The effects of familiarity on escape responses in the Trinidadian guppy (*Poecilia reticulata*)

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Predation is the main cause of mortality during early life stages. The ability to avoid and evade potential threats is, therefore, favoured to evolve during the early stages of life. It is also during these early stages that the process of familiarization occurs. It has long been recognized that associating with familiar individuals confers antipredator benefits. Yet, gaps in our knowledge remain about how predator evasion is affected by social experience during early stages. In this study, we test the hypothesis that familiarization acquired during early life stages improves escape responses. Using the guppy *Poecilia reticulata*, we examine the effect of different recent social conditions in the three main components of predator evasion. Using high-speed motion analysis, we compared the number of individuals in each test group that responded to a visual stimulus, their reactive distance and magnitude of their response (maximum speed, maximum acceleration and distance) in groups composed either of familiar or non-familiar individuals. Contrary to the prediction, groups composed of familiar individuals were less responsive than groups of unfamiliar individuals. Reactive distance and magnitude of response were more dependent on individual size rather than on familiarity. Larger individuals reached higher maximum speeds and total distances in their escape response. Our result indicates that familiarity is likely to affect behaviour earlier in a predator-prey interaction, which then affects the behavioural component of the response. Taken together our study contributes to previous ones, by distinguishing which components of an escape response are modulated by familiarity.
The effects of familiarity on escape responses in the Trinidadian guppy 

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ABSTRACT

Predation is the main cause of mortality during early life stages. The ability to avoid and evade potential threats is, therefore, favoured to evolve during the early stages of life. It is also during these early stages that the process of familiarization occurs. It has long been recognized that associating with familiar individuals confers antipredator benefits. Yet, gaps in our knowledge remain about how predator evasion is affected by social experience during early stages. In this study, we test the hypothesis that familiarization acquired during early life stages improves escape responses. Using the guppy *Poecilia reticulata*, we examine the effect of different recent social conditions in the three main components of predator evasion. Using high-speed motion analysis, we compared the number of individuals in each test group that responded to a visual stimulus, their reactive distance and magnitude of their response (maximum speed, maximum acceleration and distance) in groups composed either of familiar or non-familiar individuals. Contrary to the prediction, groups composed of familiar individuals were less responsive than groups of unfamiliar individuals. Reactive distance and magnitude of response were more dependent on individual size rather than on familiarity. Larger individuals reached higher maximum speeds and total distances in their escape response. Our result indicates that familiarity is likely to affect behaviour earlier in a predator-prey interaction, which then affects the behavioural component of the response. Taken together our study contributes to previous ones, by distinguishing which components of an escape response are modulated by familiarity.

INTRODUCTION
Predation is a powerful agent of mortality, particularly during early life stages when organisms are at heightened risk due to their smaller size (Cushing 1974). Natural selection is therefore expected to favour the development of antipredator behaviours early in life (Braithwaite & Salvanes 2005; Vilhunen & Hirvonen 2003). Antipredator behaviours are generally divided into two major types; 1) avoidance and 2) evasion (Fuiman & Magurran 1994; Weihs & Webb 1984). Avoidance includes any pre-emptive behaviours in which the individual reduces the likelihood of encountering a predator and consequently of its attack (Fuiman & Magurran 1994). Evasion, on the other hand, occurs once the predator initiates the attack. As predator avoidance is not always possible, successful predator evasion tactics are essential for survival. The behaviour and frequency at which each evasion tactic is employed is context-dependent; individuals adopt behaviours that improve their evasive response and, thus, enhance survival (Domenici 2010).

One way in which organisms may reduce the risk of predation is by associating with others, either by schooling or just by joining a group (Ruxton & Johnsen 2016; Ward & Webster 2016). Though groups might be more conspicuous to a predator, each individual within the group has a smaller probability of being predated than if alone. Among the group antipredator benefits of enhanced vigilance, dilution of risk, predator confusion and coordinated antipredator maneuvers (Krause & Ruxton 2002; Ward & Webster 2016), there is strong evidence showing that familiarity within the group enhances antipredator behaviours (Griffiths et al. 2004). Familiarity between conspecifics can be broadly defined as the ability to discriminate between individuals based on previous interactions (Griffiths 2003). The process of familiarization is based on visual, and auditory and olfactory cues (Coffin et al. 2011; Reby et al. 2001; Zajitschek & Brooks 2008). Repeated exposure to a stimulus can lead to familiarisation, in a social context
that may be conspecifics with whom an individual interacts, such as during foraging. Fitness benefits of joining a group composed of familiar conspecifics over unfamiliar individuals has been demonstrated in various taxa (Figueroa et al. 2013; Grabowska-Zhang et al. 2012; Grabowska-Zhang et al. 2011; Strodl & Schausberger 2012; Strodl & Schausberger 2013), particularly in shoaling fish (Barber & Wright 2001; Griffiths & Magurran 1997b).

The benefits in associating with familiar individuals for the social learning and for the development and acquisition of successful antipredator responses in shoaling fish are acknowledged (Swaney et al. 2001; Ward & Hart 2003). Groups composed by familiar individuals may be more cohesive and have reduced neighbour distance (Chivers et al. 1995; Höjesjö et al. 1998), characteristics which enhance predator confusion and dilute individual risk. Further, familiar groups generally experience reduced within-group aggression and evolve more stable social hierarchies (Griffiths et al. 2004; Höjesjö et al. 1998; Johnsson 1997; Tanner & Keller 2012). Reduced aggression within familiar groups allows more time for predator vigilance, which may improve escape latency (Griffiths et al. 2004; Strodl & Schausberger 2012). Additionally, individuals are more likely to perform cooperative antipredator behaviours when in familiar groups, as they may remember whether the others have behaved cooperatively in the past (Dugatkin & Alfieri 1991). For example, individuals in familiar groups may be more likely to perform more risky antipredator manoeuvres (Chivers et al. 1995), join predator mobbing (Grabowska-Zhang et al. 2012), or perform predator inspection (Dugatkin & Godin 1992). Such antipredator behaviours put individuals at higher risk, but improve group antipredator response.

While the effect and importance of familiarity on predator avoidance is well recognised, how familiarity shapes predator evasion, particularly the escape response, remains largely
unexplored For example, studies to date have focused exclusively on the effect of familiarity on the latency of the response (Griffiths et al. 2004; Strodl & Schausberger 2012) and have not considered other aspects of the escape performance. Successful escape responses depend on various components, such as latency, velocity and distance travelled in the response (Domenici & Blake 1997). For instance, latency, considered as the time between the onset of the predator attack and the start of the response, is crucial for the outcome of the interaction (Fuiman et al. 2006). Also, an effective response requires moving away from the attack trajectory fast enough so the predator cannot adjust it (Fuiman & Cowan 2003). Studies on escape behavior have focused on the aspects of the escape response which are modulated by the relative cost of escaping and perceived risk, such as latency, reactive distance (the distance between the predator and prey when the prey initiates a response) and responsiveness (whether or not a prey responds to an attack) (Domenici 2010). Kinematic aspects of escape responses, on the other hand, are less often considered, as they have been considered to be constrained by the sensory-motor system of the individual (Domenici & Blake 1997). A review by Domenici (2010) emphasizes that performance in escape responses is not always maximized to the physical capabilities of the individual, which suggests that other factors may cause variability in escape responses. Given the importance of social behaviour in reactive distance and responsiveness (Dial et al. 2016), it is plausible that the kinematic aspects of an escape response may be modulated in a similar way by familiarity. In order to fully assess the escape performance of fish, we need to employ an approach that takes into account the multiple behavioural aspects on an escape response. The aim of this study was to address the role of familiarity acquired during early life stages in affecting the different components of the antipredator escape responses in the Trinidadian guppy (Poecilia reticulata).
Guppies shoal immediately after birth (Magurran et al. 1994). These early stages are important for the establishment and reinforcement of individual discrimination and familiarity in guppies (Barbosa et al. 2016; Barbosa et al. 2013; Chapman et al. 2008a; Chapman et al. 2008b; Laland et al. 2003). Within group familiarity is likely to affect how a group of individuals respond to a potential predator. Guppies respond to a predator attack by performing a “fast-start” escape response, characteristic to most fish species (Dial et al. 2016). This evasion tactic consists of an unambiguous quick and sudden burst of swimming activity usually of only tenths of a second that propels the fish away from an oncoming predator (Domenici & Blake 1997; Fuiman et al. 2010; Webb 1978; Weihs 1973). Fast-start escape responses integrate a combination of behavioural and kinematic components (Marras et al. 2011), both of which were examined in this study.

In view of the antipredator benefits of familiarity, we predicted that juvenile guppies are also more responsive and perform more successful escape responses when in groups of familiar conspecifics. To test this prediction, we exposed familiar and unfamiliar groups of juvenile guppies to a digital display of a looming object and quantified the difference in responsiveness (number of fish responding), reactive distance (based on the size of the stimulus when the response started) and magnitude of the escape response (maximum speed and acceleration achieved during the response, and distance covered by the escaping fish). This approach allows us to identify the role of familiarity in a behaviour closely related to survival during early life stages and to pinpoint which components of an escape response are more likely to be affected by social experience.
METHODS

All guppies used were 8th generation descendants of individuals collected from the Lower sections of the Tacarigua River in Trinidad. Several species of fish predators have been reported in this locality including the pike cichlid (*Crenicichla alta*), the blue acara (*Aequidens pulcher*) and the wolf fish (*Hoplias malabaricus*), which also prey intensively on juvenile guppies (Magurran & Seghers 1994). Experimental fish were housed, and all observations recorded, at the aquarium facility at the Sir Harold Mitchell Building, University of St Andrews, UK. The aquarium has an air temperature control system, which kept the tank temperatures at a mean (±SD) temperature of 24.5°C (± 0.3 °C). All stock tanks contained similar numbers of males, females and juveniles. Lighting conditions followed a 12-hour light/dark cycle. All fish were fed daily with TetraMin® flake food. Our experimental design was examined by the Biology School Ethics Committee from the University of St Andrews and declared our study to be exempted of Animal Ethics approval.

Test Fish Collection and Rearing

Prior to the experiment, we collected three juveniles from three different stock tanks (60 x 40 x 40 cm) that contained a mix of males, females and juveniles using a dip net (there are 15 Lower Tacarigua stock tanks in at the University of St Andrews aquarium facility). This ensured that the test groups were composed neither of familiar conspecifics nor of close kin. Further, in all stock tanks there are large and smaller boulders and java moss, which allows a more natural environment for guppies. Immature juvenile guppies (i.e. age between 5 and 6 weeks) were allocated to a holding tank (20 x 22 x 30 cm) a to create a test group. Each test group was
composed of three individuals. A total of 42 holding tanks were used. Black plastic sheets were placed between each tank to ensure each test group was visually isolated from adjacent groups. Fish were of similar size and randomly distributed between holding tanks (mean (±SD) 10.8 (±1.7) mm). Nevertheless, in order to be able to identify each individual during tracking, test groups were carefully constituted of different sized individuals. Each test group remained in its holding tank for two weeks to ensure the establishment of familiarity between tank mates (Griffiths & Magurran 1997a).

**Escape Response Trials**

We split the juveniles into two treatments: a familiar and an unfamiliar. Each group was composed of three juveniles (Total 42 groups, 21 familiar and 21 unfamiliar). Each day we tested six groups, three groups with familiar individuals and three of unfamiliar individuals. In familiar groups, individuals were tested with those fish that they shared the holding tank with for two weeks prior to testing. For unfamiliar groups, we took three fish, each from a different holding tank so they had not seen each other before, and put them together in the observation chamber for testing (Figure 1). Unfamiliar groups were treated as a control. Each group was only tested once.

All tests occurred between 9:00 and 11:00 am and at least an hour after being fed. These measures were taken to avoid differences in satiation rate and time of day that might affect the behaviour of the individuals. The experimental setup used to assess escape response was based on an established protocol (Fuiman et al. 2010), but modified for this experiment (Figure 2). Each trial involved presenting a digital display of a looming object to a test group. The digital display consists 1.8-second sequence showing black oval in the middle of a white background that increases its size to simulate an approaching object (Supplementary Information). The same
stimulus has been shown to elicit a startle response in larval fish of similar size (Fuiman et al. 2006; Ojanguren & Fuiman 2010). The video was presented using a LCD screen (Braun 1210) located 0.23 cm from a 10x10x10 cm glass test chamber. Water depth within the observation chamber was kept at 225 ml to minimise vertical movement in escape responses. For each trial, a test group was transported to the observation chamber one individual at a time and given at least 10 minutes of acclimatisation to their new surroundings before testing began. Each individual fish was only tested once. After the terminus of the trials the individuals were returned to a stock tank and were not reused in the experiment.

Individual response to the visual stimulus was recorded at 240 frames s⁻¹ using a high-speed video camera (Casio EX-FH25 EXILM) through a 45°-angled mirror to obtain an overhead view of the observation chamber. The observation chamber sat on top of a black surface and was illuminated by lamps positioned left and right of the chamber so that the response could be clearly observed. All individuals tested were transferred to a small petri dish with a small amount of water and photographed from above. Individual standard length was measured to nearest millimetre using ImageJ analysis software (Abramoff et al. 2004). All tested individuals resumed normal routine swimming activity immediately after the escape responses. No fish died during the tests, or after the picture was taken. After the terminus of the study, all individuals were returned to stock tanks.

Data Analysis

Video recordings were analysed frame by frame to determine responsiveness (the number of fish that responded to the stimulus in each test group) and the reactive distance (the virtual distance between the looming object and the first individual that responded, calculated from the
size of the oval on the screen at the moment of the start of the response and the distance of the
t fish from the screen) (see (Fuiman et al. 2010) for details). The position of the fish in 2-
dimensional coordinates for the overhead view was obtained using the manual tracking plugin in
ImageJ (Cordelières 2005), this allowed us to calculate maximum speed, maximum acceleration
and total distance covered in the response (see (Fuiman et al. 2010; Fuiman et al. 2006)).

Statistical Analysis

Differences in responsiveness between familiar and unfamiliar groups were tested with a
Wilcoxon rank sum test to account for the fact that responsiveness was a discrete variable. The
responsiveness of each test group was ranked according to the number of individuals within the
group that responded (either 0, 1, 2 or 3). We considered that the response was over when the
distance travelled between three consecutive frames (12.5 milliseconds) was 1 mm or less.

In order to investigate the effect of familiarity on reactive distance and in the magnitude
of the response (maximum speed, maximum acceleration and distance covered in a response) we
used Generalised Linear Fixed Effect Models (GLM). Reactive distance, maximum speed,
maximum acceleration and distance travelled during a response were only measured on the first
fish that responded. On the only trial that two fish responded in the same frame, the fish that had
the larger reactive distance was considered the first responder. Each group was only tested once.
Each full model included familiarity as main effect treatment and standard length as a covariate
(i.e. of the individual that first responded), as well as their interaction. The linear predictor and
expected values scales were linked using a log function. Diagnostic plots revealed significant
departures from normality of the residuals for both response variables reactive distance and total
distance. Normality and homogeneity assumptions about the distributions of residual values on
the dependent variable were improved by log-transforming the response variables. To account for the effect of size in escape responses, all models included individual standard length as covariate. All analyses were performed in using R (Team 2016).

RESULTS

Individual standard length between familiar and unfamiliar treatments did not differ (mean (± SD), Familiar = 117.3 (19.7); Unfamiliar = 122.2 (27.9), $p = 0.089$)

**Responsiveness**

A total of 42 groups composed of three different sized individuals were tested. Of the 30 groups in which one or more individuals responded, 19 groups were familiar and 16 groups were unfamiliar. There was a significant effect of familiarity on responsiveness (Wilcoxon rank sum: $W=451.5$, $p < 0.001$) (Figure 3), where responsiveness was higher in unfamiliar groups. In the majority of familiar groups only one individual in the group responded, whereas the unfamiliar groups showed more instances where two or more individuals reacted to the stimulus.

**Reactive distance**

We failed to detect an effect of familiarity and individual standard length on reactive distance (Table 1, Figure 4A).
Magnitude of the response

We failed to detect an effect of social treatment on maximum speed ($p = 0.263$), maximum acceleration ($p = 0.699$) and total distance ($p = 0.698$) (Table 1, Figure 4). For maximum acceleration the effect of individual standard length was similar between treatments ($p = 0.078$). There was an increased in both maximum speed and total distance travelled as a function on increased standard length (Figure 4C, D, Table 1). Notably, we observed an almost twice-greater gradient in the familiar treatment than in the unfamiliar treatment in terms of maximum speed. There was an increase of 82.05 milliseconds in maximum speed per millimetre of standard size in the familiar treatment, while in the unfamiliar treatment the gradient was of 44.14 milliseconds per millimetre of standard size (Table 1, Figure 4B).

DISCUSSION

A novel contribution of this study is that it examines the consequences of familiarity during early stages in the performance of escape responses separating the multiple aspects of the response to determine which parts depend on the social environment. Through high-speed analysis of the escape responses in familiar and unfamiliar groups of guppies, we demonstrate that early social experience plays a role in shaping how groups of fish respond to a stimulus. Namely, we showed that unfamiliar groups had more individuals perform an escape response than those in familiar groups. Unexpectedly, other components of the escape response, namely latency and magnitude, were not affected by familiarity. Furthermore, the maximum speed and distance covered in the response were correlated with individual size rather than with level of
familiarity within the group. In combination, our study suggests, that familiarity plays a less meaningful role in determining some behavioural components of the escape response.

Our results show that familiarity affects group responsiveness. There were a greater number of individuals responding within each group among unfamiliar groups than among familiar groups (Supplementary material). While most fish species rely on the escape response to avoid a potential predator (Domenici 2010; Fuiman & Magurran 1994), escape responses may however vary within and among individuals (Lima & Dill 1990; Ward & Webster 2016; Ydenberg & Dill 1986). If there is enough information to accurately predict the level of threat in a given environment, then it is advantageous for a prey to only flee when it is necessary for survival avoiding false alarms that could in turn attract the attention of nearby predators (Ward et al. 2011). For example, minnows performed antipredator behaviours in response to a realistic pike model, whereas an unrealistic stimulus elicited no response (Magurran & Girling 1986). The lower responsiveness in familiar groups may be a result of improved vigilance. According to the theory of limited attention, performance is reduced when attention must be divided among different tasks (Dukas 2002). Therefore, if individuals are not spending time inspecting or acting aggressively toward group mates, as is often found among unfamiliar individuals (Griffiths et al. 2004; Johnsson 1997; Tanner & Keller 2012), then they are likely to have more time to dedicate to other tasks, such as predator vigilance (Strodl & Schausberger 2012; Strodl & Schausberger 2013; Zach et al. 2012). Guppies from familiar groups may have been able to accurately assess the non-threatening nature of the stimulus. An alternative explanation is that fish in familiar groups feel safer as they are with individuals they have seen before and this may be why familiar individuals are more likely to perceive the oval shape stimulus as non-threatening. On the other hand unfamiliar groups may have been more skittish and, thus more likely to be startled by the
stimulus. Interacting with unfamiliar individuals can be stressful (Choleris et al. 1998), particularly if such interactions are associated with increased aggression (Galef et al. 1984). Individuals may perceive higher risk when shoaling with unfamiliar conspecifics, as was found in fathead minnows who had a higher production of epidermal alarm substance cells when in unfamiliar shoals than familiar shoals (Wisenden & Smith 1998). Furthermore, escape responses from the digital display may be misinterpreted as an attack by the other group mates. Aggression is common among guppies, in both natural as well as laboratory conditions (Magurran 2005; Thibault 1974). Therefore, it is plausible that an individual guppy would flee from an unfamiliar group mate that is performing a fast-start response, as this could be misinterpreted as an attack.

We failed to detect an effect of familiarity on the reactive distance of an escape response. Comparable studies have found that familiarity reduces the latency of an escape response. Similarly, familiar juvenile brown trout responded 14% faster than unfamiliar ones when exposed to a simulated predator attack (Griffiths et al. 2004). In both their and our study reduction in reaction time has been attributed to the associated benefits of the theory of limited attention. Our results, therefore, suggest that familiarity is more important in antipredator behaviours earlier in a predator sequence. A predator must successfully encounter, attack and capture a prey, where a prey’s strategy is to interrupt this sequence. It has been suggested that avoiding the encounter and attack, are prey’s best strategy (Fuiman & Magurran 1994). Previous experiments included an entire predator interaction, such as a model heron swinging forward and plunging its beak into the water (Griffiths et al. 2004) or a live predator (Strodl & Schausberger 2012), and could, therefore elicit such behaviours. In contrast, our experiment only elicited behaviours seen in the last few milliseconds of the attack.
Familiarity has been found to enhance avoidance tactics. For example, predator confusion was enhanced in shoals of familiar fathead minnows that had reduced neighbour distance and more shoal cohesion in response to predator stimuli compared to unfamiliar shoals (Chivers et al. 1995). Tighter shoal cohesion reduces the probability of being captured by a predator (Mathis & Smith 1993). In addition, familiar shoals exhibited a greater number of predator inspections with more inspectors per inspection when faced with a model pike (Chivers et al. 1995). Predator inspection, where an individual or small group of individuals approach a predator, pause and swim away (Pitcher 1991), enables prey to gain valuable information on the threat of a predator. This behaviour, though risky to inspectors, is associated with improved avoidance of a predator attack (Godin & Davis 1995; Magurran 1990; Magurran & Pitcher 1987). Therefore, it is likely that familiarity is more crucial in antipredator behaviour associated with predator avoidance than predator evasion.

The effect of familiarity on the magnitude of the response was not significant. The kinematic aspects of escape responses are often assumed to be constrained by the sensory-motor system of the individual (Domenici & Blake 1997). However, juvenile guppies reared in an environment with intense social aggression travelled a greater distance in the first five frames after a simulated avian attack than those reared in absence of social aggression (Chapman et al. 2008a). It is then recognized the need to implement an integrative approach that accounts for all aspects of an escape response in order to obtain a clear understanding of the mechanisms of response to a predator (Domenici 2010). While other behavioural variables may affect the magnitude of an escape response, our study provides evidence that familiarity is not one of them. Our results showed that size, rather than familiarity, influenced the magnitude of the response than familiarity. This result is consistent with previous
studies that have shown that the magnitude of the fast-start response in young fish increases with body length (Dial et al. 2016). While behavioural effects on the locomotive performance cannot be ruled out (Domenici 2010), our study and others (Gibb et al. 2006; Ojanguren & Braña 2003) lend strong support that the magnitude of a fast-start response is largely determined by morphology, rather than by social conditions.

In this study, we provided a test for the relative effect of familiarity in modulating predator avoidance behaviour by measuring several components of the escape responses using high speed video analysis. Our results suggest that familiar groups may have improved antipredator performance, as individuals conserve energy and are less conspicuous by not fleeing in a non-threatening situation. Nevertheless, further studies are necessary to elucidate this. Future studies may try to tease the contribution of group size and familiarity in modulating the predator escape response, by testing familiar and non-familiar groups composed of different number of individuals. Our results also suggest that the effects of familiarity on the response are perhaps unlikely to play a role on escape performance in the last few milliseconds of a predator attack. Instead, we believe that familiarity is more likely to affect behaviour earlier in a predator-prey interaction, which then affects the quality of the response.

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Diagram of the two experimental treatments (familiar and unfamiliar). Individuals were allocated to a holding tank with two other conspecifics for two weeks. Each testing day, three groups were tested where fish remained with those they had been sharing a tank with (familiar treatment). The other three groups had the individuals swapped so that none of the fish had encountered each other previously (unfamiliar treatment). Forty-two groups were tested in total, 21 of each treatment.
Illustration of the experimental setup. A camera was placed 1 m away from a glass tank (10 x 10 x 10 cm) positioned before the LDC screen that showed the digital display of a looming object. The front of the tank and the overhead view of the tank were recorded in high-speed video for each trial. The distance in centimetres of the digital looming object was displayed on the top left of the screen.
Figure 3

Responsiveness for familiar and unfamiliar groups in terms of how many individuals in a group of three responded to the stimulus. The numbers within the bubbles give the number of groups.
Figure 4

Figure 4

Variation in reactive distance (A), maximum speed (B), maximum acceleration (C) and total distance (D), in familiar (open circles) and unfamiliar (closed circles) groups. Lines were fitted using the coefficients of linear models.
A: Log Reactive distance (mm) vs. Standard Length (mm)
B: Maximum speed (mm/s) vs. Standard Length (mm)
C: Maximum acceleration (mm/s^2) vs. Standard Length (mm)
D: Log Total distance (mm) vs. Standard Length (mm)
Generalised linear models for testing the effect of familiarity on different qualitative measures of response.
| Response variable | Explanatory variable | Estimate | Std Error | T-value | p-value |
|-------------------|----------------------|----------|-----------|---------|---------|
| Reactive distance | Intercept            | 2.526    | 1.819     | 1.389   | 0.175   |
|                   | Unfamiliar           | 1.985    | 2.879     | 0.690   | 0.496   |
|                   | Length               | 0.069    | 0.142     | 0.488   | 0.629   |
|                   | Unfamiliar: length   | -0.178   | 0.243     | -0.737  | 0.467   |
| Maximum speed     | Intercept            | 175.7    | 269.9     | 0.651   | 0.519   |
|                   | Familiar             | -487.8   | 427.2     | -1.140  | 0.263   |
|                   | Length               | 44.14    | 21.16     | 2.086   | 0.045   |
|                   | Familiar: length     | 37.91    | 36.06     | 1.051   | 0.301   |
| Maximum acceleration | Intercept         | -147.6   | 4846      | -0.003  | 0.997   |
|                   | Familiar             | 2989     | 7671      | 0.390   | 0.699   |
|                   | Length               | 6909     | 3799      | 1.819   | 0.078   |
|                   | Familiar: length     | -3032    | 6473      | -0.468  | 0.642   |
| Total distance    | Intercept            | 0.699    | 0.908     | 0.771   | 0.447   |
|                   | Familiar             | 0.562    | 1.437     | 0.391   | 0.698   |
|                   | Length               | 0.194    | 0.071     | 2.733   | 0.010   |
|                   | Familiar: length     | -0.055   | 0.121     | -0.454  | 0.653   |