enclosures. These 30 fish were a representative sample of the 108, in terms of habitat complexity, with visual distances that varied from 23.4 to 100 cm (mean ±SE = 57.7 ± 17.7 cm, $N = 30$). The mean (t test: $t_{48.3} = 0.72$, $P = 0.48$) and distribution (Kolmogorov–Smirnov test: $D = 0.13$, $N_1 = 30$, $N_2 = 108$, $P = 0.84$) of visual distances in the two samples did not differ significantly (Fig. 3.1a, b).

Behavioural Traits

Contrary to our expectations, the behavioural tests did not measure qualitatively different behavioural traits, as fish showed a more generalized neophobic response across the different contexts (Table 3.1). Subsequently, we used a principal components analysis to reduce the 16 behavioural variables from the observation and tests into three composite behavioural traits (Martin & Réale, 2008) with significant ($P = 0.01$) eigenvalues (Table 3.1). The first composite behavioural trait, PC1, was associated with activity and aggression, with high rates of movement, high FIDs with short emergence latencies and a high rate of aggression with conspecifics. The second trait, PC2, was associated with avoidance, high FIDs, short distances fled and long emergence latencies, while the third trait, PC3, was associated with site attachment and short distances fled. Hereafter, we will refer to the three PC axes as ‘activity and aggression’, 'avoidance' and 'site attachment', respectively.

Factors Influencing Behaviour

Contrary to the prediction of habitat sorting, none of the composite behavioural traits were affected by habitat complexity at the site of capture, and no interaction was found between the habitat complexity of the original sites and the enclosures; this variable was not retained for any of the final models (Table 3.2). However, the behaviour of focal fish in the enclosures differed significantly between the open and complex habitats. In accordance with our predictions, activity and aggression was higher (Fig. 3.2a) and site attachment was lower (Fig. 3.2c) in the open habitat than in the complex habitat. Contrary to our predictions, however, avoidance did not differ significantly between habitats (LMM: $t_{88.9} = -1.65$, $P = 0.103$; Fig. 3.2b).

Regarding abiotic variables within the enclosures, the influence of date and velocity differed among the behavioural traits (Table 3.2). Activity and aggression decreased over the summer, as did site attachment, indicating that fish moved less as the summer progressed but fled farther when disturbed. Site attachment was also lower in faster velocities, with fish moving farther in faster currents.

Quantifying Personality

YOY salmon exhibited significant, repeatable behaviour over time for avoidance and site attachment but not for activity and aggression (ANOVA, model 2 versus model 1: $\chi^2_1 = 0.84$, $P = 0.36$; CIs: 0.000, 0.302). Individual differences were found for avoidance (ANOVA, model 2 versus model 1: $\chi^2_1 = 8.84$, $P = 0.003$) with a repeatability of 0.287 (CIs: 0.049, 0.481), and for site attachment (ANOVA, model 2 versus model 1: $\chi^2_1 = 5.08$, $P = 0.024$), with a repeatability of 0.206 (CIs: 0.001, 0.429).

Personality and Growth

Contrary to our predictions, the SGR of focal fish during trials was not higher for active and aggressive fish (LM: $t_{25} = 0.02$, $P = 0.98$) or lower for avoidant individuals (LM: $t_{25} = -1.36$, $P = 0.19$). SGR was higher for site-attached fish (LM: $t_{25} = 2.19$, $P = 0.039$). As predicted, initial body size, or growth rate in the wild, was positively associated with higher activity and aggression (LM: $t_{26} = 2.23$, $P = 0.035$), but, contrary to our predictions, was not related with avoidance (LM: $t_{26} = 0.63$, $P = 0.54$). Site-attached fish were also smaller initially (LM: $t_{26} = -2.72$, $P = 0.012$). No significant relationships were found between growth and original body size (LM: $t_{27} = -1.07$, $P = 0.29$), or the characteristics of the site of capture.

DISCUSSION

Our study shows that YOY Atlantic salmon have personality, or consistent individual behavioural differences across contexts (Réale et al., 2007), for avoidance and site attachment, traits which reflect a generalized neophobic response. Avoidance was characterized by high FIDs, short distances fled and long emergence latencies in response to stimuli, which are often typical of shy fish (e.g. Bell, 2005; Ydenberg & Dill, 1986), while site attachment was characterized by inconsistencies in shy or bold responses while remaining close to the site of origin. Although habitat complexity can induce a plastic behavioural response in YOY salmon, this behavioural response is not mutually exclusive with the maintenance of individual differences in personality. Contrary to our predictions, habitat complexity of the site of capture was not a significant predictor of personality. Within the enclosures, behaviour differed between the open and complex habitats, with activity and aggression higher in the open habitat, and site attachment higher in the complex habitat. Higher activity and aggression levels predicted higher growth in the wild, whereas increased site attachment predicted higher growth during the trials but lower growth in the wild. In summary, our study demonstrates that YOY Atlantic salmon: (1) exhibit personality across open and complex habitats when observed in a seminatural setting, (2) show no evidence for habitat sorting by personality, (3) alter their behaviour in response to habitat complexity and (4) exhibit a link between fitness and personality.

Activity and aggression, one of the three axes of behaviour found in our study, were included among the five personality trait categories summarized by Réale et al. (2007). Additionally, avoidance is associated with shyness, while site attachment can also be considered as a correlate of territory size. The repeatability of our two behavioural traits ranged from 0.206 to 0.286, within the range of the average repeatability of 0.370 found for behavioural traits (Bell et al., 2009). Although repeatability is used to quantify behavioural consistency over both time and contexts, time-related changes are not directly accounted for, resulting in a lower statistical power when quantifying change over time (Biro & Stamps, 2015). However, this warning is less relevant to our study, as it focused on individual behaviour that occurred across contexts, with brief intervals between the behavioural observations. Our study is one of the first to assess salmonid personality through direct behavioural testing conducted in a seminatural environment. Previous studies of personality in salmonids have found that fitness or social status observed in the wild is not easily predicted by behavioural measures obtained in a laboratory (Adriaenssens & Johnsson, 2011; Höjesjö et al., 2011; Závorka et al., 2015), while studies that assess personality in the wild have been largely confined to more passive observations of behaviour (Härkönen et al., 2014; Taylor & Cooke, 2014).

Contrary to our predictions, avoidant or bold/shy behaviour did not differ between the complex and open habitats, although activity and aggression were higher in the open habitat. Similar results were found in a previous study on Atlantic salmon at the same location, with aggression decreasing in complex habitats (Bilhete & Grant, 2016). However, contrary to our findings, brown trout, *Salmo trutta*, showed no significant differences in aggression between habitats, although activity was higher in the open habitat (Enefalk & Bergman, 2016). Consistent with our results, bluegill sunfish, *Lepomis macrochirus*, and golden shiner, *Notemigonus crysoleucas*, do not adjust their boldness or distance from a muskellunge predator (*Esox masquinongy*) in open relative to complex habitats (Deboom & Wahl, 2013).

Previous research suggests that salmonid fry adopt one of two distinct behavioural strategies shortly after emergence, with larger, more active and aggressive individuals quickly establishing and defending a territory, while smaller, less active individuals passively dispersing downstream, away from sites of high competition (Näslund & Johnsson, 2016; Skoglund & Barlaup, 2006). Although we also found that active fish were larger and more aggressive, they were not more site-attached, and did not exhibit a more territorial behavioural strategy. Avoidant fish did not show lower fitness before or during the trials, although more aggressive and active fish were larger initially. These data suggest that different life histories may not be driving personality differences for these traits (Biro & Stamps, 2008). However, fish with higher fitness in the wild were less site-attached, indicating larger territories, a measure of competitive success in territorial species. Although territory size was not explicitly measured in this study, higher site attachment in complex habitats corresponded to the prediction that individuals would have smaller territories in complex habitats (Eason & Stamps, 1992). Similarly, a closely related behaviour, site fidelity, or time spent within a given territory, is also a repeatable behavioural trait (Harrison et al., 2015) found to be higher for juvenile Atlantic salmon in more complex habitats (Reid et al., 2012). Although dominant individuals may have a competitive advantage in simple laboratory habitats (Thorpe et al., 1992; Yamamoto et al., 1998), this benefit can disappear in complex and unpredictable habitats (Basquill & Grant, 1998; Grand & Grant, 1994; Reid et al., 2012), or even reverse (Höjesjö et al., 2004). Hence, fish with lower fitness in the wild appeared to gain a competitive advantage while in the enclosures, while fish with higher fitness in the wild appeared to lose their competitive advantage during the trials.

Habitat sorting by size or personality did not occur in our study, as no significant relationships were found between habitat complexity of the original site and personality or growth rate. Contrary to our findings, bolder sea anemones, *Condylactis gigantean* (Hensley et al., 2012) settle in more open habitats, as do more aggressive bluebirds, *Sialia mexicana* (Duckworth et al., 2006). More research is needed to determine whether habitat sorting by personality occurs in salmonids.

Overall, our study demonstrates that the addition of physical structure to streams has a significant effect on Atlantic salmon behaviour, but a negligible effect on personality. The complexity of the open and complex enclosure habitats were ecologically relevant to the study site, Catamaran Brook (Fig. 3.1a). The complex habitats, with an average visual distance of approximately 35 cm, represented a commonly used habitat in the wild, whereas the open habitats, with a mean visual distance closer to 100 cm, represented a more extreme habitat type. Although very open sites were rare in our pristine study site, they are likely to be abundant in more degraded streams. Habitat loss is one of the primary causes of salmonid population decline (e.g. Gibson et al., 2011; Koljonen et al., 2013). However it may not be the destruction of the habitat per se that is most damaging, but the transformation of a dynamic freshwater habitat to one that is increasingly uniform in both space and time (Beechie & Bolton, 1999). As opposed to the simplification of natural habitats that is often a result of anthropogenic effects, the addition of physical complexity to stream habitats successfully increases population density (Dolinsek et al., 2007a; Whiteway et al., 2010). Our results imply that the many beneficial aspects of increasing habitat complexity for stream salmonids will affect their behaviour in predictable ways but will not favour any particular personality type.

Table 3.1

Retained principal components representing composite behavioural traits from 16 behavioural variables obtained from 10 min observations and four personality tests of focal fish conducted at least twice (*N* = 27) or at least once (*N* = 3) in the open and complex enclosure habitats

Variables	PC 1	PC 2	PC 3
Observation – movement	**0.560**[1]	-0.106	0.266
Observation – hiding	-0.210	0.212	0.026
Novel object – FID	**0.354**	**0.511**	0.284
Novel object – latency to emerge	**-0.490**	**0.328**	**0.329**
Novel object – distance fled	0.256	**0.596**	-0.291
Mirror test – FID	**0.335**	**0.379**	0.218
Mirror test – latency to emerge	**-0.319**	**0.498**	0.134
Mirror test – distance fled	-0.050	0.225	**-0.621**
Fish predator – FID	**0.623**	0.157	**0.343**
Fish predator – latency to emerge	**-0.403**	**0.448**	0.129
Fish predator – distance fled	0.081	**0.349**	**-0.600**
Spider model – FID	**0.460**	0.219	**0.404**
Spider model – latency to emerge	**-0.447**	0.263	**0.353**
Spider model – distance fled	0.230	**0.399**	**-0.405**
Number of times – chasing fish	**0.468**	-0.072	-0.059
Number of times – chased by fish	**0.398**	-0.033	-0.228
Eigenvalue	2.41	1.85	1.80

P	0.01	0.01	0.01
% Total variance	15.04	11.58	11.24
Cumulative proportion of variance	15.04	26.62	37.86

FID: flight initiation distance.

[1] Coefficients larger than 0.3 in absolute value are indicated in bold, and indicate behaviours characteristic of each composite behavioural trait

Table 3.2

Significant fixed effects of the final mixed models[1] ($N = 30$) that predicted the behaviour of young-of-the-year salmon in open and complex habitats in enclosures

Composite behavioural trait	Fixed effects	Coefficient	SE	*t*	*P*
Activity and aggression	Habitat[2] – open	0.677	0.305	2.22	0.035
	Date	-0.685	0.141	-4.88	0.00001
Site attachment	Habitat – open	-1.168	0.190	-6.16	<0.00001
	Velocity	-0.018	0.007	-2.47	0.016
	Date	-0.394	0.144	-2.74	0.010

[1] Final models were reduced using backwards stepwise multiple regression with analysis of variance likelihood ratio tests and were used to calculate repeatabilities and individual behavioural profiles (BLUPs).

[2] Habitat refers to differences between treatments in the enclosures.

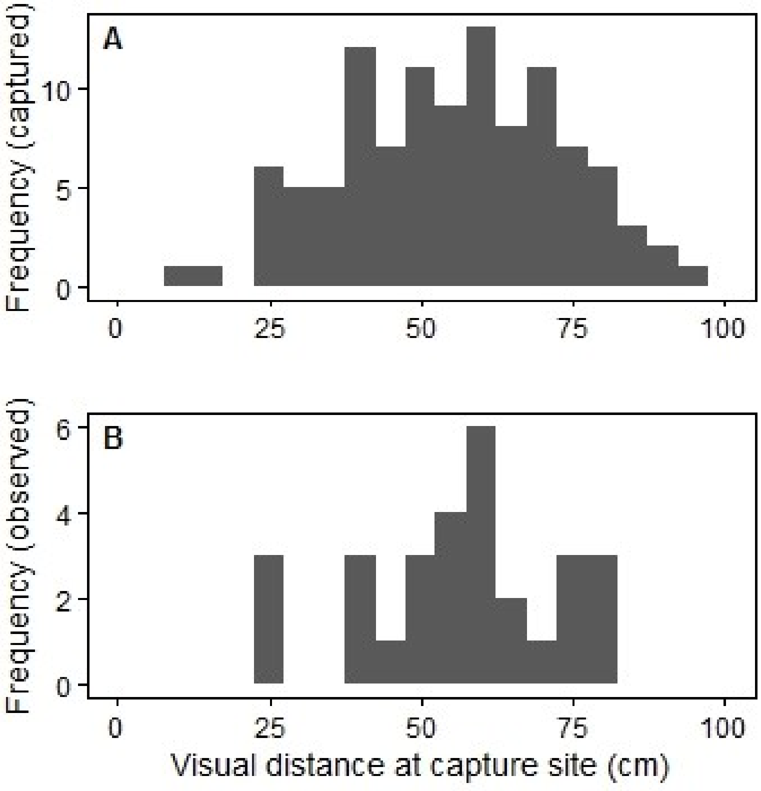


Figure 3.1. Frequency distributions of young-of-the-year Atlantic salmon (a) captured (*N* = 108) and (b) observed at least once in both enclosure habitats (*N* = 30), in relation to visual distance at the original capture location in Catamaran Brook.

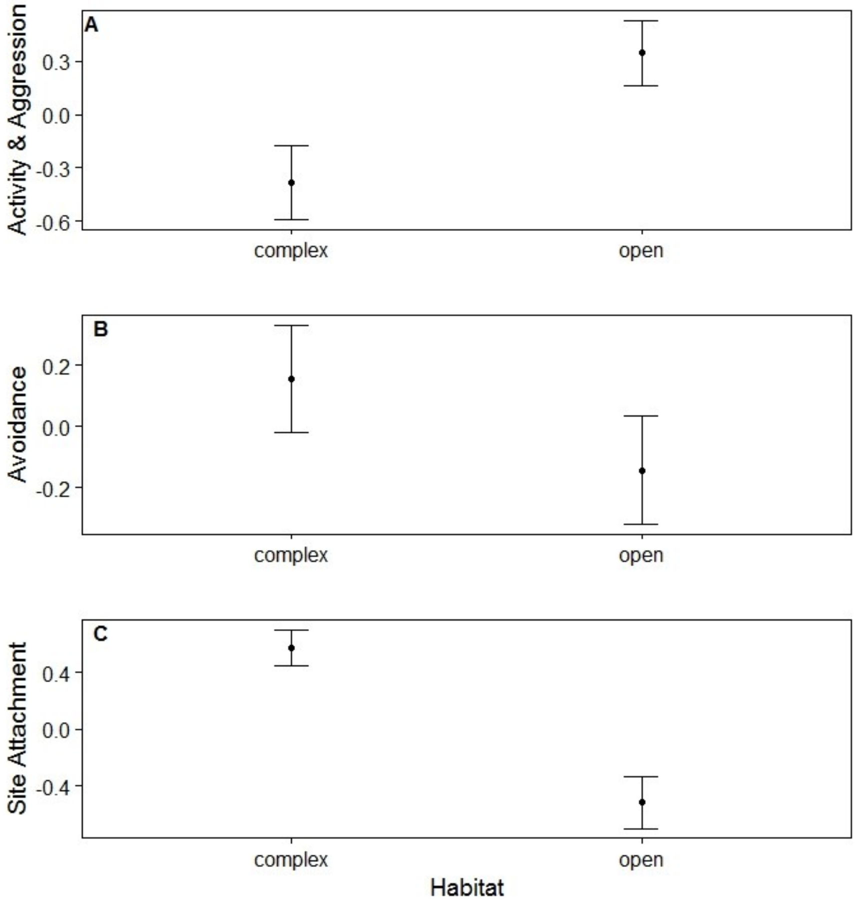


Figure 3.2. Mean ±SE (*N* = 30) (a) activity and aggression (PC1 scores), (b) avoidance (PC2 scores) and (c) site attachment (PC3 scores) behaviour of wild young-of-the-year Atlantic salmon captured from habitats of varying complexity and observed in open and complex seminatural enclosure habitats.

Chapter 4: A meta-analysis of the effects of habitat complexity and territoriality on foraging, aggressive and social behaviour

Abstract

The addition of structure to increase habitat complexity is frequently used to increase the population density of territorial species and to reduce aggression among captive animals. However, it is unknown if territorial species in general are uniquely affected by habitat complexity. We conducted a meta-analysis to compare the behaviour of a wide range of territorial and non-territorial taxa in complex and open habitats in order to determine the effects of habitat complexity on 1) territory size, 2) population density, 3) rate and time spent on aggression, 4) rate and time devoted to foraging, 5) rate and time of activity, 6) shyness, 7) survival rate, 8) exploration behaviour, and 9) social behaviour. Overall, habitat complexity significantly affected all measures except shyness and sociality, while territorial and non-territorial species tended to respond differently to complexity. Territorial species showed lower aggression, foraging, and activity in complex habitats, while non-territorial species showed the opposite pattern, with higher aggression, foraging, and activity in complex habitats. The effects of habitat complexity on density and activity were strong and highly predictable for territorial species, with consistent increases in density and decreases in activity. Survival of territorial species remained unaffected by complexity, while in contrast, non-territorial species suffered less mortality in complex habitats, thereby suggesting that they experience less predation risk in open habitats. This meta-analysis demonstrates that territorial and non-territorial animals respond differently to habitat complexity, likely due to territorial species strong reliance on visual cues.

Introduction

Abiotic and biotic components of habitat complexity play important roles in a variety of aquatic and terrestrial ecosystems. Invertebrates, fish, reptiles, birds and mammals are affected by many natural forms of habitat structure, including boulders in streams (Kemp et al. 2005; Venter et al. 2008), vegetation in lakes, grassland and forests (Bhat et al. 2015; Kruidhof et al. 2015; Lassau et al. 2005), coral in coral reefs (Geange & Stier 2010; Kok et al. 2016), as well as substrate and nest material (Fuller et al. 2010; Hutchinson et al. 2012). Animals are also affected by artificial structures in zoos, experimental, and farm settings, such as dividers (Eason & Stamps 1992; Hasegawa & Maekawa 2009; Ninomiyo & Sato 2009), bricks (Baird et al. 2006; Jensen et al. 2005), straws (Lukasik et al. 2006), tires (Miranda-de la Lama et al. 2013), hammocks and pulleys (Anderson 2016), barrier perches (Ventura et al. 2012), and dowels (Bartholomew et al. 2000).

Habitat complexity is predicted to affect the behaviour of animals in a variety of ways. In territorial species, the reduced visual distance in complex habitats increases the costs of territorial defence, resulting in smaller predicted territory sizes (Prediction 1, Table 4.1; Eason & Stamps 1992; Imre et al. 2002) and higher population densities (Prediction 2, Table 4.1; Semmens et al. 2005; Venter et al. 2008). Consequently, the theory on how habitat complexity affects behaviour is perhaps better developed for territorial than non-territorial species (e.g. Clayton 1987; Sundbaum & Näslund 1998; Venter et al. 2008).

By reducing visual distance, increasing habitat complexity is also predicted to decrease the encounter rate between conspecifics, leading to lower rates of, or time devoted to, aggression (Prediction 3, Table 4.1; Chaloupkova et al. 2006; Clayton 1987; Danley 2011). Similarly, the reduced visual distance will decrease encounter rates with potential prey (Kemp et al. 2005), and may also interfere with movement (Butler & Gillings 2004), leading to lower foraging rates or times (Prediction 4, Table 1; Kemp et al. 2005; but see Laegdsgaard & Johnson 2001). Although prey detectability and capture tends to be impeded in complex habitats, this effect is more pronounced for actively hunting predators. Indeed, ambush predators that rely more on camouflage or surprise, may use habitat strucuture to their advantage (Flynn & Ritz 1999; Skov & Koed 2004). Hence, complex habitats may benefit predators that employ sit-and-wait strategies (Prediction 4, Table 4.1; Eklöv & Diehl 1994; Flynn & Ritz 1999). Moreover, an increase in habitat complexity may provide more surface area for prey, increasing food abundance (Laegdsgaard & Johnson 2001; Venter et al. 2008), which leads to higher foraging rates (Prediction 4, Table 4.1: Semmens et al. 2005; Wilkinson & Feener 2007).

Because smaller territories and complex habitats constrain or slow the movements of animals, activity rates and times are predicted to be lower in complex habitats (Prediction 5, Table 4.1; Blakey et al. 2017; Sundbaum & Naslund 1998). Animals may also experience lower physiological distress while in complex habitats (Fischer 2000; Millidine et al. 2006), likely due to complex habitats being safer in terms of predation risk (Church & Grant submitted; Gilliam & Fraser 2001). Animals are often attracted to complex habitats for anti-predator reasons, as complexity may decrease the risk of more conspicuous behaviour by providing refuges from predators (Orpwood et al. 2008) and reducing predator efficiency (Candolin & Voigt 2001; Kaiser 1983; Wong 2013). If predation risk is indeed lower, then individuals may engage in riskier behaviour in complex habitats – i.e. shy behaviour, or tendency to avoid risk (Wilson 1993), will be lower in complex habitats (Prediction 6, Table 4.1; e.g. Orpwood et al. 2008). Alternatively, complex habitats may attract individuals with shyer personalities (e.g. Hensley et al. 2012; Wilson et al. 1993), leading to shyer behaviour in these habitats (Prediction 6, Table 4.1).

Additionally, lower foraging success in complex habitats also indicates that from a prey individual's point of view, predation risk should also be lower. Hence, the survival rate of animals should be higher in complex habitats (Prediction 7, Table 4.1; Bartholomew et al. 2000; Hovel & Lipcius 2001; Laegdsgaard & Johnson 2001). However, the opposite effect is expected for species preyed upon by ambush predators, which should have lower rates of survival in complex habitats (Prediction 7, Table 4.1; Eklöv & Diehl 1994; Flynn & Ritz 1999).

From an animal welfare point of view, complex "artificial" habitats, found in zoos, agricultural facilities and laboratory environments, are more "enriched" from a structural point of view (Naslund & Johnsson 2016), and may promote more exploratory behaviour, or positive reactions toward novel objects (Prediction 8, Table 4.1; Mettke-Hofmann et al. 2002). Similarly, as exploratory behaviour is negatively related to risk of predation (Russell 1973), then it may increase in relatively safer, complex habitats. Alternatively, if shyer, more neophobic individuals settle in complex habitats (e.g. Wilson et al. 1993), then exploration will decrease (Prediction 8, Table 4.1). Additionally, exploratory behaviour may also be positively correlated with movement (e.g. Cenni et al. 2010), and may be likewise impeded by habitat complexity (Prediction 8, Table 4.1). It is largely unknown how habitat complexity affects sociality, or time spent associating with a known conspecific, including play behaviour. However, if sociality is the opposite of aggressive behaviour, then we might expect sociality to increase in complex habitats (Prediction 9, Table 4.1).

We conducted a meta-analysis to test the predicted effects of habitat complexity on a variety of behavioural and ecological variables in a wide range of territorial and non-territorial taxa (see Table 4.1). As the predicted effect of habitat complexity differed between territorial and non-territorial species for some of the variables, we retained this distinction for all variables in Table 4.1.

Methods

Google scholar and BIOSIS were searched for published comparisons of the dependent variables in Table 4.1 in open and complex habitats using combinations of the terms “habitat”, “enclosure*”, “pen”, and “complex*”, “struct*”, “enrich*”, “simple”, “open”, and “unstruct*” with “territory size”, “density”, “abundance”, “aggress*”, “agon*”, “forag*”, “feed*”, “predat*”, “move*”, “active*”, “bold*”, “shy*”, “risk*”, “survival”, “mortality”, “explor*”, “neophob*”, “novelty”, and “social*”. Additionally, references of relevant papers were scanned to include papers overlooked by the search engine. Searches were conducted in 2016 and 2017, with the last update occurring in December 2017.

Papers were selected if they provided the i) mean of any of the dependent variables in Table 4.1 that was measured in both an open and a structurally complex habitat, along with ii) the standard error or standard deviation and iii) a sample size for each habitat. Papers were excluded if they measured physiological (i.e. hormones, heart rate), life history or morphological features, or had sample sizes of two or less for each group, with a pooled sample size of four or less. All of the species used in these studies were also classified as either territorial or non-territorial at the time of the study, based on information within the paper. For example, a species that exhibits territorial behaviour only during mating or only as an adult would be classified as non-territorial if reproductive behaviour did not occur during the study, or if only juveniles were observed. If detailed information was lacking in the individual paper, we used general references (e.g. Grzimek's Animal Life Encyclopedia). A total of approximately 7 000 different papers were found by the two search engines from different combinations of the search terms. Abstracts were scanned to identify potential papers, then potential papers were skimmed to determine if they met the three criteria specified above.

Most studies measured either aggression rates or the proportion of time engaged in aggression, foraging and activity. As these two measures appeared to measure different aspects of a particular behaviour, and often showed opposite trends in the same study, they were analyzed separately for each of the three behaviours and were not aggregated. I included behavioural responses to risk, including movement, shoal distance, and time to recover as measures of shyness, and positive reactions to novelty in the absence of risk as a measure of exploration. Studies on social behaviour, or sociality, measured time associating with conspecifics, including play, in the absence of risk. Multiple estimates from the same study were often encountered. If a study compared one open habitat with multiple complex habitats, the average of the multiple habitat treatments was compared to the single control, or vice versa. In contrast, multiple effect sizes were reported for studies that included comparisons from multiple independent populations, or in studies with multiple treatments applied to both open and complex habitats. For studies with multiple measures of the same behavioural trait for the same individuals, such as the inclusion of two measures of boldness/shyness (e.g. Bhat et al. 2015; Suriyampola et al. 2016), effect sizes were calculated for both measures, then aggregated into a single effect using the package "MAd" (Del Re & Hoyt 2014). Standard deviations for each habitat and the mean difference between habitats were then manually extracted for each composite effect size, before inclusion in the final analysis (sensu Del Re 2015). If aggregated effect sizes included inverse measures of the same dependent variable (e.g. boldness rather than shyness), these measures were multiplied by -1, to ensure all reported effect sizes were consistent.

The meta-analysis for each ecological trait was then conducted using the "meta" package (Schwarzer 2007) in R (R Core Team 2017), which calculated the effect size using the formula for Cohen's d:

$$d = (m_{open} - m_{complex}) / \delta$$

where d is the calculated effect size, m_{open} is the mean calculated in the open habitat, $m_{complex}$ is the mean calculated in the complex habitat, and δ is the standard error (Cohen 1988).

The presence of heterogeneity within the effect size was detected by the Q statistic, and quantified with the I^2 statistic, with values of 25%, 50% and 75% indicative of low, medium and high levels of heterogeneity, respectively (Del Re 2015). A high value of Q indicates a lack of precision in the effect size estimate, often recognized by wide confidence limits (Viechtbauer 2010). Funnel plots and fail-safe numbers were also used to identify bias in the included studies that showed significant differences between habitats, indicating a "file-drawer" effect (Rosenthal 1979); fail-safe numbers were calculated using the weighted average effect size (Rosenberg 2005). Funnel plots comparing the distribution of effect sizes across different sample sizes (Light & Pillemer 1984) were constructed using the "cowplot" (Wilke 2017) and "ggplot2" (Wickham 2009) packages in R, and the relationship between the two factors quantified using Pearson's correlation coefficient. Minimal publication bias is indicated by graphs with wide openings at smaller sample sizes and a small number of gaps between data points (Rosenberg et al. 2000). Fail-safe numbers, which indicate the number of unpublished or insignificant studies needed to change the calculated results, were calculated using the "metafor" package

(Viechtbauer 2010). A high fail-safe number, relative to the number of included studies, indicates validity in the calculated results (Rosenberg et al. 2000).

Results

A total of 339 data points were analyzed in the meta-analysis of 12 dependent variables, taken from 113 papers, with a total of 113 different species or species groupings (e.g. insectivorous bats); summaries of the included studies are presented in the Supplementary Tables (4.1-9). Fish accounted for 179 of the 339 data points, including 40 for salmonids alone, followed by 80 for mammals, 55 for invertebrates (21 for decapods alone), 17 for birds, and 3 for reptiles. Seven species of domestic animals were included in the analysis. Ten studies were conducted in agricultural facilities with another six in zoos.

Territory Size

Ten comparisons from 10 studies analyzed the territory sizes of 7 species of fish, 1 bird and 1 lizard in complex and open habitats (Supplementary Table 4.1). As predicted, territories were smaller in complex than in open habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.63 [-0.83, -0.43], z=-6.19, p<0.0001; Fig. 4.1). A high degree of heterogeneity was found for the effect of habitat complexity on territory size (I^2, 95% C.I.'s [LCI, UCI]: 96.3% [94.7%, 97.9%], Q=244.34, df=9, p<0.0001). No bias was evident from the funnel plot (Pearson's, r_8 =0.33, p=0.35; Supplementary Figure 4.1) or the fail-safe number (Rosenberg's N: 392).

Density

We included 43 comparisons of population densities in open and complex habitats from 18 different studies, including fish, invertebrates, and one rabbit (Supplementary Table 4.2). Overall, population density was higher in complex relative to the open habitats (Cohen's d ±

95% C.I.'s [LCI, UCI]: 0.35 [0.19, 0.51], z=4.21, $p<0.0001$; Fig. 4.1). As predicted, the effect of habitat complexity was stronger in territorial (Cohen's d, 95% C.I.'s [LCI, UCI]: 0.77 [0.50, 1.04]) than in non-territorial (Cohen's d, 95% C.I.'s [LCI, UCI]: 0.07 [-0.14, 0.28]) species (Fixed effect model, $Q_1=16.16$, $p<0.0001$; Fig. 4.2). Heterogeneity was moderately high overall ($I^2=71.2\%$, Q=145.89, df=42, $p<0.0001$), but was lower for non-territorial species ($I^2=64.9\%$, Q=62.67, df=23, $p<0.0001$), and non-significant for territorial species ($I^2=29.8\%$, Q=27.08, df=19, p=0.10), indicating a strong, predictable effect. No biases were revealed by the funnel plot (Pearson's, $r_{41}=0.07$, p=0.65; Supplementary Figure 4.2), or the fail-safe number (Rosenberg's N: 8,705,046).

Aggression

A total of 84 comparisons were included in the analysis, including data from fish, mammals, invertebrates, a chicken and a gecko (Supplementary Table 4.3). Seventy different comparisons from 37 papers quantified the number of aggressive acts, while only 14 comparisons from 11 papers quantified time spent engaged in aggressive behaviour. As only 6 of 42 studies quantified both measures of aggression, we analyzed the frequency and duration of aggressive behaviour separately.

As predicted, the number of aggressive acts tended to be lower in the complex relative to open habitats, but not significantly (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.09 [-0.18, 0.00], z=-1.83, p=0.067; Fig. 4.1). When species were separated by territoriality, opposite patterns emerged (Fixed effect model, $Q_1=40.64$, $p<0.0001$; Fig. 4.2): as predicted, territorial species showed moderately lower aggression in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.21 [-0.32, -0.11]), but contrary to predictions, non-territorial species were more aggressive in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: 0.64 [0.40, 0.88]). Aggression rates showed a moderately high degree of heterogeneity overall (I^2=79.3%, Q=333.96, df=69, p<0.0001), with slightly lower heterogeneity for both territorial (I^2=72.6%, Q=204.40, df=56, p<0.0001) and non-territorial species (I^2=75.9%, Q=49.88, df=12, p=0.016). No biases were revealed by the funnel plot (Pearson's, r_{68}=-0.18, p=0.13; Supplementary Figure 4.3a), or by the fail-safe number (Rosenberg's N: 1,767).

As predicted, time spent engaging in aggressive activity was significantly lower in complex relative to open habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.19 [-0.35, -0.03], z=-2.25, p=0.024; Fig. 4.1). However, this effect tended to be stronger for non-territorial species (Fixed effect model, Q_1=2.95, p=0.086; Fig. 4.2), which spent less time on aggression in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.63 [-1.16, -0.10]), whereas territorial species did not differ significantly between habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.13 [-0.30, 0.04]). Heterogeneity was moderately high overall (I^2: 73.0%, Q=48.21, df=13, p<0.0001) as well as for non-territorial species (I^2=76.9%, Q=4.33, df=1, p=0.037), but was slightly lower for territorial species (I^2=69.1%, Q=35.58, df=11, p=0.0002). No biases were revealed by either the funnel plot (Pearson's, r_{12}=-0.39, p=0.17; Supplementary Figure 4.3b), or the fail-safe number (Rosenberg's N: 3,032).

Foraging Activity

Our analysis included 34 comparisons from 20 studies of foraging rates in fishes, mammals, birds, insects, and a crab (Supplementary Table 4.4). As predicted, foraging rate was lower in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.23 [-0.33, -0.13], z=-4.29, p<0.0001; Fig. 4.1), but this effect was stronger for non-territorial (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.91 [-1.17, -0.66]) and nonsignificant in territorial (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.07 [-0.19, 0.05]) animals (Fixed effect model, Q_1=34.51, p<0.0001; Fig. 4.2). Overall, foraging rates showed high heterogeneity (I^2: 90.0%, Q=331.42, df=33, p<0.0001), with similarly high heterogeneity for both territorial (I^2=88.1%, Q=201.90, df=24, p<0.0001) and non-territorial species (I^2=89.0%, Q=72.50, df=8, p<0.0001). The funnel plot (Pearson's, r_{32}=-0.11, p=0.52; Supplementary Figure 4.4a) and the high fail-safe number (Rosenberg's N: 3,571) revealed no biases.

Twenty-two comparisons from 16 studies quantified the proportion of time spent foraging in open and complex habitats, including 9 species of mammals (5 primates), 4 species of fish and 3 birds (Supplementary Table 4.4b). Similar to foraging rate, time spent foraging decreased in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.24 [-0.40, -0.08], z=-2.83, p=0.0005; Fig. 4.1). However, in contrast to foraging rate, territorial and non-territorial species responded differently to structure (Fixed effect model, Q_1=9.84, p=0.0017; Fig. 4.2); territorial species foraged less in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.43 [-0.64, -0.22]), while non-territorial species foraged similarly in both habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: 0.11 [-0.16, 0.38]). Time spent foraging also showed high heterogeneity (I^2=80.9%, Q=109.71, df=21, p<0.0001), which remained high for non-territorial (I^2=78.7%, Q=46.87, df=10, p<0.0001), but was moderate for territorial species (I^2=67.8%, Q=31.01, df=10, p<0.0001). No biases were evident from the funnel plot (Pearson's, r_{20}=0.12, p=0.58; Supplementary Figure 4.4b) or the fail-safe number (Rosenberg's N: 46,394).

Activity

Rates of activity were analyzed using 14 comparisons from seven studies; all were fish and mammals (Supplementary Table 4.5). As predicted, habitat complexity had a moderately strong negative effect on activity rates (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.59 [-0.79, -0.39], z=-5.69, p<0.0001; Fig. 4.1), but this effect was stronger in territorial (Cohen's d, 95% C.I.'s

[LCI, UCI]: -0.64 [-0.93, -0.35]) than in non-territorial (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.49 [-0.77, -0.21]) species, although not to a significant degree (Fixed effect model, Q_1=0.50, p=0.48; Fig. 4.2). Heterogeneity was lower for activity rate, although still substantial (I^2= 63.3%, Q=34.38, df=13, p=0.0006); similar results were found for territorial species (I^2=63.9%, Q=19.37, df=7, p=0.0036). However, heterogeneity was not significant for non-territorial species (I^2=53.7%, Q=10.81, df=5, p=0.15), indicating highly predictable effects of complexity on activity rates. No biases were apparent from either the funnel plot (Pearson's, r_{12}=-0.16, p=0.58; Supplementary Figure 4.5a) or the fail-safe number (Rosenberg's N: 1,653).

Proportion of time engaged in activity was analyzed using 27 comparisons from 13 studies involving fishes, mammals and birds (Supplementary Table 4.5a). Overall, habitat complexity had a small, positive effect on the proportion of time active (Cohen's d, 95% C.I.'s [LCI, UCI]: 0.13 [0.02, 0.24], z=2.24, p=0.025; Fig. 4.1), contrary to predictions. However, habitat complexity had opposite effects on territorial and non-territorial (Fixed effect model, Q_1=50.85, p<0.0001). As predicted, territorial species were less active in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.50 [-0.71, -0.29]), while contrary to predictions, non-territorial animals were more active in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: 0.40 [0.27, 0.53]; Fig. 4.2). This effect showed a high degree of heterogeneity (I^2=84.0%, Q=162.88, df=26, p<0.0001), which tended to be lower for territorial (I^2=71.8%, Q=70.93, df=20, p<0.0001), and was not significant for non-territorial species (I^2=50.4%, Q=10.07, df=5, p=0.073). No biases were revealed by the funnel plot (Pearson's, r_{25}=-0.30, p=0.13 Supplementary Figure 4.5b), or by the fail-safe number (Rosenberg's N: 6,188).

Shyness & Boldness

Thirty-four measures of shyness and boldness in open and complex habitats were obtained from 18 studies, including fishes, mammals, birds, a lizard and a crab (Supplementary Table 4.6). Contrary to predictions, habitat complexity had no overall effect on shyness (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.12 [-0.25, 0.01], $z=-1.79$, $p=0.074$; Fig. 4.1). No differences were found when species were separated by territoriality (Fixed effect model, $Q_1=0.59$, $p=0.44$; Fig. 4.2). Heterogeneity in shyness was moderately high overall ($I^2=68.4\%$, $Q=104.36$, $df=33$, $p<0.0001$), and for territorial species ($I^2=83.6\%$, $Q=61.16$, $df=10$, $p<0.0001$), but was lower for non-territorial species ($I^2=27.8\%$, $Q=30.47$, $df=22$, $p=0.014$). The funnel plot revealed bias, with larger effects occurring in studies with smaller sample sizes (Pearson's, $r_{34}=-0.36$, $p=0.04$; Supplementary Figure 4.6), while the fail-safe number was not applicable for a non-significant effect.

Survival

Forty-nine comparisons of survival and mortality in open and complex habitats were obtained from 21 studies, including fishes, invertebrates, and one species of gull (Supplementary Table 4.7). As predicted, survival was significantly higher in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: 0.46 [0.36, 0.56], $z=9.16$, $p<0.0001$; Fig. 4.1). However, this effect differed markedly between territorial and non-territorial species (Fixed effect model, $Q_1=21.09$, $p<0.0001$; Fig. 4.2); survival was higher in complex habitats for non-territorial (Cohen's d, 95% C.I.'s [LCI, UCI]: 0.56 [0.45, 0.67]), but not for territorial (Cohen's d, 95% C.I.'s [LCI, UCI]: -0.03 [-0.26, 0.20]) species. Heterogeneity was high overall ($I^2=83.1\%$, $Q=284.69$, $df=48$, $p<0.0001$), but was lower for territorial ($I^2=74.9\%$, $Q=87.76$, $df=22$, $p<0.0001$) and non-territorial ($I^2=72.9\%$, $Q=92.34$, $df=25$, $p<0.0001$) species. No apparent biases were revealed by the funnel plot (Pearson's, r_{47}=0.16, p=0.28; Supplementary Figure 4.7), or by the fail-safe number (Rosenberg's N: 24,687).

Exploration

Twelve comparisons of exploratory behaviour from 9 studies were included in the analysis, involving 6 mammal species and 1 lobster (Supplementary Table 4.8), all of which were territorial. As predicted, exploration increased significantly in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: 0.47 [0.29, 0.65], z=5.17, p<0.0001; Fig. 4.1). By chance, exploration in the lobster, the sole aquatic species, was atypical in how strongly it increased in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: 3.21 [1.46, 4.96]). Exploration showed high levels of heterogeneity (I^2=92.2%, Q=140.60, df=11, p<0.0001). No bias was evident in the funnel plot (Pearson's, r_{10}=-0.11, p=0.74 Supplementary Figure 4.8), or from the fail-safe number (Rosenberg's N: 60).

Social Behaviour

Ten comparisons from eight studies were included in the analysis of social behaviour, defined as time spent associating with a known conspecific in the absence of risk, including grooming and play behaviour. The social behaviour of six species of mammals and two fish were assessed (Supplementary Table 4.9). Contrary to predictions, habitat complexity had no consistent effect on sociality overall (Cohen's d, 95% C.I.'s [LCI, UCI]: 0.01 [-0.17, 0.19], z=0.07, p=0.94; Fig. 4.1); this effect did not differ significantly between territorial and non-territorial animals (Fixed effect model, Q_1=0.41, p=0.52; Fig. 4.2). Social behaviour was characterized by moderately high heterogeneity (I^2, 95% C.I.'s [LCI, UCI]: 63.0% [44.7%, 81.3%], Q=24.35, df=9, p=0.0038), which was lower and non-significant for non-territorial species (I^2=42.3%, Q=3.47, df=2, p=0.18), but slightly higher for territorial species (I^2=69.1%,

$Q=19.39$, $df=6$, $p=0.0036$). However, bias was evident with the funnel plot (Pearson's, $r_8=0.69$, $p=0.027$; Supplementary Figure 4.9), while the fail-safe number was not applicable for a nonsignificant effect.

Aquatic vs. Terrestrial

Aquatic and terrestrial species differed in their aggression rates (Fixed effect model, non-territorial species: $Q_1=13.26$, $p=0.0003$), time spent foraging (Fixed effect model, non-territorial species: $Q_1=12.92$, $p=0.0003$) and exploration (Fixed effect model, territorial species: $Q_1=9.55$, $p=0.002$) in open and complex habitats. However these differences were all driven by the behaviour of a single species. Rates of aggression differed between aquatic and terrestrial species, as the sole terrestrial species, calves (*Bos taurus*), were more aggressive in open habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: -1.07 [-2.02, -0.12]). Similarly, time spent foraging differed as the roach (*Rutilus rutilus*), the sole aquatic species, spent much more time foraging in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: 6.90 [3.35, 10.45]). Finally, differences in exploration were also due to one species, the lobster (*Homarus americanus*), which became much more exploratory in complex habitats (Cohen's d, 95% C.I.'s [LCI, UCI]: 3.21 [1.46, 4.96]). Habitat complexity tended to more positively affect the density of terrestrial species (Fixed effect model, non-territorial species: $Q_1=3.25$, $p=0.007$), and to more negatively affect the foraging rates of terrestrial species (Fixed effect model, territorial species: $Q_1=2.95$, $p=0.086$), although these effects were not significant. Aquatic and terrestrial species showed no differences in territory size, time spent aggressive, foraging rates, activity, shyness, survival or social behaviour in open and complex habitats (Fixed effect models, all $p>0.10$).

Discussion

Territorial species responded in the predicted way to increasing habitat complexity by decreasing territory size, increasing population density, and decreasing the rate of aggression. These predictable responses seem to be related to the decrease in visibility in complex habitats, as suggested by Eason & Stamps (1992). Despite the decrease in visibility and some rates of behaviour, which may have decreased susceptibility to predators, the survival rate of territorial individuals was not affected by habitat complexity. This may be due to the decreased risk of predation for territorial species in habitats with greater visibility (Rilov et al. 2007).

In general, non-territorial animals differed from territorial animals in how they responded to habitat complexity. Some differences were predicted, such as no change in population density, whereas others were unexpected. Notable differences included an increase in aggression rates, and in the time spent foraging and active in complex habitats, all behaviours which might have increased their risk of predation (Jakobsson et al. 1995; Metcalfe et al. 1987). The increased safety of complex habitats must have more than compensated for the increase in these rates of behaviour, because the survival rate of non-territorial animals increased in complex habitats. However, territorial and non-territorial species showed similar responses to habitat complexity for shyness, sociality and time spent engaging in aggression. Contrary to predictions, shyness, sociality and time spent being aggressive were not significantly affected by habitat complexity. In contrast to the distinction between territorial and non-territorial species, aquatic and terrestrial species tended to respond similarly to habitat complexity. Although aquatic and terrestrial species differed in aggression, foraging and exploration, these differences were largely driven by the atypical behaviour of a single species, rather than signifying a general tendency.

Overall, heterogeneity was fairly high, and largely not accounted for by territoriality. Although 7 of the 9 variables were significantly affected by complexity, the high degree of heterogeneity indicates that precise estimates of their magnitude were not possible, perhaps due to the variety of included species and differences in study design. However, three exceptions were characterized by low heterogeneity: the effects of habitat complexity on population density and activity rates in territorial species, and the effects of complexity on time spent active in non-territorial species. The population densities and activity rates of territorial species showed nonsignificant heterogeneity and a consistently strong effect of habitat complexity, with densities positively affected by complexity and activity rates negatively affected by structure in territorial species; non-territorial species also showed a highly predictable yet moderate and positive effect of complexity on time spent active. This lack of heterogeneity demonstrates the consistency of these strong effects of habitat complexity, in contrast to the high degree of heterogeneity observed for the majority of the variables in our study. Unsurprisingly, the general high levels of heterogeneity in the results illustrates that species differences generally affect the degree to which behaviour alters in response to habitat complexity. A key example of this is illustrated within the analysis of exploratory behaviour. Although exploration is generally positively affected by habitat structure, this effect was over five times stronger for lobsters (*Homarus americanus*), the sole aquatic species in this analysis. Decapods, like lobsters, show a strong tendency to increase exploratory behaviour in complex habitats (Cenni et al. 2010), which is likely due to their unique and particular reliance on tactile cues to monitor and detect subtle topographical changes within their territories (Basil & Sandeman 2000).

Although generalizations can be made on the effect of habitat complexity on behaviour, these general effects are also mediated by different susceptibilities to predation, as well as species-specific ecological differences. Such differences may include varying morphology (Nyström & Pérez 1998), modes of foraging (Diehl 1988; Reid et al. 2012;), or reliance on different forms of sensory input (i.e. visual vs chemical or tactile); these differences also interact to determine susceptibility to predation. Species differences also determine the degree to which other physical factors, such as light (James & Heck 1994; Mandelik et al. 2003), temperature (Jeppesen et al. 2010; Stoner et al. 2010), proximity to humans (Thompson & McGarigal 2002; Zeige et al. 2015), and water velocity (Bhat et al. 2015; Vehanen et al. 2000) influence habitat use and the relative benefits of habitat complexity. In many cases, habitat selection is driven primarily by species-specific habitat preferences (Boström & Mattila 1999; Ryer et al. 2004), or the effects of competition (Schofield 2003), rather than by predation risk. Similarly, a high degree of variability exists in the overall effect of habitat complexity on marine fish survival, due to differences in predator search tactics and variability in the habitat preferences and avoidance responses of prey between different predator and prey species combinations (Scharf et al. 2006).

The tendency to form smaller territories in complex habitats is used to practical advantage in salmonid conservation, with stream restorations that focus on increasing habitat complexity to effectively increase the population density of territorial salmonids (Whiteway et al. 2010), and no effects on the densities of non-territorial species (Dolinsek et al. 2007; Venter et al. 2008). Our results support the consistency of response to complexity across species. Artificial environments with added complexity also provide captive animals with stimulation and promote overall well-being relative to more barren habitats (Mellen & MacPhee 2001; Shepherdson 1994). Additionally, captive animals in zoos (Doane et al. 2013; Jaman & Huffman 2008), aquaculture (Batzina & Karakatsouli 2012, 2014) and agricultural facilities (Bøe et al. 2012; Bozicovich et al. 2016; Melotti et al. 2011) often benefit from increased physical complexity as a simple yet effective method of reducing overall levels of aggression, as well as the frequency and severity of injuries (Keck et al. 2015; Naslund et al. 2013).

However, our results challenge the notion that habitat complexity is universally beneficial. Across species, the benefits of complex habitats, especially reductions in aggression and activity, appear to exist primarily for territorial species, while the opposite response is observed in non-territorial species. These results suggest that complexity should be used cautiously as a source of enrichment for non-territorial species in captive habitats, in order to avoid unexpected negative effects. To ensure that undesireable behaviour like aggression will not increase with complexity in non-territorial species, the specific ecology of the target species must also be considered. Overall, this meta-analysis demonstrates that the ecology of the target species, including whether or not it is territotorial, is crucial when predicting behavioural responses to habitat complexity.

Table 4.1: Predicted effects of habitat complexity on nine dependent variables for territorial (T) and non-terrritorial (NT) species.

Variable	**Prediction: T**	**Prediction: NT**	**Mechanism**	**Result (T / NT)**
1. Territory size	Smaller in complex	N/A	Reduced visual distance	True / NA
2. Density	Higher in complex	No change	Smaller territories allow higher densities	True / True
3. Aggression				
Aggressive rate	Lower in complex	Lower in complex	Reduced visual distance reduces encounter rates	True / False
Aggressive time	Lower in complex	Lower in complex	Reduced visual distance reduces encounter rates	False / True
4. Foraging				

Foraging rate	Lower in complex	Lower in complex	Complex habitats constrain movement & visual foraging	True / True
	Higher in complex	Higher in complex	Complex habitats improve foraging for ambush predators & have more food	False / False
Foraging time	Lower in complex	Lower in complex	Complex habitats constrain movement & visual foraging	True / False
	Higher in complex	Higher in complex	Complex habitats improve foraging for	False / True

			ambush predators & have more food	
5. Activity				
Activity rates	Lower in complex	Lower in complex	Complexity & smaller territories constrain movement	True / False
Activity time	Lower in complex	Lower in complex	Complexity & smaller territories constrain movement	True / False
6. Shyness	Lower in complex	Lower in complex	More risk-taking in “safer” habitat	False / False
	Higher in complex	Higher in complex	Shyer fish prefer complex	False / False

7. Survival	Higher in complex	Higher in complex	Complexity provides refuge from predators	False / True
	Lower in complex	Lower in complex	Complexity improves foraging success of ambush predators	False / False
8. Exploration	Higher in complex	Higher in complex	More exploratory individuals prefer complex habitats & more novelty in more complex habitats	True / NA
	Lower in complex	Lower in complex	More risk taking in “safer” habitat	False / NA
9. Sociality	Higher in complex	Higher in complex	Opposite of aggression	False / False

Figure 4.1: The overall effect of habitat complexity on the mean effect size (95% C.I.'s) for all 9 dependent variables, ordered by effect size. Negative numbers indicate a decrease in the variable in the complex relative to the open habitat, and vice-versa for positive numbers.

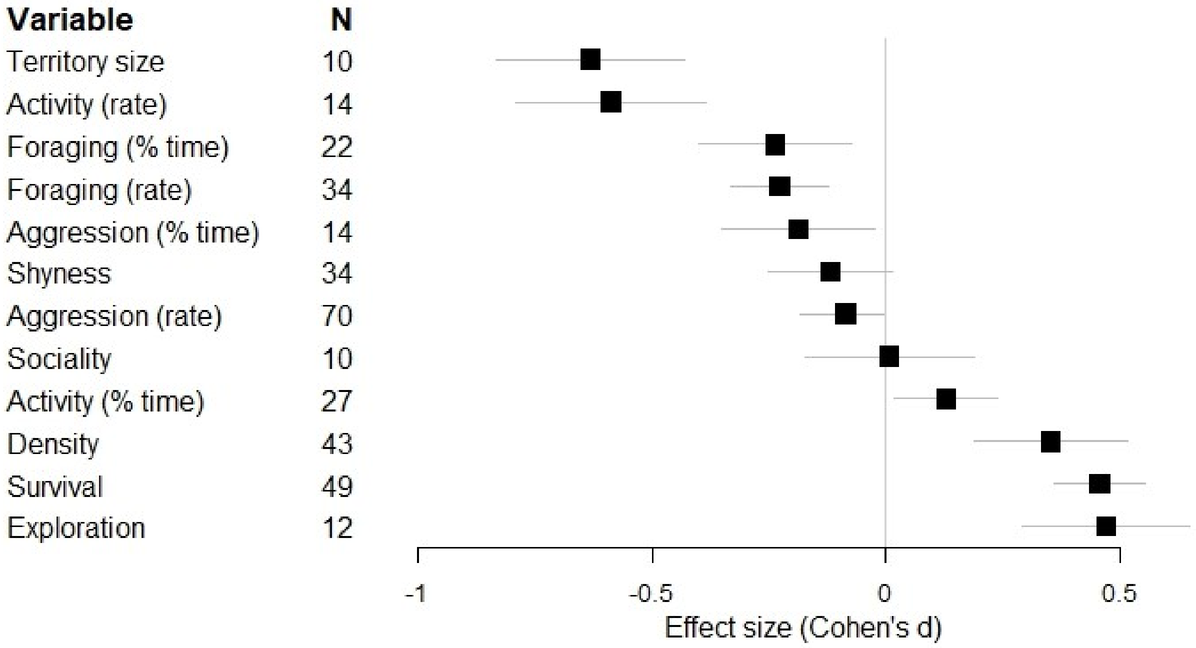
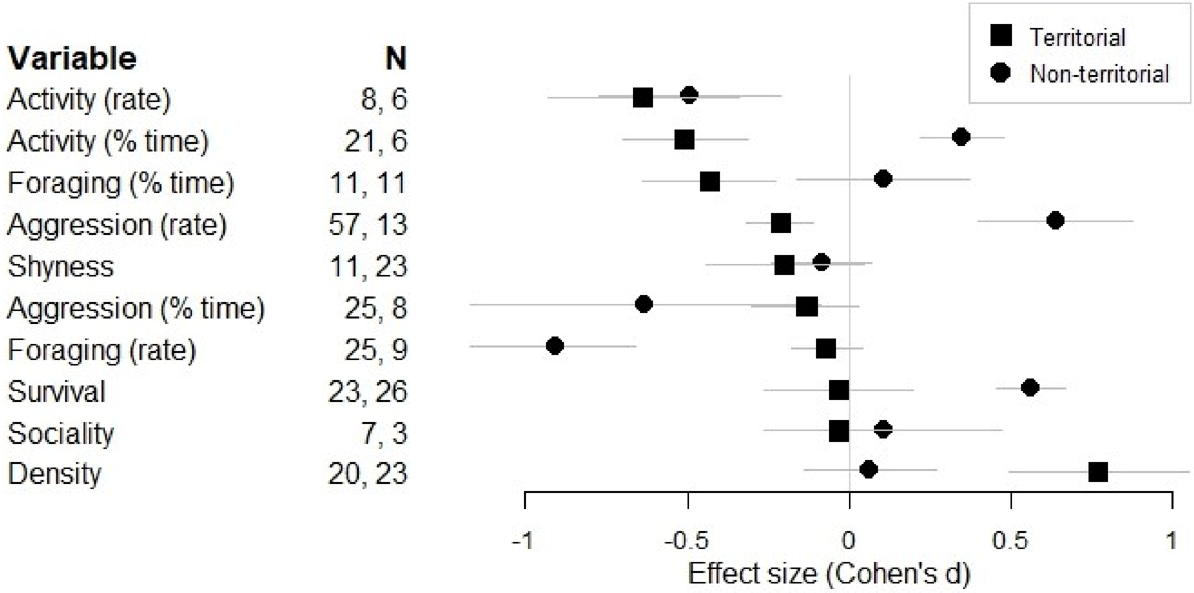


Figure 4.2: The overall effect of habitat complexity on the mean effect size (95% C.I.'s) for 7 of 9 behavioural variables for territorial and non-territorial species, ordered by effect size for territorial species (*N* = territorial, non-territorial). Negative numbers indicate a decrease in the variable in the complex relative to the open habitat, and vice-versa for positive numbers.



Supplementary Figures: Funnel plots

Figure 4.1: Funnel plot of effect size relative to the pooled sample size for territory size in open and complex habitats (corr=0.33, p=0.35).

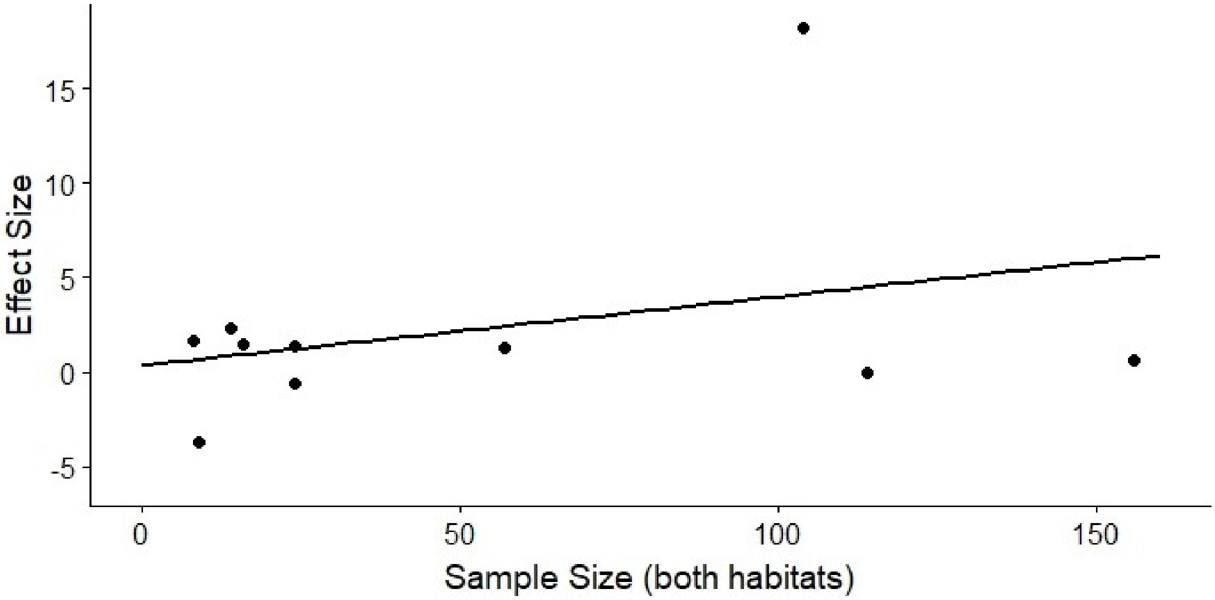


Figure 4.2: Funnel plot of effect size relative to the pooled sample size of the population density, or number of individuals found in open and complex habitats (cor=0.07, p=0.65).

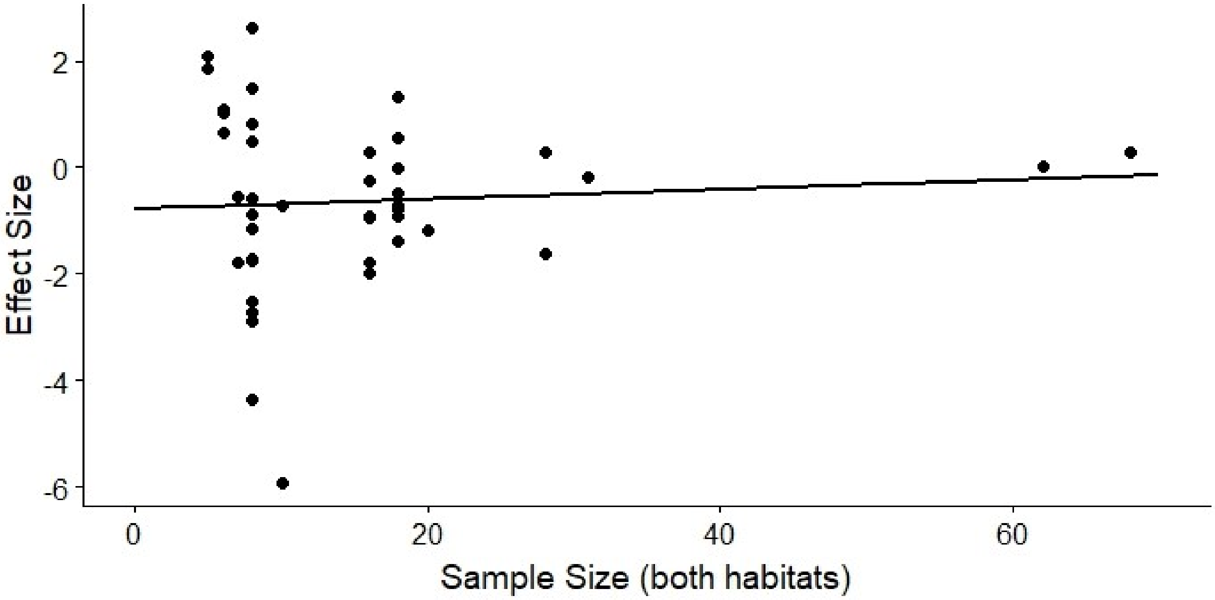


Figure 4.3: Funnel plot of effect size relative to the pooled sample size of A) number of aggressive acts (cor=-0.18, p=0.13), and B) proportion of time engaged in aggressive activity (cor=-0.39, p=0.17) in open and complex habitats.

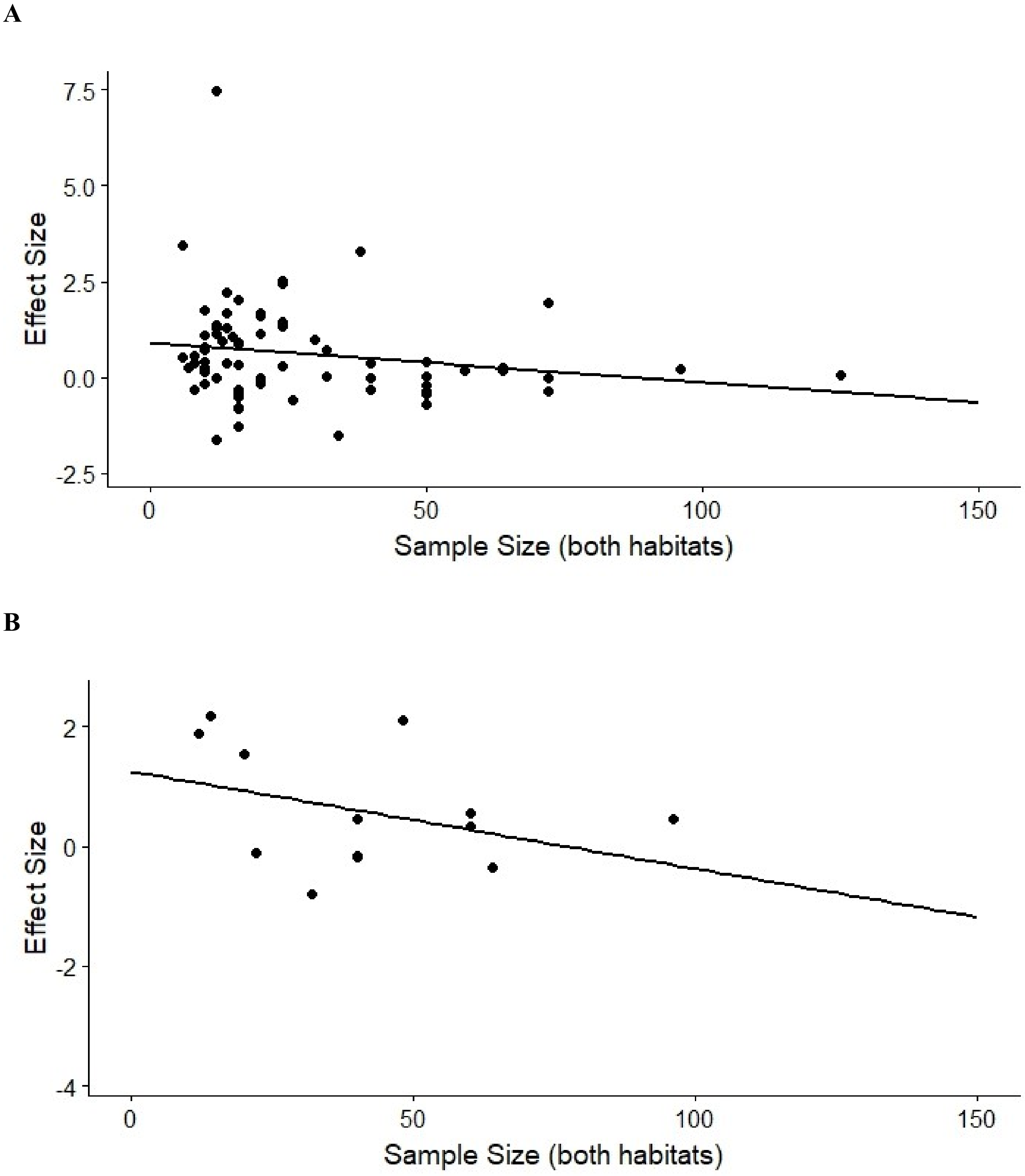
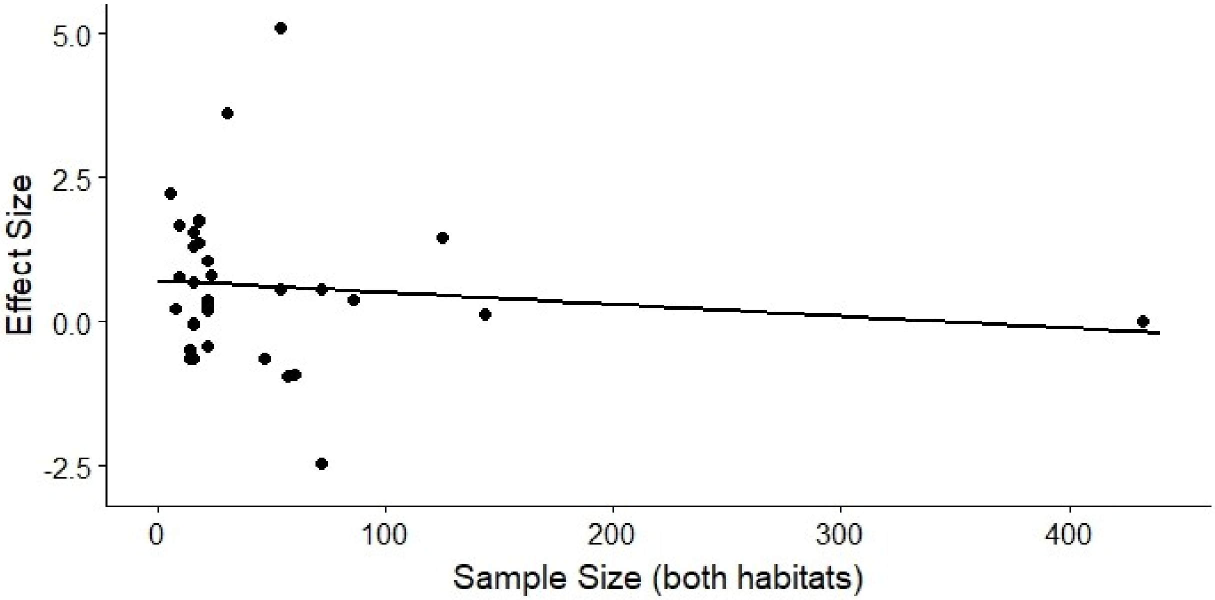


Figure 4.4: Funnel plot of effect size relative to pooled sample size of A) foraging rate (cor=-0.11, p=0.52) and B) proportion of time foraging (cor=0.12, p=0.58) in open and complex habitats.

A



B

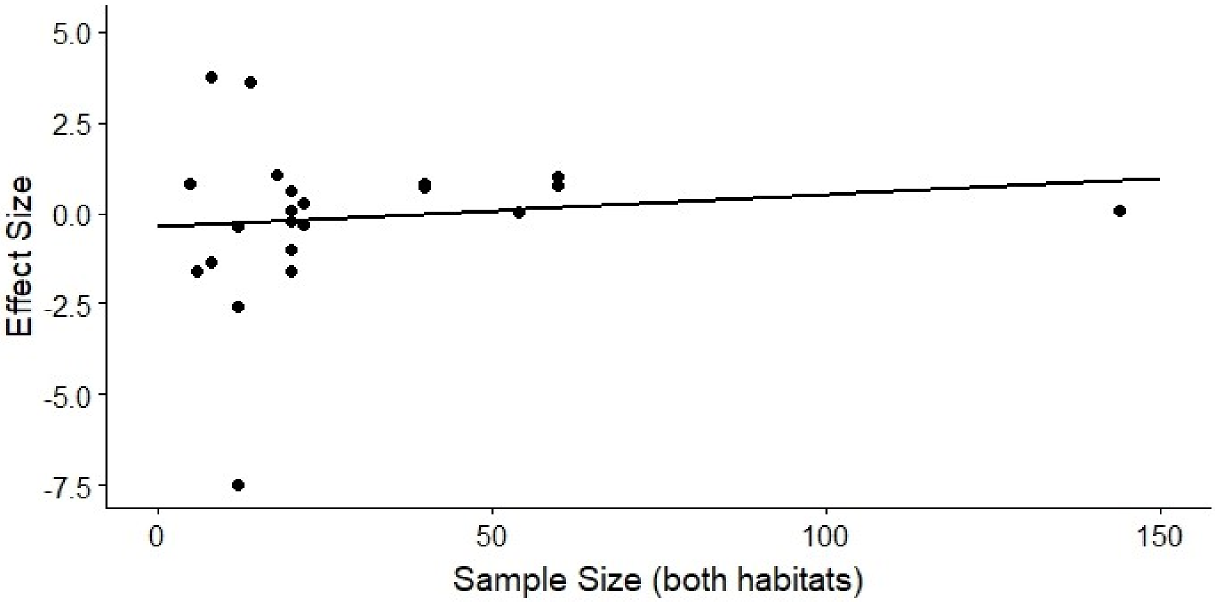
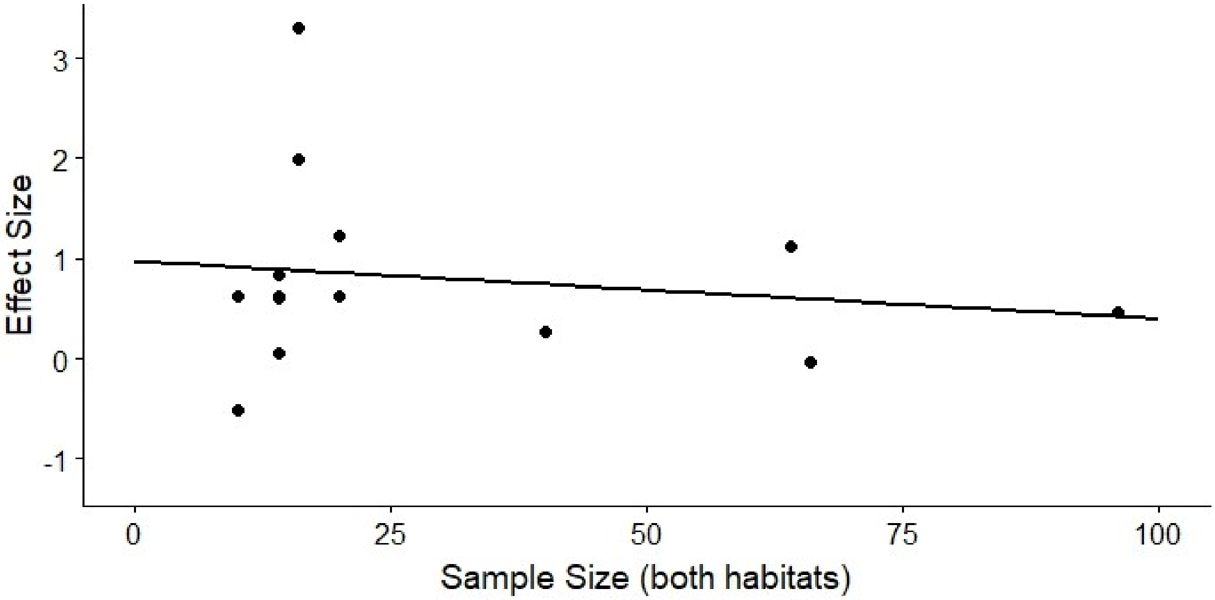


Figure 4.5: Funnel plot of effect size relative to the pooled sample size of A) activity rates (cor=-0.16. p=0.58), and B) proportion of time active (cor=-0.28, p=0.12) in open and complex habitats

A



B

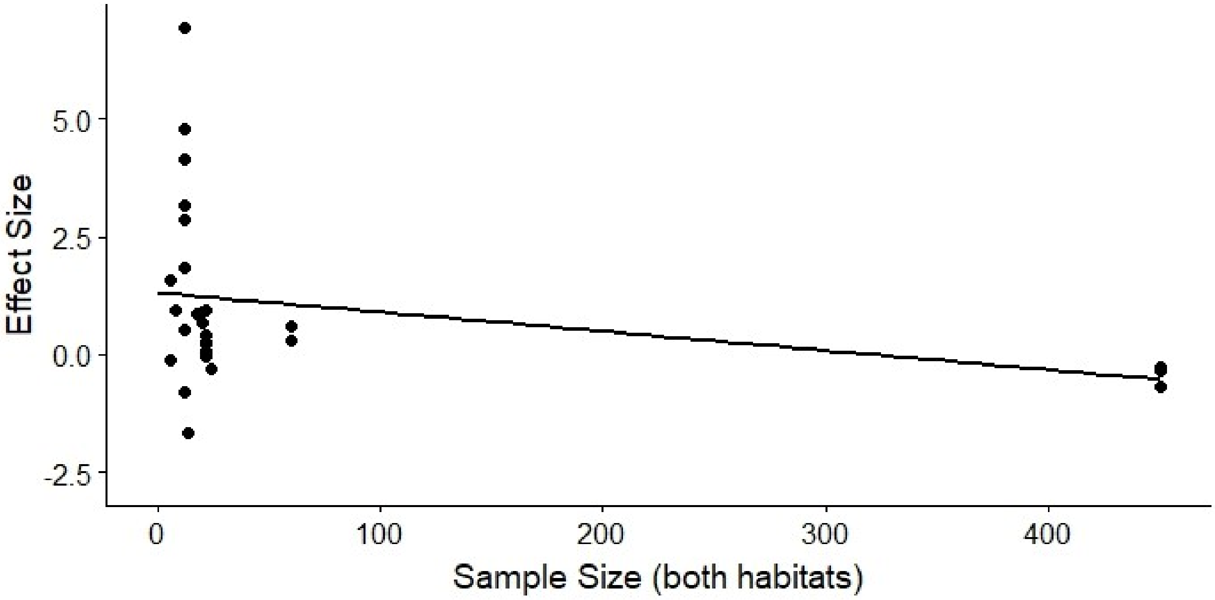


Figure 4.6: Funnel plot of effect size relative to the pooled sample size for shyness in open and complex habitats (cor = -0.36, p=0.036).

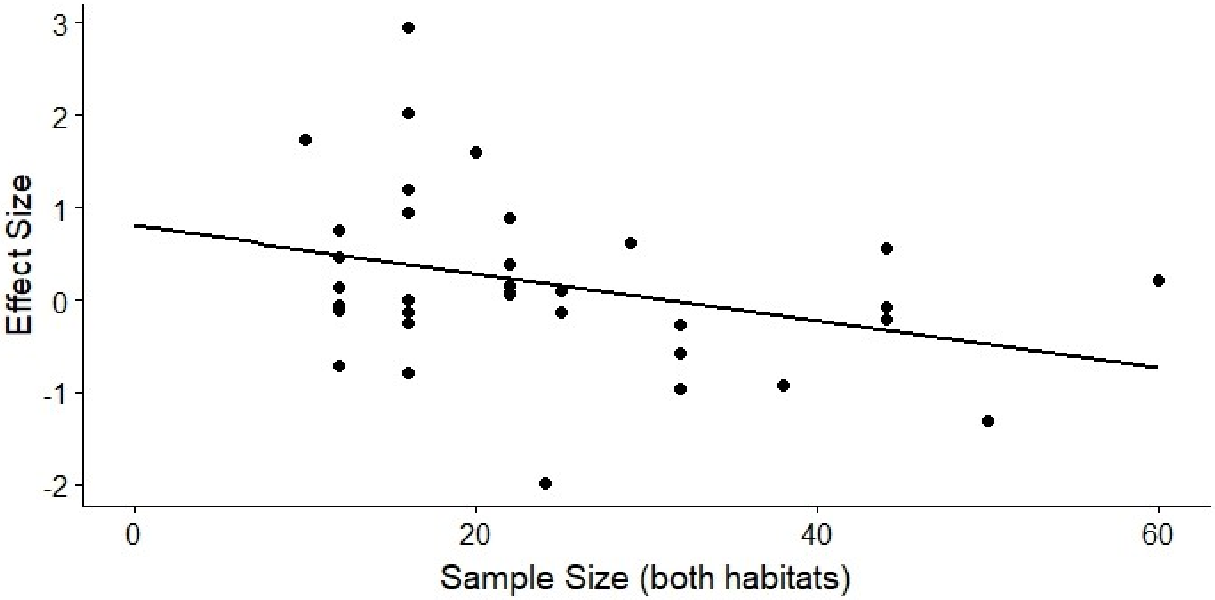


Figure 4.7: Funnel plot of effect size relative to the pooled sample size for survival in open and complex habitats (cor=0.16, p=0.3).

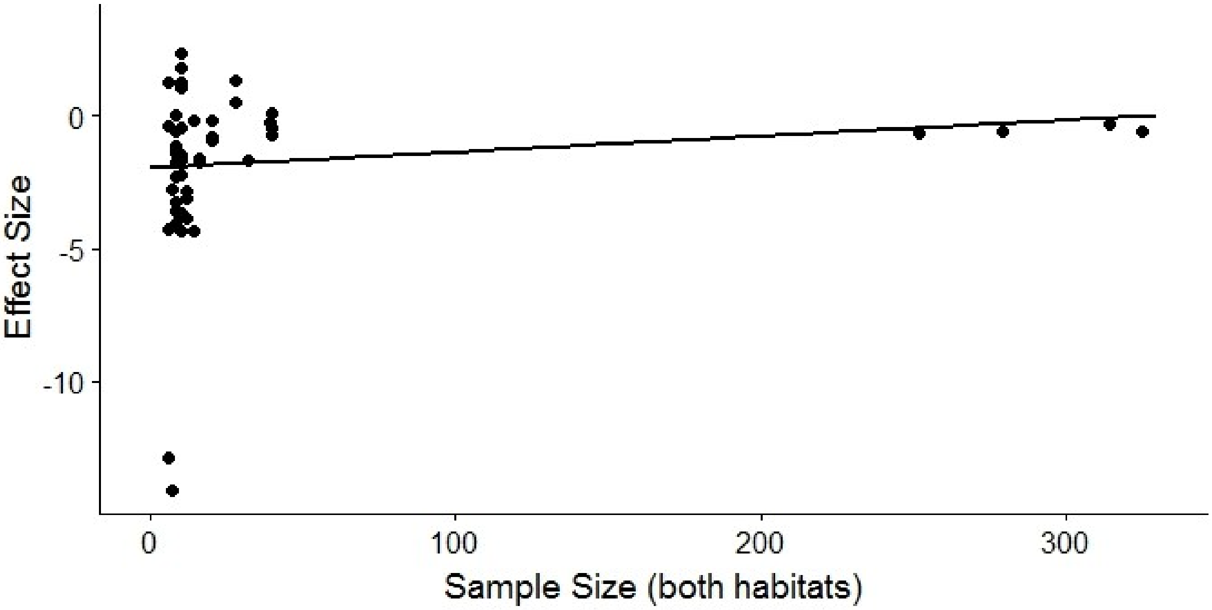


Figure 4.8: Funnel plot of effect size relative to the pooled sample size for exploration in open and complex habitats (p=0.74, cor=0.11).

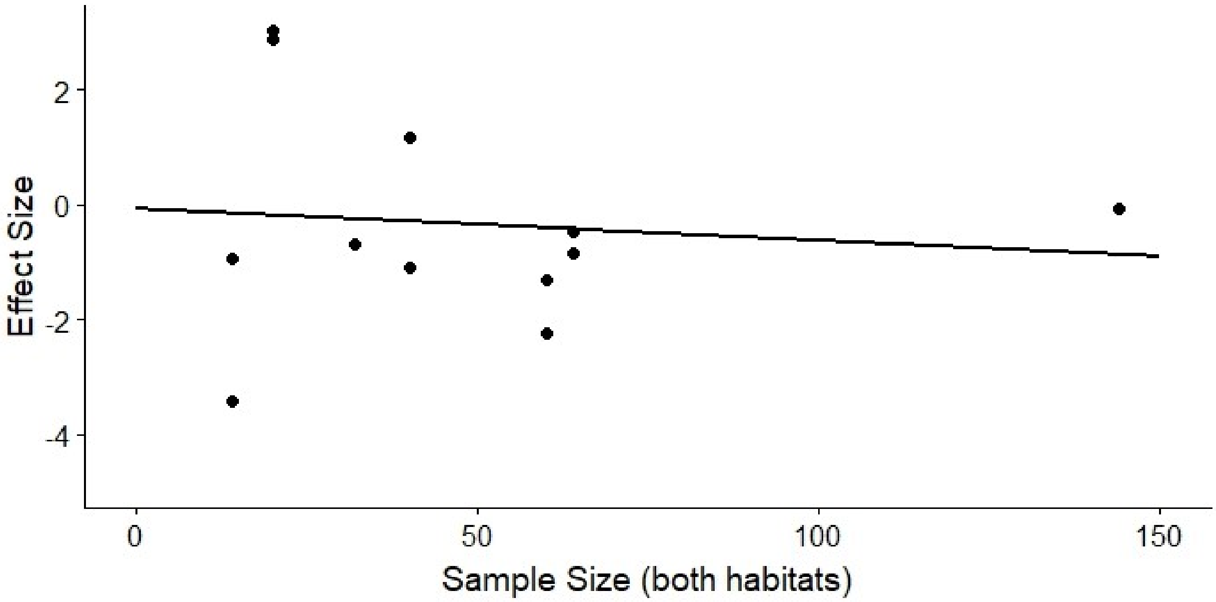
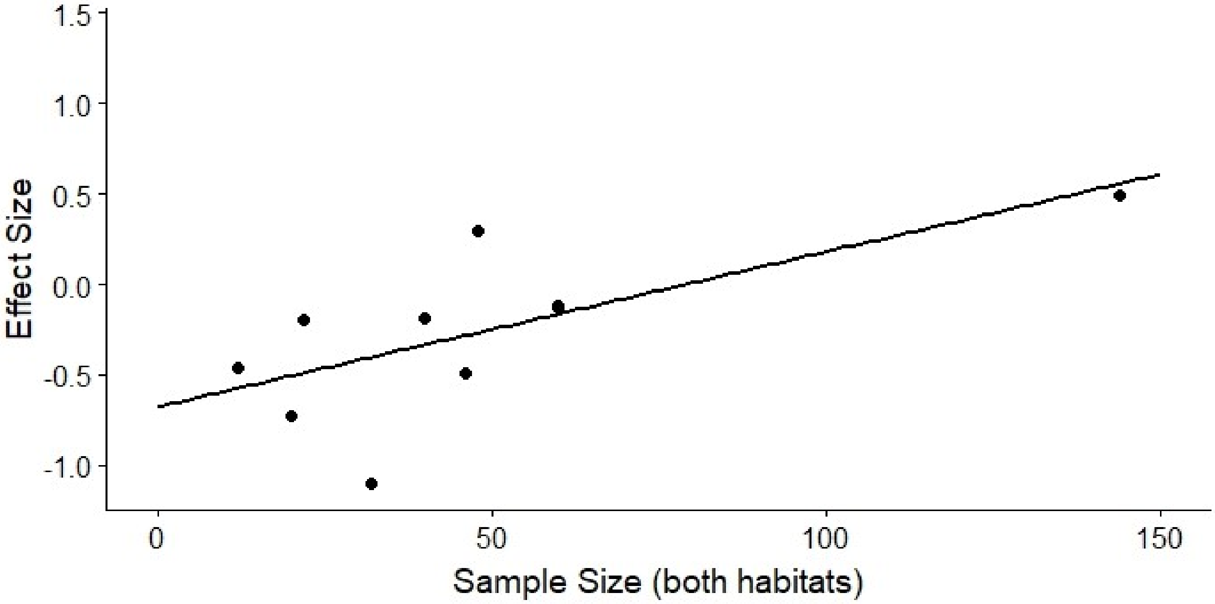


Figure 4.9: Funnel plot of effect size relative to the pooled sample size for sociality in open and complex habitats (cor = 0.69, p=0.027).



List of papers used in meta-analysis

(legend: ts=territory size, d=density, ag=aggression, f=foraging, ac=activity, sh=shyness, su=survival, e=exploration, so=sociality)

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Supplementary Table 4.1: Territory size

Species	Sample size (open; complex)	Complexity Treatment[1]	Territoriality (reference)[2]	Reference
Atlantic salmon, *Salmo salar*	56; 58	Boulders	Yes	Bilhete & Grant 2016
Convict cichlid, *Amatitlania nigrofasciata*	7; 7	Plastic plants	Yes	Breau & Grant 2002
Threespine sticklebacks, *Gasterosteus aculeatus*	12; 12	Stones & algae, -20% vs +20%	Yes	Candolin & Voigt 2001
Redband parrotfish, *Sparisoma aurofrenatum*	79; 77	Coral reef, unprotected vs protected sites	Yes	Catano et al. 2015
Juvenile lizards, *Anolis aeneu*	12; 12	Opaque dividers	Yes	Eason & Stamps 1992
Western gulls, *Larus occidentalis*	5; 4	Natural vegetation	Yes	Ewald et al. 1980

Rainbow trout, *Oncorhynchus mykiss*	4; 4	Cobbles & plywood dividers (mean of 2 complex habitats)	Yes	Imre et al. 2002
Peacock grouper, *Cephalopholis argus*	52; 52	Coral reef, low vs high complexity	Yes	Karkarey et al. 2017
Blue tang, *Acanthurus coeruleus*	27; 30	Uncolonized pavement vs reef	Yes	Semmens et al. 2005
Atlantic salmon, *Salmo salar*	8; 8	Boulders, boulders removed vs added	Yes	Venter et al. 2008

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[1] Unless otherwise specified, all papers compared behaviour in one complex treatment with the structures listed, versus in one open treatment without these structures.

[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

Supplementary Table 4.2: Density

Species	**Sample size (open; complex)**	**Complexity Treatment**[1]	**Territoriality (reference)**[2]	**Reference**
Surgeonfish (Acanthuridae), butterflyfish (Chaetodontidae), wrasse (Labridae), angelfish (Pomacanthidae), damselfish (Pomacentridae)	4; 4	Coral reef, low vs high complexity (4 treatments)	Yes	Almany 2004b
Chironomid larvae, *Chironomus anthraci*	5; 5	Plastic macrophytes	No (Hutchins et al. 2003b)	Diehl 1988
Atlantic salmon, *Salmo salar*	8; 8	Boulders (2 treatments)	Yes	Dolinsek et al. 2007
Blacknose dace, *Rhinichthys atratulus*, creek chub, *Semotilus atromaculatus*, white sucker, *Catostomus*	8; 8	Boulders (all species together, 2 treatments)	No	Dolinsek et al. 2007

commersonii, American eel, *Anguilla rostrate*				
Macroinvertebrates, perch, *Perca fluviatilis*	3; 4 (1), 3; 3 (2-4)	Lake natural vegetation (3 populations)	No	Eklöv 1997
Snapper (taape), *Lutjanus kasmira*	16; 15	Reef habitat, Open vs complex	Yes	Friedlander et al. 2002
Brown trout, *Salmo trutta*	10; 10	Plastic plants, shredded plastic	Yes	Höjesjö et al. 2015
Blue crabs, *Callinectes sapidus*	4; 4	Seagrass shoot density (2 treatments)	Yes (Burggren & McMahon 1998)	Hovel & Lipcius 2001
Rainbow trout, *Oncorhynchus mykiss*	4; 4	Cobbles & plywood (mean of 2 complex habitats)	Yes	Imre et al. 2002
Damselfish, *Pomacentrus moluccensis, P. amboinensis, Dischistodus perspicillatus*	8; 8	Coral reef habitat, complex vs simple (all species together)	Yes	Kok et al. 2016

Rotifers (phylum Rotifera)	34; 34 (1), 31;31 (2)	Macrophytes (2 treatments)	No (Hutchins et al. 2003f)	Kuczyńska-Kippen & Wiśniewska 2011
Flat-tail mullet, *Liza argentea* (1), Sillago, *Sillago* spp (2), Obtuse barricuda, *Sphyraena obtusata* (3)	4; 4	Fake mangrove stems (2 treatments)	No, (1, 2 – Hutchins et al. 2003e)	Laegdsgaard & Johnson 2001
Various beetle families	14; 14	Trees & shrubs, rocks, debris (2 treatments)	No (Hutchins et al. 2003b)	Lassau et al. 2005
Coral reef fish, (Scaridae, Acanthuridae, Pomacentridae, Haemulidae, Lutjanidae)	5; 5	Live coral reef, degraded vs living (all species together)	Yes (Thresher 1984)	Lemoine & Valentine 2012
Bicolor damselfish, *Stegastes partitus*	3; 2	Live coral, fore vs back reef sites (2 treatments)	Yes	Rilov et al. 2007
Blue tang, *Acanthurus coeruleus*	8; 8	Uncolonized pavement vs reef crest sites	Yes	Semmens et al. 2005

Water boatmen (Corixidae), water beetles (Dystiscidae), chironomids (Chironomidae), larvae of dragonflies & damselflies (Odonata), alderflies (Sialidae), midges (Tanypodinae), mayflies (Ephemeroptera), caddisflies (Trichoptera)	9; 9	Macrophytes (<10 vs >50 stems)	No (Hutchins et al. 2003b)	Tolonen et al. 2003
Atlantic salmon, *Salmo salar*	8; 8	Boulders, boulders removed vs added	Yes	Venter et al. 2008
European rabbit, *Oryctolagus cuniculus*	3; 4	Pavement vs natural cover & plants	Yes (Bozicovich et al. 2016)	Ziege et al. 2015

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[1] Unless otherwise specified, all papers compared behaviour in one complex treatment with the structures listed, versus in one open treatment without these structures.

[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

Supplementary Table 4.3a: Aggression rate

Species	**Sample size (open; complex)**	**Complexity Treatment**[1]	**Territoriality (reference)**[2]	**Reference**
Crayfish, *Cherax destructor*	10; 10	Brick pieces	Yes	Baird et al. 2006
Zebrafish, *Danio rerio*	5; 5	Simulated vegetation	No	Basquill & Grant 1998
Gilthead seabream, *Sparus aurata*	3; 3	Gravel (mean of 2 open habitats)	No (Thresher 1984)	Batzina & Karakatsouli 2014
Zebrafish, *Danio rerio*	12; 12	Plastic plants (3 pops, 2 treatments)	No	Bhat et al. 2015
Atlantic salmon, *Salmo salar*	63; 62	Boulders	Yes	Bilhete & Grant 2016
Convict cichlid, *Amatitlania nigrofasciata*	7; 7	Plastic plants	Yes	Breau & Grant 2002
Zebrafish, *Danio rerio*	4; 4 (1), 5; 5 (2)	Plastic plants (2 experiments)	No (Baquill & Grant 1998)	Carfagnini et al. 2009

American lobster, *Homarus americanus*	7; 7	Bricks	Yes	Cenni et al. 2010
Domestic pigs, *Sus scrofa domesticus*	9; 11	Straw substrate	Yes (Sparklin et al. 2009)	Chaloupkova et al. 2007
Crayfish, *Orconectes propinquus*	6; 6	Flowerpots	Yes (Baird et al. 2006)	Corkum & Cronin 2004
Mbuna cichlids, *Maylandia callainos* & *M. aurora* (1), *M. benetos* & *M. zebra* (2)	18; 20 (1), 15; 15 (2)	Bedrock vs cobble (2 populations)	Yes	Danley 2011
Brown trout, *Salmo trutta*	3; 4	Fine wood	Yes	Enefalk & Bergman 2016
Fivestripe wrasse, *Thalassoma quinquevittatum*	10; 10	Branching coral (2 vs 4) (3 treatments)	Yes	Geange & Stier 2010
House mouse, *Mus domesticus*	20; 20	Bricks (mean of 2 obs.)	Yes	Gray et al. 2000

Brown trout, *Salmo trutta*	6; 6	Wooden logs (2 treatments)	Yes	Gustafsson et al. 2012
Western buffalo bream, *Kyphosus cornelii*	17; 17	Plastic vegetation	Yes	Hamilton & Dill 2003
Whitespotted charr, *Salvelinus leucomaenis*, brown trout, *Salmo trutta*	36; 36	Barriers (bricks) (3 treatments)	Yes	Hasegawa & Maekawa 2009
BALB/c mice, *Mus domesticus*	20; 20	Plastic hut & 2 balls (2 treatments)	Yes (Gray et al. 2000)	Hutchinson et al. 2012
Rainbow trout, *Oncorhynchus mykiss*	4; 4	Cobbles & plywood (mean of 2 complex habitats)	Yes	Imre et al. 2002
Squirrel monkeys, *Saimiri sciureus*	7; 7	Toys, pool, metal chain	Yes (Mitchell et al. 1991)	Izzo et al. 2011
House mouse, *Mus domesticus*	10; 4 (1), 4; 4 (2), 2; 10 (3), 8; 8 (4), 12; 12 (5), 14; 12 (6)	Bricks (2 pops, 6 treatments)	Yes	Jensen et al. 2005

Dwarf cichlid, *Apistogramma agassizii*	8; 8	Two plastic tubes	Yes	Kochhann & Val 2016
Juvenile damselfish, P*omacentrus moluccensis, P. amboinensis, Dischistodus perspicillatus*	8; 8	Coral reef habitat, Complex vs simple	Yes	Kok et al. 2016
China rockfish, *Sebastes nebulosus*	5; 5	Rocks & plastic plants (2 treatments)	Yes	Lee & Berejikian 2009
Domestic pigs, *Sus scrofa domesticus*	32; 32	Straw, peat, shavings, branches (2 treatments)	Yes (Sparklin et al. 2009)	Melotti et al. 2011
Dairy goats, *Capra aegagrus hircus*	6; 6	Two fences, earth filled tires (2 treatments)	Yes (Macdonald 2006)	Miranda-de la lama et al. 2013
Two spotted goby, *Gobiusculus flavescens*	48; 48	Plastic plants and dividers	Yes	Myhre et al. 2012
Japanese shorthorn calves, *Bos Taurus*	10; 10	Wall dividers	No (Macdonald 2006)	Ninomiyo & Sato 2009

Midas cichlid, *Amphilophus citrinellus*	8; 8 (1, 2, 3), 8; 5 (4)	Stones, clay, tile, moss (4 treatments)	Yes	Oldfield 2011
Blue tang, *Acanthurus coeruleus*	27; 30	Uncolonized pavement vs reef crest sites	Yes	Semmens et al. 2005
Brown trout, *Salmo trutta*	8; 8	Woody debris	Yes (Höjesjö et al. 2004)	Sundbaum & Naslund 1998
Zebrafish, *Danio rerio*	25; 25	Plastic plants (2 treatments)	No	Suriyampola et al. 2016
Mosquitofish, *Gambusia holbrooki*, platyfish, *Xiphophorus variatus*, swordtail, *X. hellerii*	3; 3	Plastic plants	Yes (Hutchins et al. 2003e)	Thompson et al. 2012
Red breast tilapia, *Tilapia rendalli*	8; 7	Pebbles & plastic plants	Yes	Torrezani et al. 2013
Atlantic salmon, *Salmo salar*	8; 8	Boulders, removed vs added	Yes	Venter et al. 2008

Brook trout, *Salvelinus fontinalis,* bull trout, *Salvelinus confluentus*	5; 5	Cobbles (2 treatments)	Yes (Scott & Crossman 1973)	Warnock & Rasmussen 2013
Fiddler crabs, *Uca terpsichores*	20; 20	Mud shelters (4 treatments)	Yes	Zucker 1974

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[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

Supplementary Table 4.3b: Time spent engaging in aggression

Species	**Sample size (open; complex)**	**Complexity Treatment**[1]	**Territoriality (reference)**[2]	**Reference**
Crayfish, *Cherax destructor*	10; 10	Brick pieces	Yes	Baird et al. 2006
Nile tilapia, *Oreochromis niloticus*	11; 11	Pebbles, plastic kelp	Yes	Barreto et al. 2011
Domestic pigs, *Sus scrofa domesticus*	30; 30	Straw substrate (2 treatments)	Yes (Sparklin et al. 2009)	Bolhuis et al. 2004
Rhesus macaques, *Macaca mulatta*	4; 8	Pine & aspen shavings	No (Hutchins et al. 2003c)	Doane et al. 2013
House mouse, *Mus domesticus*	20; 20	Bricks	Yes	Gray et al. 2000
BALB/c mice, *Mus domesticus*	20; 20	Plastic hut, 2 balls (2 treatments)	Yes (Gray et al. 2000)	Hutchinson et al. 2012
Domestic pigs, *Sus scrofa domesticus*	32; 32	Straw, peat, shavings, branches (2 treatments)	Yes (Sparklin et al. 2009)	Melotti et al. 2011

Domestic mouse, *Mus musculus*	16; 16	House, wheel, tunnel, toys	Yes	Mesa-Gresa et al. 2013
Two spotted goby, *Gobiusculus flavescens*	48; 48	Plastic plants, dividers	Yes	Myrhe et al. 2012
Midas cichlid, *Amphilophus citrinellus*	8; 6	Stones, clay, tile, moss	Yes	Oldfield 2011
Gecko, *Lepidodactylus lugubris*	24; 24	Opaque plastic moulding	No (Hutchins et al. 2003d)	Short & Petren 2008

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[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

Supplementary Table 4.4a: Foraging rate

Species	Sample size (open; complex)	Complexity Treatment[1]	Territoriality (reference)[2]	Reference
Atlantic salmon, *Salmo salar*	63; 62	Boulders	Yes	Bilhete & Grant 2016
Bats, *Austronomus australis, Saccolaimus flaviventris, Mormopterus ridei, M. planiceps*	58; 28	Forest stand vegetation (<90 vs >90stems) (all species together)	No (Hutchins et al. 2003c)	Blakey et al. 2017
Domestic rabbits, *Oryctolagus cuniculus*	72; 72	Eucalyptus sticks	Yes	Bozicovich et al. 2016
Threespine sticklebacks, *Gasterosteus aculeatus* (1), Terns, *Sterna hirundo* & *S. paradisaea* (2)	12; 12 (1), 8; 8 (2)	Stones and algae, -20% vs +20%	Yes (2 - Hutchins et al. 2002)	Candolin & Voigt 2001

Largemouth bass, *Micropterus salmoides* & muskellunge, *Esox masquinongy* (predators), bluegill sunfish, *Lepomis macrochirus* & golden shiner, *Notemigonus crysoleucas* (prey)	11; 11	Coarse woody debris (4 species combinations)	Yes	Deboom & Wahl 2013
Seahorses, *Hippocampus abdominalis* (1, 2), Australian salmon, *Arripis trutta* (3)	16; 16 (1), 24; 24 (2), 27; 27 (3)	Artificial seagrass (1-juvenile, 2-adult)	Yes (1, 2), No (3),	Flynn & Ritz 1999
Ants (Formicidae)	216; 216	Leaf litter, cones & rocks	Yes (Hutchins et al. 2003b)	Gibb & Parr 2010
Mud crab, *Panopeus herbstii*, toadfish, *Opsanus tau*	5; 5	Vertically placed oysters (2 treatments)	Yes (1- Burggren & McMahon 1998, 2- Campbell & Dawes 2004)	Grabowski 2004
Whitespotted charr, *Salvelinus leucomaenis*,	36; 36	Barriers (bricks) (2 treatments)	Yes	Hasegawa & Maekawa 2009

brown trout, *Salmo trutta*				
Rainbow trout, *Oncorhynchus mykiss*	4; 4	Cobbles, plywood (mean of 2 complex habitats)	Yes	Imre et al. 2002
Atlantic salmon, *Salmo salar*	8; 8	Boulders (mean of 3 groups)	Yes	Kemp et al. 2005
Parasitoid wasp, *Cotesia glomerata*, host, *Pieris brassicae*	9; 9	Natural vegetation (3 treatments)	No	Kruidhof et al. 2015
Arctic charr, *Salvelinus alpinus*	30; 30	Cobble with water moss	Yes	Larranaga & Steingrímsson 2015
Coral reef fish, (Scaridae, Acanthuridae, Pomacentridae, Haemulidae, Lutjanidae)	3; 3	Live coral, degraded vs living (all fish together)	Yes (Thresher 1984)	Lemoine & Valentine 2012
Blue tang, *Acanthurus coeruleus*	27; 30	Uncolonized pavement vs reef crest sites	Yes	Semmens et al. 2005

Brown trout, *Salmo trutta*	8; 8	Woody debris	Yes (Höjesjö et al. 2004)	Sundbaum & Naslund 1998
Atlantic salmon, *Salmo salar*	8; 8	Boulders, boulders removed vs added	Yes	Venter et al. 2008
Chaffinches, *Fringilla coelebs*	27; 27	Artificial stubble habitat	No (Hutchins et al. 2002)	Whittingham et al. 2004
Ants, *Pheidole diversipilosa* & *P. bicarinata,* parasitoids, *Apocephalus. pocephalus* sp. 8 & *A.* sp. 23	7; 8	Leaf litter (2 treatments)	Yes (Hutchins et al. 2003b)	Wilkinson & Feener 2007
Bats, (Emballonuridae, Mormoopidae, Vespertilionidae)	10; 12	Tree canopy, high vs low management sites (2 groups of bats)	No (Hutchins et al. 2003c)	Williams-Guillen & Perfecto 2011

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[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

Supplementary Table 4.4b: Time spent foraging

Species	**Sample size (open; complex)**	**Complexity Treatment[1]**	**Territoriality (reference)[2]**	**Reference**
Gibbons, *Nomascus leucogenys, Symphalangus syndactylus*	6; 6	Bridge, pulleys, hammocks	Yes (Hutchins et al. 2003c)	Anderson 2016
Dairy goats, *Capra aegagrus hircus*	20; 20	Branches (Mean of 2 obs)	Yes (Macdonald 2006)	Bøe et al. 2012
Domestic pigs, *Sus scrofa domesticus*	30; 30	Straw substrate (2 treatments)	Yes (Sparklin et al. 2009)	Bolhuis et al. 2004
Domestic rabbits, *Oryctolagus cuniculus*	72; 72	Eucalyptus sticks	Yes	Bozicovich et al. 2016
Rhesus macaques, *Macaca mulatta*	4; 8	Pine and aspen shavings	No (Hutchins et al. 2003c)	Doane et al. 2013
Brown trout, *Salmo trutta*	3; 4	Fine wood (2 treatments)	Yes	Enefalk & Bergman 2016
Goldfish,	10; 10 (1, 3),	Plastic plants	No	Ingrum et al. 2010

Carassius auratus	20; 20 (2)	(3 treatments)		
Japanese macaques, *Macaca fuscata*	10; 12	Natural vegetation	No	Jaman & Huffman 2008
Roach, *Rutilus rutilus*	6; 6	Gravel	No (Christensen & Persson 1993)	Murray et al. 2016
Japanese shorthorn calves, *Bos Taurus*	10; 10	Wall dividers	No (Macdonald 2006)	Ninomiyo & Sato 2009
Midas cichlid, *Amphilophus citrinellus*	8; 8 (1, 2, 3), 8; 5 (4)	Stones, clay, tile, moss (4 treatments)	Yes	Oldfield 2011
Eurasian skylark, *Alauda arvensis*	10; 10	Fake cereal straw (2 treatments)	No	Powolny et al. 2015
Cotton top tamarin, *Saguinus oedipus (1)*, Goeldi's monkey, *Callimico goeldii (2)*	2; 4 (1), 2; 3 (2)	Trees & branches	Yes (Epple 1975)	Sha et al. 2015

Broiler chicken, *Gallus gallus domesticus*	4; 4	Barrier perches	No (Leone et al. 2007)	Ventura et al. 2012
Chaffinches, *Fringilla coelebs*	27; 27	Artificial stubble habitat	No (Hutchins et al. 2002)	Whittingham et al. 2004

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[1] Unless otherwise specified, all papers compared behaviour in one complex treatment with the structures listed, versus in one open treatment without these structures.

[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

Supplementary Table 4.5a: Activity Rate

Species	**Sample size (open; complex)**	**Complexity Treatment**^{1}	**Territoriality (reference)**^{2}	**Reference**
Threespine sticklebacks, *Gasterosteus aculeatus*	7; 7	Artificial eelgrass (3 treatments)	No	Ajemian et al. 2015
Chaffinch, *Fringilla coelebs*	32; 32	Artificial cereal crop	No (Hutchins et al. 2002)	Butler & Gillings 2004
House mouse, *Mus domesticus*	7; 7 (1), 5; 5 (2, 4), 9; 7 (3)	Bricks (2 pops, 2 treatments)	Yes	Jensen et al. 2003
Albino Swiss mice, *Mus musculus*	10; 10	Nesting material, tunnels, hiding spaces	Yes	Loss et al. 2015
Two spotted goby, *Gobiusculus flavescens*	48; 48	Plastic plants and dividers	Yes	Myhre et al. 2012
European minnow, *Phoxinus phoxinus*	28; 38 (1), 25; 15 (2)	Boulders	No	Orpwood et al. 2008
Brown trout, *Salmo trutta*	8; 8	Woody debris	Yes (Höjesjö et al. 2004)	Sundbaum & Naslund 1998

[1] Unless otherwise specified, all papers compared behaviour in one complex treatment with the structures listed, versus in one open treatment without these structures.

[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

Supplementary Table 4.5b: Time spent active

Species	Sample size (open; complex)	Complexity Treatment^1	Territoriality (reference)^2	Reference
Gibbons, *Nomascus leucogenys, Symphalangus syndactylus*	6; 6	Bridge, pulleys, hammocks	Yes (Hutchins et al. 2003c)	Anderson 2016
Domestic pigs, *Sus scrofa domesticus*	30; 30	Straw substrate (2 treatments)	Yes (Sparklin et al. 2009)	Bolhuis et al. 2004
Threespine sticklebacks, *Gasterosteus aculeatus*	12; 12	Stones and algae, -20% vs +20%	Yes	Candolin & Voigt 2001
Perch, *Perca fluviatilis*	6; 6	Strings covered with periphyton	No	Christensen & Persson 1993
Largemouth bass, *Micropterus salmoides* & muskellunge, *Esox masquinongy* (predators), bluegill sunfish, *Lepomis*	11; 11	Coarse woody debris (4 species combinations)	Yes	Deboom & Wahl 2013

macrochirus & golden shiner, *Notemigonus crysoleucas* (prey)				
Brown trout, *Salmo trutta*	3; 4	Fine wood (2 treatments)	Yes	Enefalk & Bergman 2016
Bats, *Eptesicus serotinus, E. nilssonii, Vespertilio murinus, Nyctalus leisleri, N. noctula* (1), *Hypsugo savii, Pipistrellus kuhlii, P. nathusii, P. pipistrellus, P. pygmaeus* (2), *Myotis blythii, M. daubentonii, M. emarginatus, M. myotis, M. mystacinus, M. nattereri, Barbastella barbastellus, Plecotus auritus, P. austriacus* (3)	90; 360	Sand vs vegetation >1.5m above ground (3 groups of bats)	No (Hutchins et al. 2003c)	Frey-Ehrenbold et al. 2013

Brown trout, *Salmo trutta*	6; 6	Wooden logs (6 treatments)	Yes	Gustafsson et al. 2012
Japanese macaques, *Macaca fuscata*	10; 12	Natural vegetation	No	Jaman & Huffman 2008
Albino Swiss mice, *Mus musculuc*	10; 10	Nesting material, tunnels, hiding spaces (2 treatments)	Yes	Loss et al. 2015
Midas cichlid, *Amphilophus citrinellus*	8; 6	Stones, clay, tile, moss	Yes	Oldfield 2011
Cotton top tamarin, *Saguinus oedipus (1)*, Goeldi's monkey, *Callimico goeldii (2)*	2; 4 (1), 2; 3 (2)	Trees & branches	Yes (Epple 1975)	Sha et al. 2015
Broiler chicken, *Gallus gallus domesticus*	4; 4	Barrier perches	No (Leone et al. 2007)	Ventura et al. 2012

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[1] Unless otherwise specified, all papers compared behaviour in one complex treatment with the structures listed, versus in one open treatment without these structures.

[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

Supplementary Table 4.6: Shyness & Boldness

Species	Sample size (open; complex)	Complexity Treatment[1]	Territoriality (reference)[2]	Reference
Lesser scaup, *Aythya affinis*	16; 16	Macrophytes (3 treatments)	No	Austin et al. 2017
Zebrafish, *Danio rerio*	12; 12	Plastic plants (3 pops, 2 treatments)	No	Bhat et al. 2015
Perch, *Perca fluviatilis,* Roach, *Rutilus rutilus*	6; 6	Strings covered with periphyton	No	Christensen & Persson 1993
Atlantic salmon, *Salmo salar*	30; 30	Boulders	Yes	Church & Grant 2018
Largemouth bass, *Micropterus salmoides,* & muskellunge, *Esox masquinongy* (predators), bluegill sunfish, *Lepomis macrochirus* (1) & golden	11; 11	Coarse woody debris (4 species combinations, 2 behaviours aggregated)	Yes (1), No (2),	Deboom & Wahl 2013

shiner (2), *Notemigonus crysoleucas* (prey)				
Killifish, *Rivulus hartii* (prey), Wolffish, *Hoplias malabaricus* (predator)	5; 5 (1), 8; 8 (2)	Cobbles (2 treatments)	Non-territorial (Hutchins et al. 2003e)	Gilliam & Fraser 2001
Mud crab, *Panopeus herbstii* (prey), toadfish, *Opsanus tau* (predator)	5; 5	Vertically placed oysters	Yes (1-Burggren & McMahon 1998, 2-Campbell & Dawes 2004)	Grabowski 2004
Japanese macaques, *Macaca fuscata*	10; 12	Natural vegetation	No	Jaman & Huffman 2008
House mouse, *Mus domesticus*	26; 24	Bricks	Yes	Jensen et al. 2003
Domestic fowl, *Gallus gallus domesticus*	8; 8	PVC pipe with screen mesh (3 treatments)	No	Leone et al. 2007
Lizard, *Psammodromus algirus*	20; 9 (1), 38; 21 (2)	Leaves in shrubs (2 behaviours aggregated)	Yes (Hutchins et al. 2003d)	Martin & Lopez 2000

Dairy goats, *Capra aegagrus hircus*	6; 6	Two fences, earth filled tires (2 treatments)	Yes (Macdonald 2006)	Miranda-de la lama et al. 2013
Common brushtail possum, *Trichosurus vulpecula*	8; 8	Burlap sack, woody debris	No (Macdonald 2006)	Nersesian et al. 2012
European minnow, *Phoxinus phoxinus*	28; 38 (1), 25; 15 (2)	Boulders (2 pops., 2 behaviours aggregated)	No	Orpwood et al. 2008
Perch, *Perca flavescens*	19; 19	Natural lake habitat	No	Radabaugh et al. 2010
Zebrafish, *Danio rerio*	25; 25	Plastic plants (2 treatments)	No	Suriyampola et al. 2016
Atlantic salmon, *Salmo salar*	8; 8	Boulders, boulders removed vs added	Yes	Venter et al. 2008
Chaffinches, *Fringilla coelebs*	4; 7 (1), 23; 20 (2)	Artificial stubble habitat, (2 behaviours aggregated)	No (Hutchins et al. 2002)	Whittingham et al. 2004

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[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

Supplementary Table 4.7: Survival

Species	**Sample size (open; complex)**	**Complexity Treatment[1]**	**Territoriality (reference)[2]**	**Reference**
Beaugregory damselfish, *Stegastes leucostictus*	4; 4	Coral reef, low vs high complexity (2 treatments)	Yes	Almany 2004a
Surgeonfish (Acanthuridae), butterflyfish (Chaetodontidae), wrasse (Labridae), angelfish (Pomacanthidae), damselfish (Pomacentridae)	4; 4	Coral reef, low vs high complexity (2 treatments)	Yes	Almany 2004b
Amphipods, *Gammarus mucronatus* (prey), Mummichog, *Fundulus heteroclitus* (predator)	6; 6	Evenly spaced dowels (2 treatments)	No	Bartholomew et al. 2000
Daphnia, *Daphnia pulex* (prey), roach, *Rutilus rutilus*	3; 3 (1), 4; 4 (2)	Plastic (1) & real (2) macrophytes	No (Hutchins et al. 2003a)	Burks et al. 2001

& perch, *Perca fluviatilis* (predators)				
Blue crabs, *Callinectes sapidus* (prey), bonnet head sharks, *Sphyrna tiburo* (predator)	8; 8	Oyster reef habitat compared to mudflats	Yes (Burggren & McMahon 1998)	Byers et al. 2017
Pinfish, *Lagodon rhomboids*	5; 5	Artificial seagrass (2 treatments)	Yes	Chacin & Stallings 2016
Copepods (Maxillopoda) & larval damselfly *Ischnura posita* (prey), predatory damselfly	3; 3	Plastic plants	No (2–Hutchins et al. 2003b)	Delclos & Rudolph 2011
Fivestripe wrasse, *Thalassoma quinquevittatum*	10; 10	Branching coral quantity (2 vs 4) (3 treatments)	Yes	Geange & Stier 2010
Western / Glaucous-winged gull hybrid, *Larus occidentalis x glaucescens*	178; 147 (1), 174; 140 (2), 145; 134 (3),	Sand vs vegetated habitats (4 treatments)	No	Good 2002

	133; 119 (4)			
Mud crab, *Panopeus herbstii*, toadfish, *Opsanus tau*	5; 5	Vertically placed oysters (2 treatments)	Yes (Burggren & McMahon 1998)	Grabowski 2004
Bluebanded goby, *Lythrypnus dalli*	7; 7, 15; 24	Small vs large stones (1), artificial habitats (2)	Yes	Gregor & Anderson 2016
Brown trout, *Salmo trutta*	13; 15 (2)	Boulders (2 treatments)	Yes	Höjesjö et al. 2004
Blue crabs, *Callinectes sapidus*	5; 5	Seagrass shoot density (3 treatments)	Yes (Burggren & McMahon 1998)	Hovel & Lipcius 2001
Infaunal bivalve, *Mercenaria mercenaria*	4; 4	Seagrass cover (23 vs 99%) (2 treatments)	No (Hutchins et al. 2003a)	Irlandi 1994
Sillago, *Sillago* spp	4; 4	Fake mangrove stems	No (Hutchins et al. 2003e)	Laegdsgaard & Johnson 2001

Balmerino mites, *Sancassania berlesei*	20; 20	Vertical plastic drinking straws (3 groups of mites)	Yes (1), No (2 & 3),	Lukasik et al. 2006
Crayfish, *Pacifastacus leniusculus*	8; 8	Cobbles	Yes (Baird et al. 2006)	Olsson & Nystrom 2009
Juvenile perch, *Perca fluviatilis*, & roach, *Rutilus rutilus* (prey), adult perch (predator)	4; 4 (1), 4; 3 (2)	Simulated vegetation (2 treatments)	No (Christensen & Persson 1993)	Persson & Eklov 1995
Amphipods (prey), *Lembos macromanus* & *Maera insignis* (1), *M. pacifica* (2), gray damselfish, *Abudefduf sordidus* (predator)	7; 7 (1), 6; 6 (2)	Nylon bottle brushes (2 treatments)	No (Hutchins et al. 2003a)	Russo 1987
Damselflies, (Coenagrionidae)	16; 16	Artificial macrophyte stems (low vs high)	No (Hutchins et al. 2003b)	Tavares et al. 2017

Platyfish, *Xiphophorus variatus* & swordtail, *X. hellerii* (prey), Mosquitofish, *Gambusia holbrooki* (predator)	5; 5	Artificial plant stems (low vs high)	Yes (Hutchins et al. 2003e)	Thompson et al. 2012

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[1] Unless otherwise specified, all papers compared behaviour in one complex treatment with the structures listed, versus in one open treatment without these structures.

[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

Supplementary Table 4.8: Exploration

Species	**Sample size (open; complex)**	**Complexity Treatment**[1]	**Territoriality (reference)**[2]	**Reference**
Dairy goats, *Capra aegagrus hircus*	20; 20	Branches (mean of 2 obs.)	Yes (Macdonald 2006)	Bøe et al. 2012
Domestic pigs, *Sus scrofa domesticus*	30; 30	Straw substrate (2 treatments)	Yes (Sparklin et al. 2009)	Bolhuis et al. 2004
Domestic rabbits, *Oryctolagus cuniculus*	72; 72	Eucalyptus sticks	Yes	Bozicovich et al. 2016
American lobster, *Homarus americanus*	7; 7	Bricks	Yes	Cenni et al. 2010
House mouse, *Mus domesticus*	20; 20	Bricks	Yes	Gray et al. 2000
Squirrel monkeys, *Saimiri sciureus*	7; 7	Toys, pool, metal chain	Yes (Mitchell et al. 1991)	Izzo et al. 2011
Albino Swiss mice, *Mus musculus*	10; 10	Nesting material, tunnels, hiding spaces (2 treatments)	Yes	Loss et al. 2015

Domestic pigs, *Sus scrofa domesticus*	32; 32	Straw, peat, shavings, branches (2 treatments)	Yes (Sparklin et al. 2009)	Melotti et al. 2011
Domestic mouse, *Mus musculus*	16; 16	House, wheel, tunnel, toys	Yes	Mesa-Gresa et al. 2013

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[1] Unless otherwise specified, all papers compared behaviour in one complex treatment with the structures listed, versus in one open treatment without these structures.

[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

Supplementary Table 4.9: Sociality

Species	**Sample size (open; complex)**	**Complexity Treatment**[1]	**Territoriality (reference)**[2]	**Reference**
Gibbons, *Nomascus leucogenys,* *Symphalangus syndactylus*	6; 6	Bridge, pulleys, hammocks	Yes (Hutchins et al. 2003c)	Anderson 2016
Dairy goats, *Capra aegagrus hircus*	20; 20	Branches (mean of 2 obs.)	Yes (Macdonald 2006)	Bøe et al. 2012
Domestic pigs, *Sus scrofa domesticus*	30; 30	Straw substrate (4 treatments, 2 behaviours aggregated)	Yes (Sparklin et al. 2009)	Bolhuis et al. 2004
Domestic rabbits, *Oryctolagus cuniculus*	72; 72	Eucalyptus sticks	Yes	Bozicovich et al. 2016
Domestic pigs, *Sus scrofa domesticus*	9; 11	Straw substrate	Yes (Sparklin et al. 2009)	Chaloupkova et al. 2007
Japanese macaques, *Macaca fuscata*	10; 12	Natural vegetation	No	Jaman & Huffman 2008

Domestic mouse, *Mus musculus*	16; 16	House, wheel, tunnel, toys	Yes	Mesa-Gresa et al. 2013
European minnow, *Phoxinus phoxinus*	23; 25 (1), 22; 24 (2)	Boulders (2 pops.)	No	Orpwood et al. 2008

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[1] Unless otherwise specified, all papers compared behaviour in one complex treatment with the structures listed, versus in one open treatment without these structures.

[2] If no reference is listed, occurrence of territoriality was scored based on information in the original reference.

General Discussion

Overall, this thesis has shown that the effects of anthropogenic reductions in habitat complexity will likely be modified by dominance status and territoriality, but not by personality. In future scenarios with reduced habitat complexity, Chapters 1 and 2 suggest that dominant and subordinate individuals will be differentially affected by losses of complexity, with dominants more adversely affected. Subordinates are likely to experience minimal effects in areas with low predation pressure and more adverse effects when exposed to a predator, while dominants will suffer more from significantly greater energy costs and behavioural inhibition in open habitats, regardless of predation risk. Losses of habitat complexity are not likely to select for particular personality types, as different personalities will likely be similarly affected by losses of complexity, according to the results of Chapter 3. Finally, Chapter 4 demonstrates that habitat complexity will likely reduce the density of both territorial and non-territorial species, albeit through different mechanisms. While reductions of habitat complexity will decrease the densities of territorial species through increases in territory size, densities of non-territorial species will decrease through increased rates of mortality in open habitats.

Surprisingly, no measureable differences were detected in the behavioural assays in Chapter 1, for fish which became dominant among conspecifics of the same size; this suggests that aggression toward conspecifics may not have been accurately assessed by the assays. As personality assessments generally use three or fewer individual behavioural tests (e.g. Briffa & Greenaway 2011; Höjesjö et al. 2011; Réale et al. 2009; but see David et al. 2011), the six tests conducted in the individual behavioural assays were sufficient to observe a range of behaviour under different experimental conditions for a substantial length of time (~1 hr / fish). However, the behavioural assays were conducted in open experimental tanks, which may have inhibited the dominant's observed aggression, as shown in the results of both laboratory studies.

Consequently, further research on individual behaviour in convict cichlids will benefit from individual behavioural assays conducted in complex, rather than open habitats.

The four and six fish laboratory experiments in Chapters 1 and 2 both suggest that energy costs of dominance are higher than for subordinates, and that these costs are reduced in complex, relative to open habitats. Previous research has shown that dominants may inherently experience greater energetic costs, due to a higher metabolic rate (Bryant & Newton 1994; Careau et al. 2008; Millidine et al. 2009; Røskaft et al. 1986), and from engaging in more energetically expensive aggression (Hogstad 1987; Ros et al. 2006). Future work should use direct measures of energy expenditure for dominants and subordinates in both complex and open habitats to directly test these interpretations. Although personality can initially develop from differences in energy reserves (Luttbeg & Sih 2010), physical state continues to affect foraging (Lendvai et al. 2004), aggression (Fokidis et al. 2013; Sakakura & Tsukamoto 1998), and risk-taking behaviour (Heithaus et al. 2007; Lima 1988) throughout an individual's life. Like the similarly sized dominants that emerged in the same-size fish experiments, a recent meta-analysis (Niemelä & Dingemanse 2018) concluded that differences in body state, i.e. body size or metabolism, only accounted for about 5 % of the variation in personality. However, as both laboratory studies suggest that changes in energetic state affect dominants more than subordinates, a reaction norms approach, to distinguish between the effects of metabolism and energy stores, may be effective to assess how energetics affect personality.

The field study in Chapter 3 suggests that salmonid habitat restorations are not likely to select for particular personality traits. Although juvenile Atlantic salmon do have personalities and habitat complexity does affect their behaviour, no associations were found between personality and habitat complexity. These findings are encouraging, as conservation practices that introduce new selective pressures are prone to backfire, either by reducing the overall viability in non-restored habitats (Stockwell et al. 2003), or by increasing individual susceptibility to predation (Geffroy et al. 2015). Similar to our findings, Landsman et al. (2017) found no relationship between personality and successful passage through a fishway in rainbow smelt (*Osmerus mordax*), although it appears that the converse may be more common. Consideration of personality is frequently a crucial determinant of success in many conservation strategies (Merrick & Koprowski 2017), including captive breeding (Tetley & O'Hara 2012), reintroduction programs (Reading et al. 2013), and evaluating impacts of invasive species (Hirsch et al. 2017); personality traits also affect an individual's vulnerability to hunting (Madden & Whiteside 2014), angling (Sutter et al. 2012; Wilson et al. 2011) and anthropogenic disturbance (Naguib et al. 2013; Sol et al. 2013). This study contributes to the growing literature on the benefits and lack of unintentional ecological consequences of stream habitat restorations.

The meta-analysis in Chapter 4 elucidated several substantial differences between the effects of habitat complexity on territorial and non-territorial species. Only territorial species behaved as predicted in complex habitats, with lower foraging, activity, and aggression, while non-territorial species showed the opposite response to complexity. Territorial species also had higher densities and smaller territory sizes in complex habitats as predicted, but only non-territorial species showed higher survival in complex habitats. As previous work has shown that it is the reduced visual distance in complex habitats that leads to lower foraging (Kemp et al. 2005), aggression (Clayton 1987; Oldfield 2011), and risk of predation (Rilov et al. 2007), as well as higher densities (Whiteway et al. 2010) and smaller territories (Eason & Stamps 1992; Imre et al. 2002), the meta-analysis results solidify and synthesize the overall importance of visual distance on the behaviour of territorial species. In contrast, non-territorial species behaved opposite to our predictions in complex habitats, but unlike territorial species, they also experienced higher survival in complex habitats. It appears that for non-territorial species, the higher risk of mortality in open habitats drives reductions in behaviours that increase predation risk, like foraging, activity, and aggression (Jakobsson et al. 1995; Metcalfe et al. 1987), which then increase in safer, more complex habitats. Territorial species may use the increased visibility of open habitats to better avoid predators, and thus compensate for increased conspicuousness (Rilov et al. 2007); in contrast, non-territorial species suffer greater mortality in open habitats, and consequently, their behavioural response to habitat complexity is driven by risk avoidance. It is this key difference that drives the effects of habitat complexity on territorial and non-territorial behaviour: in open and complex habitats, territorial species respond to visual distance, while non-territorial species respond to predation risk, particularly conspicuousness to predators. These conclusive findings from the meta-analysis demonstrate that despite the myriad species and ecological differences found between the included species and studies, general principles of behaviour can be used to predict how territoriality and habitat complexity will affect behaviour.

The role of habitat complexity

Overall, it appears that habitat complexity provides different things to different individuals, and to different types of species. Complexity provides convict cichlids with protection from predators, while also providing dominants with lower energy costs. Similarly, the behaviour of both territorial and non-territorial species are altered in complex habitats, but driven by different mechanisms. While habitat complexity affects the behaviour of territorial species by providing visual obstructions, complexity alters non-territorial behaviour through increased protection from predators. When it can be determined what habitat complexity provides for a given individual or species, its effects on behaviour become highly predictable.

The role of personality

Although evidence for personality was found, as well as associations with fitness (body size in convict cichlids, body size and growth in Atlantic salmon), no relationships were found between personality and habitat use in either the field or laboratory experiments. Thus, personality did not predict the habitat use of either species. Atlantic salmon personality was not related to use of either complex or open habitats, while in convict cichlids, it was relative dominance that predicted habitat use, while personality did not account for variation in habitat use among dominants. Although cichlids with subordinate personality traits were found more frequently in open habitats in Chapter 1, this was not a case of personality determining habitat choice, but of subordinates being excluded from the dominants' preferred habitat. Additionally, although large dominants in Chapter 2 were bolder in personality, they preferred complex habitats, contrary to expectations. In general, personality does not appear to determine habitat preference.

What does personality explain?

Overall, the results of this thesis demonstrate that although personality does exist, it does not explain everything. The inclusion of personality within this thesis largely failed to generate new insights into the behaviour quantified in this thesis (see also, Beekman & Jordan 2017), rather emphasizing the importance of context in determining behaviour (Sinn et al. 2010). These results suggest that future research on behavioural and fitness responses to habitat complexity will benefit from more integrative approaches, which enable the simultaneous assessment of personality and energy metabolism, i.e. a pace-of-life syndrome approach (e.g. Binder et al. 2016; Biro & Stamps 2008, 2010; Careau & Garland Jr. 2012; Gangloff et al. 2017; Réale et al. 2010; Roche et al. 2016).

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