The effects of background risk on behavioural lateralization in a coral reef fish

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Summary

1. Behavioural lateralization – the preferential use of one side of the body or either of the bilateral organs or limbs – has been well documented in many species, in a number of contexts. While the benefits reported are numerous, existing latent variability in the degree of lateralization within and across populations, species and taxa indicates that existing costs may modulate its expression.

2. Few studies have reported *changes* in the degree of lateralization at the individual level, in response to long-term changes in environmental conditions, but not in response to short-term changes in environmental conditions. Predation is highly variable both temporally and spatially and hence is a good candidate for testing lateralization effects based on short-term changes in environmental conditions.

3. Here, we tested the hypothesis that the degree of behavioural lateralization changes following short-term exposure to different levels of risk. We tested whether wild-caught juvenile damselfish exposed to a high or low background level of risk for 4 days would subsequently differ in their turning bias, a trait that has been linked to predator escape behaviour in fishes.

4. We found that 4 days is enough to induce a difference in the absolute lateralization scores of the fish, with high-risk fish being more strongly lateralized than low-risk fish. Practically, this difference stemmed from decreasing lateralization scores for newly recruiting coral reef fishes that were kept in low-risk environments, with the concurrent maintenance of higher lateralization scores for fish maintained under high-risk conditions. Fish from the high-risk background had higher survival than those from the low-risk background upon release into mesocosms containing reef predators.

5. Our study highlights how early exposure to differential predation risk affects the degree of behavioural lateralization. Given the profound effects of lateralization on many aspects of an animal's life from its ability to discriminate conspecifics to how it forages and interacts during agonistic interactions, predation risk may be a key driver of animal development.

Key-words: antipredator defences, coral reef fishes, detour test, plasticity, predation risk

Introduction

Behavioural lateralization – the preferential use of one side of the body or either of the bilateral organs or limbs – can be traced back to the common ancestors of echinoderms and chordates (Andrew 2002) and has been well documented in all vertebrate taxa (Csermely 2013). Such lateralization is commonly displayed in a number of ecological contexts. For instance, during exploratory or migratory behaviours, the eyes are often used asymmetrically, with general environmental cues being processed preferentially by the left eye (Wiltschko *et al.* 2002; Vallortigara & Rogers 2005). Similar asymmetries in sensory inputs have been reported during agonistic interactions (Hews & Worthington 2002), predator detection (Franklin & Lima 2001; Rogers & Kaplan 2006) or during conspecific recognition tasks (Basile *et al.* 2009). The asymmetry can also be displayed through 'handedness'. The preferential handling of

tools and food items by one hand/paw/foot is relatively common in birds and mammals (Rogers & Workman 1993; Rogers 2009).

The evolution of behavioural lateralization is linked to the benefits it provides. Rogers, Zucca & Vallortigara (2004) reported that lateralized chicks (*Gallus domesticus*) could perform simultaneous tasks (pecking and predator vigilance) at the same time using different parts of their brain. In contrast, non-lateralized chicks performed poorly in both tasks when forced to multitask. These results demonstrate clear multitasking benefits (increased foraging gain and predator avoidance) due to lateralization. In addition to the advantages provided at the individual level, groups of social animals benefit from having similar levels of lateralization as it enhances group escape behaviour and allows for the formation of more stable social groups (Vallortigara & Rogers 2005). These improvements would certainly provide a fitness benefit explaining the spread of this trait through selection (Rogers, Zucca & Vallortigara 2004). Despite the overwhelming list of benefits documented in the literature, evidence suggests a surprising variation in the degree of lateralization (or lack thereof) of many species (Vallortigara, Rogers & Bisazza 1999; Bisazza *et al.* 2000a), suggesting that lateralized individuals may incur costs that would prevent the selection for this trait in certain contexts and hence would maintain species-level variability. Among the list of potential costs, Vallortigara & Rogers (2005) argue that lateralization may be disadvantageous if cues processed preferentially by one side tend to appear at random in the environment. Others have argued that strongly lateralized individuals may perform poorly when tasks require coordination between hemispheres (Dadda *et al.* 2009; Dadda, Koolhaas & Domenici 2010). Just like any other trait, the trade-off between the costs and benefits of being lateralized should determine the expression of this trait for specific tasks and contexts, in specific environmental conditions.

Lateralization can be heritable (Hopkins 1999; Bisazza, Facchin & Vallortigara 2000b) or be expressed as a result of specific hormone levels or environmental factors (Vallortigara & Rogers 2005). For instance, light exposure during embryonic development determines the degree of eye lateralization in chicks (Rogers 1997). In the context of predation, Brown, Gardner & Braithwaite (2004) showed that wild-caught fish (*Brachyrhaphis episcopi*) taken from high- and low-risk streams differed in their degree of lateralization with individuals from the high-risk environment displaying stronger lateralization. Similarly, many studies have reported how individuals from different populations exposed to different environmental conditions can differ in their degree of lateralization. However, very little is known about the plasticity associated with the expression of lateralization bias at the individual level. In one study, Bisazza *et al.* (1998) reported that limiting access to mates for 2 months would affect the turning bias in fish (*Girardinus falcatus*) exposed to sexual stimuli. Cantalupo, Bisazza & Vallortigara (1995)

reported changes in side bias upon repeated exposure to simulated predatory attacks. Such results provide some evidence that the existence (or lack thereof) of bias at the individual level may not be as fixed as previously thought, but rather could change within an individual's life depending on recent experience. If the expression of a bias provides greater benefits in one type of environment than another, and an individual can find itself in both types of conditions, then selection should favour individuals able to modulate the expression of this bias – a form of behavioural plasticity.

Predation is a strong selective force, known to affect many facets of an animal's life, including its behaviour, life history and morphology. Predation is highly variable in space and time (Lima & Bednekoff 1999), with risk changing on a moment-to-moment basis, or on a daily, monthly or yearly cycle. In response to this variation, many of a prey's antipredator traits are highly plastic, and their expression is dependent on the level of threat detected by the individuals (Helfman 1989). Some antipredator traits, such as vigilance or the decision to hide, can be tuned to match their perceived level of predation risk within seconds (Lima & Dill 1990). Others, such as the development of defensive morphological traits (spines, deeper body) (Ferrari, Wisenden & Chivers 2010), may take more time to change and may or may not be reversible (Chivers *et al.* 2008).

The goal of our study was to investigate the effect of background level of risk on the expression of lateralization in juvenile coral reef fishes. Our experiment is similar to the work of Brown, Gardner & Braithwaite (2004) except that rather than examining fish that have been raised for many generations under differential risk, here we manipulate risk over a shorter time frame. In the context of predation, behavioural lateralization could be expressed in bias of eye use (De Santi *et al.* 2001) or turning bias of prey individuals in a detour test (Cantalupo, Bisazza & Vallortigara 1995; Bisazza *et al.* 1998; Bisazza, Dadda & Cantalupo 2005). Some have argued these two traits stemmed from the same bias in eye use in the context of vigilance or predator inspection (Facchin, Bisazza & Vallortigara 1999). Last-minute antipredator strategies often rest on the ability of the prey to evade and/or survive a predatory attack. Prey can deceive predators into directing their attacks towards a less vital portion of their body via the use of morphological lures such as eye spots (Stevens 2005). They can also quickly dash away from the predator, which usually involves the escape of the fish in a direction perpendicular to the axis of attack of the predator. In this type of situation, displaying a turning bias would likely allow the prey to save time in processing and decision-making, and would increase its chances of escaping, while maintaining the predator on the eye side that preferentially process predator-related information. Here, we argue that if turning bias is a trait that offers increased benefits in conditions of high predation risk, its expression should be greater in individuals raised in a high-risk environment.

This scenario assumes that turning bias is not fixed genetically and that variation in early predation risk leads individuals down to different irreversible lateralization trajectories or alternatively that the degree of lateralization is a plastic trait that can change through an animal's life depending on risk level. Such plasticity, if it exists, should be associated with inherent costs, such as lower performance in other tasks, or other disadvantages associated with having a side preference (Vallortigara & Rogers 2005).

In this study, we used wild-caught juvenile whitetail damselfish, *Pomacentrus chrysurus*, as they have been shown, like many other fish species, to exhibit turning bias (Bisazza *et al.* 2000a; Domenici *et al.* 2012; Bibost, Kydd & Brown 2013). We exposed them for 4 days to conditions of high or low predation risk, following the established protocol (Brown *et al.* 2013; Chivers *et al.* 2014). After this period, we tested the turning bias of the fish using a detour test commonly used in fish and birds (Bisazza *et al.* 1998; Vallortigara, Rogers & Bisazza 1999) and investigated any difference seen between fish from the two risk groups. We also recorded the existing (if any) turning bias of the wild-caught fish prior to the risk treatment. To further assess the potential benefits associated with any behavioural bias, we compared the survival of high- and low-risk fish exposed to predators in large mesocosms.

Materials and methods

TEST SPECIES

The whitetail damselfish, *Pomacentrus chrysurus*, is a common coral reef fish in the Indo-Pacific region, typically associated with coral rubble in shallow (<10 m depth) reef waters. It has a bipartite life history typical of many reef fishes, with a planktonic larval stage maintained for ~20–25 days, before young fish recruit to coral reefs and transition to benthic juveniles that are highly territorial. This transition involves a severe population bottleneck, with more than 60% of individuals succumbing to predation within 1–2 days of settlement to the reef (Almany & Webster 2006). These results highlight the importance of predation in structuring these communities. Indeed, juveniles are vulnerable to a diverse range of predators including dottybacks *Pseudochromis fuscus,* which can be routinely observed to consume juveniles that venture too far from shelter.

Settlement-stage juveniles of the whitetail damselfish were collected overnight using light traps moored in open water around Lizard Island (14′40°S, 145′28°E), in the northern Great Barrier Reef, Australia in November 2013. Adult predatory dottybacks (Feeney *et al.* 2012) were captured from a lagoon using hand nets and dilute clove oil, kept individually in mesh baskets placed in flow-through tanks and fed daily with 2 juvenile damselfish.

LATERALIZATION TRIALS

Lateralization trials were performed on newly caught fish (settlement-stage juveniles) to assess the lateralization scores of the fish prior to any risk treatment. Other fish underwent a 4-day risk treatment, during which they were exposed to a high- or low-risk environment. They were then tested for their behavioural lateralization after the end of the treatment. Each fish was only tested once. All tests temporally overlapped, to control for possible temporal confounds in the results.

To assess the behavioural lateralization of the fish, we used a detour test. The apparatus used in this study was based on a design used previously by Bisazza *et al.* (1998) and Dadda, Koolhaas & Domenici (2010). Briefly, it consisted of an opaque Perspex tank (60 cm length × 30 cm width × 15·4 cm height), with a runway in the middle (25 cm length × 3 cm width × 12 cm height), and at both ends of the runway (3 cm ahead of the runway), an opaque barrier (12 cm length × 12 cm height) was positioned perpendicular to the orientation of the runway. Water in the tank was 6 cm deep. At the start of each trial, a single fish was introduced into the middle of the runway and left for 2 min to become accustomed to the environment. During each trial, fish were gently manoeuvered to the starting point of the runway. The fish then swam along the runway until it faced the barrier. Fish then had to make a decision to turn left or right around the barrier. To account for any possible asymmetry in the set-up, tests were carried out alternately on the two ends of the runway (Bisazza *et al.* 1998). To avoid fish taking 'a familiar route', the fish entered the runway from a different side from which they exited. Turning was scored by direct observation. The criterion used for scoring was the first turning direction taken by the fish when exiting from the runaway. Ten consecutive tests were conducted for each fish. To avoid changes in water temperature and dissolved oxygen levels, both of which have been found to influence neural function (Domenici, Lefrancois & Shingles 2007), the tank water was changed every ten trials. Water temperature in the experimental tank was maintained at 27–28 °C.

In order to compare the high- and low-risk groups with respect to their left–right preference in the detour test, we first calculated a relative lateralization index (L_R) according to the following formula (Bisazza *et al.* 1998): [(#right turn - #left turn)/(total # of trials, i.e. 10)*100. Mean L_R is used to assess turning preference (i.e. bias in left or right turns) at the *population* level. On the basis of the L_R index, individuals were classified between the extreme values of '100' (fish that turned right on all 10 trials) and '−100' (fish that turned left on all 10 trials). A mean L_R near zero indicates that a given sample of the population is neither left- nor right-biased in its turning tendency (Bisazza *et al.* 2000a). A sample that is not left- or right-biased may include individuals that are themselves right or left biased. Given that our fish were sampled over a long time period (3 weeks) and likely do not belong to the same population, we used the absolute lateralization index (L_A) of each fish to evaluate the strength of *individual* lateralization in the detour test irrespective of their preference for right or left turning. The L_A index corresponds to the absolute value of L_R, thus ranging from 0 (an individual that turned in equal proportion to the right and to the left) to 100 (an individual that turned in the same direction in all 10 trials). L_A thus allowed us to compare the strength of the lateralization (irrespective of its direction) among groups at the individual level. We tested 30 fish per treatment group.

CREATING HIGH AND LOW BACKGROUND LEVELS OF RISK

To create a high-risk environment that would not provide specific information about the diversity, density and predator species causing it and bias the response towards a specific predator type, we decided to use non-predator specific general risk cues. Injured conspecific cues (hereafter alarm cues) are chemicals that innately elicit an overt antipredator response when detected by nearby conspecifics (Ferrari, Wisenden & Chivers 2010). Given that these cues are located in the skin of prey and thus can only be released in the water column via mechanical damage to the skin (which would usually occur during a predator attack), they represent a

reliable indicator of risk and mediate many antipredator adaptations in aquatic species (Ferrari, Wisenden & Chivers 2010). Many damselfish species, including the whitetail damselfish, are known to possess and respond to cues from injured conspecifics (Ferrari *et al.* 2011a; Lienart *et al.* 2014).

Following their capture, juvenile damselfish were immediately taken to the laboratory and placed in groups of 10 in a series of 3-L flow-through plastic aquaria with a flow rate of approximately 3 L h^{-1}. The fish were fed *ad libitum* with newly hatched brine shrimp 3 times per day. We left them to acclimate for 24 h before starting the experimental treatment. Fish were then exposed to high- or low-risk conditions by introducing a solution of alarm cues (high risk) or a seawater control (low risk) into the tanks 3 times per day for 4 days. Half the fish received the high-risk treatment, while the remainder of the fish received the low-risk treatment. The alarm cue solution was prepared minutes prior to being used, by making 6 vertical cuts on each side of 6, freshly euthanized, donor conspecific fish and then rinsing the fish in 60 mL of seawater. We injected 5 mL of this standard alarm cues solution into the conditioning tanks, giving us a concentration of 2 cuts L^{-1} when it was injected into the tanks. This concentration has been shown to elicit strong antipredator responses in our test species (Chivers *et al.* 2014). The timing of the 3 injections occurred randomly between 0800 and 1800 h, with a minimum of 1·5 h between consecutive injections. There was no mortality in either of the holding tanks over the 4-days conditioning period.

SURVIVAL TRIALS

To assess whether changes in lateralization scores would confer a fitness advantage, we tested whether high- and low-risk juveniles would differ in survival, using a well-established protocol (Ferrari *et al.* 2011b). Groups of 4 fish of matching risk treatment (day 1 post-treatment) were placed in outdoors flow-through mesocosm pools (111 cm diameter, 45 cm high, 368 L) containing a 1-cm-deep sand substrate, an airstone and 2 pieces of dead bushy hard coral (*Pocillopora damicornis*) placed beside each other. These 2 pieces formed a coral patch of ~90 cm in circumference and ~20 cm in height. The water was pumped directly from the ocean, so it followed natural temperature fluctuations. Thirty minutes after the introduction of the damselfish, we introduced a single dottyback in each mesocosm. Both prey and predator were left undisturbed, except for 2 feeding events (1100 and 1700 h), in which we injected 60 mL of a solution of freshly hatched *Artemia* sp (~ 250 mL^{-1}) in the pool. The next day, all the fish were removed from the pool and we recorded the number of surviving fish. The water was drained, the water flow increased and the pool reset for the next trial.

One week prior to the start of the experiment, the predators were fed juvenile damselfish, but starved for 24 h prior to being used in a trial. To control for the effect of predator (size, experience, hunting success, etc.), we used each predator as its own control. The predators (16 in total) were randomly allocated to either the high- or low-risk group, in a balanced design (8 in the high-risk treatment and 8 in the low-risk treatment). After the end of their first trials, the predators were fed, and then starved for a day prior to being used in their second trials, which took place 48 h after their first one. The treatment with which each predator was associated was switched between the first and second trial.

Results

BEHAVIOURAL LATERALIZATION

There was significant variation in absolute lateralization (L_A) scores among the groups (one-way ANOVA, $F_{2,87} = 5·1$,
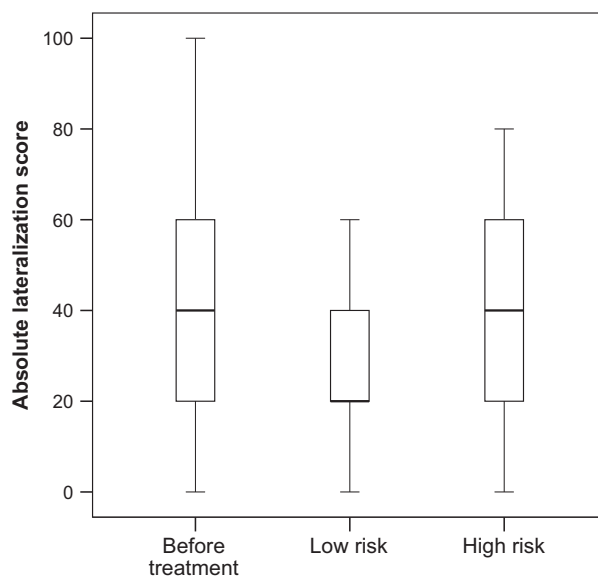

Fig. 1. Boxplot of the absolute lateralization index of wild-caught whitetail damselfish (*Pomacentrus chrysurus*) in a detour test. Fish were tested prior to treatment exposure (before treatment), or were exposed to high- or low-risk conditions for 4 days and tested the following day.

$P = 0·008$). Newly caught fish and high-risk fish did not differ in their L_A scores (Tukey *post-hoc* tests, $P > 0·99$), with both of these groups being significantly more lateralized than low-risk fish ($P = 0·016$ and $P = 0·021$, respectively, Fig. 1).

SURVIVAL

Prey in the high-risk treatment survived significantly more than those in the low-risk treatment (difference: 29·7%, paired *t*-test, $t_{15} = 3·4$, $P = 0·004$, Fig. 2).

Discussion

Our results clearly indicate that juvenile fish experiencing high-risk conditions were more strongly lateralized than those experiencing low-risk conditions. This result followed our predictions that, if behavioural lateralization provided a fitness-related advantage in a predation context, its expression should be more pronounced in individuals from the high-risk environment. It is striking that such short exposure (4-day) to a general risk cue has the potential to modulate the expression of a behavioural lateralization trait. Previous studies have reported changes in lateralization bias, but the duration of stimulus exposure was much longer, with juveniles or subadults tested after being exposed to varying conditions from weeks, months or from birth (Rogers 1997; Bisazza *et al.* 1998; Brown, Western & Braithwaite 2007; Bibost, Kydd & Brown 2013). To our knowledge, this is the first study to find measurable differences in behavioural lateralization in response to variation in environmental conditions over
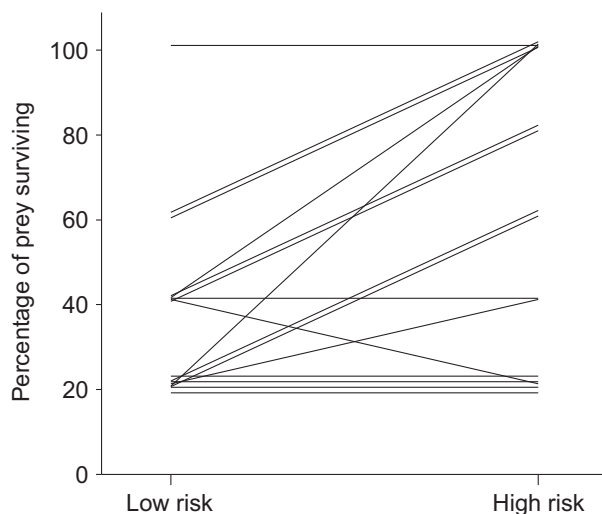
Fig. 2. Mean (±SE) proportion of juvenile whitetail damselfish (*Pomacentrus chrysurus*) surviving in mesocosm experiments with a predator. Fish were exposed to high- or low-risk conditions for 4 days and subsequently put in groups of 4 fish in a mesocosm and left to interact with a predatory dottyback (*Pseudochromis fuscus*) for 22 h. Each predator was used once in each treatment (paired design).

such a short time frame. This finding highlights that early predation risk starts fish down a specific irreversible lateralization trajectory or alternatively that the degree of lateralization is a plastic trait that can change through an animal's life depending on risk level. In either case, our results suggest that the expression of the bias does not directly stem from a change in cerebral organization per se. In this study, we also provide the first documentation that the expression of such a trait could potentially lead to increased survival during predator encounters. Of course, caution should be used as other behavioural and physiological traits may have been altered by the risk exposure.

A few studies have documented a change in the degree of lateralization of individuals due to learning or habituation to a stimulus. Bibost, Kydd & Brown (2013) argue that this change is a result from a re-categorization of the stimulus by the individual. For instance, lateralization bias may differ for novel vs. familiar stimuli (Tang & Verstynen 2002), and repeated exposure to the same stimulus would eventually lead the individual to change its categorization from novel to familiar, changing the behavioural bias observed in response to that stimulus. This type of learning or experience may help explain the experience-related change in lateralization observed in some species. In our experiment, the repeated exposure was to a chemical stimulus, but the testing involved a non-alarm cue-related apparatus. Thus, learning via habituation or re-categorization cannot explain our results, but rather, it is likely that such exposure would turn on a suite of antipredator traits, some of which could manifest themselves as a turning bias or eye bias related to ways in which prey deal with predation-related information (Cantalupo, Bisazza &

Vallortigara 1995; Bisazza *et al.* 1998; De Santi *et al.* 2001; Bisazza, Dadda & Cantalupo 2005).

We documented that wild-caught juveniles were already displaying a strong turning bias prior to the risk treatment. This indicates that the differences observed in lateralization scores stemmed from high-risk fish maintaining their bias, while low-risk fish underwent a relaxation or decrease in the expression of their behavioural lateralization. This could result from individuals reducing their degree of laterality while maintaining their original laterality direction or from some individuals reversing their laterality direction. The expression of a turning bias in wild-caught juveniles may not be surprising, if we consider that juveniles recruiting to the reef are likely exposed to pelagic predators, and likely travel in large groups (Bernardi *et al.* 2012). A population bias for turning in the same direction may allow for a greater coordination in group escape behaviour during this recruitment journey. The decrease in the degree of lateralization found in low-risk fish would indicate that predation is an important driver in the maintenance of this trait and that the cost incurred by maintaining a pronounced lateralization may override the benefits in low-predation environments. While our study has focused on demonstrating the benefits (survival) associated with the expression of this trait, we are unfortunately lacking evidence as to the costs of this turning bias. Further work should focus on comparing the performance of lateralized vs. non-lateralized individuals in non-predation-related tasks. For our test species, competition plays a great role in the success of individuals in their new environment (McCormick & Weaver 2012). The ability to gain access to "prime" coral patch real estate is dictated by the outcome of agonistic interactions between conspecifics and also heterospecifics (Munday, Jones & Caley 2001). While size is a great predictor of competitive outcome (Maynard-Smith & Parker 1976), it would be interesting to compare the outcome of competitive interactions between size-matched individuals that differ in their lateralization bias.

While we linked variation in environmental risk to variation in turning bias, other traits could also be affected by the treatment and mediate the survival differences reported here. Reddon & Hurd (2008, 2009) reported that differences in turning bias in fish were linked to differences in the expression of personality traits such as boldness and aggression. However, boldness is usually considered a non-advantageous trait in high-risk situations (Conrad *et al.* 2011), hence unlikely to explain our present results. Similarly, exposures to high levels of background risk have been linked to the expression of a neophobic phenotype, with prey displaying fear responses to novel stimuli (Brown *et al.* 2013; Chivers *et al.* 2014). Dadda, Koolhaas & Domenici (2010) also demonstrated that fish receiving high lateralization scores in a detour test also showed a higher escape reactivity, higher turning rates and longer distances travelled in escape performance tasks. Hence, while we undoubtedly linked the background level of risk to the expression of behavioural lateralization in our

juveniles, we cannot ascertain which particular mechanism (s) is (are) responsible for the increased survival we observed. However, there is little doubt that high-risk fish are overall performing better in antipredator-related tasks than fish with a history of low risk.

Acknowledgements

Data accessibility

Data for this study (Ferrari *et al.* 2015) are in the Dryad Digital Repository: doi:10.5061/dryad.4q7s8.

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