



Ectoparasites modify escape behaviour, but not performance, in a coral reef fish



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Survival depends on escape responses and when to flee a predator. As a result, factors affecting the escape performance of prey species, including parasite infection, may profoundly influence the outcome of predator–prey encounters. Several hypotheses predict the responses of prey to simulated predator attacks based on intrinsic characteristics such as individual reproductive value and flight costs: as predation risk and reproductive value increase, so should the distance at which an organism begins to flee an escaping predator (flight initiation distance; FID). Conversely, FID should decrease if the costs of fleeing are high. Despite providing testable hypotheses, rarely have these theories been used to predict the escape behaviour of parasitized individuals. The bridled monacle bream, *Scolopsis bilineata*, is parasitized by a large cymothoid isopod, *Anilocra nemipteri*, which attaches above the eye. In this species, ectoparasite infection is associated with increased energy costs and decreased endurance. We investigated the effects of infection on escape performance and FID. Maximum velocity, maximum acceleration, cumulative distance travelled and response latency did not differ between parasitized fish, unparasitized fish and fish that had their parasite experimentally removed. Parasitized fish were smaller, on average, than unparasitized individuals. Smaller, parasitized individuals allowed a threat to approach closer before fleeing (shorter FID) than larger parasitized or uninfected individuals. Since parasite infection has known effects on host growth and metabolism, we suggest that parasitism alters fish escape behaviour as predicted by two nonexclusive hypotheses: (1) by decreasing reproductive value (the asset protection hypothesis) and (2) by increasing the relative costs of fleeing (the economic hypothesis) compared with uninfected and large parasitized fish. The relative importance of each hypothesis in driving the trends observed remains to be tested.

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When to escape from a predator is a key behaviour influencing the fitness of mobile species. This decision must consider the time, energy and opportunity costs associated with fleeing as well as intrinsic traits such as size, previous experience and measures of kinematic performance such as maximum achievable speed and acceleration (Domenici, 2010; Januchowski-Hartley, Graham, Feary, Morove, & Cinner, 2011; Lagos et al., 2009; Lima & Dill, 1990; Møller, Grim, Ibanez-Alamo, Marko, & Tryjanowski, 2013; Stankowich & Blumstein, 2005). Extrinsic factors (e.g. predator approach speed, ambient temperature, habitat complexity, distance to shelter) can

also influence an individual's decision making when evaluating whether an approaching organism constitutes a threat (Bonenfant & Kramer, 1996; Cooper, 2006; Dill & Houtman, 1989; Domenici, 2010; Domenici, Claireaux, & McKenzie, 2007; Møller et al., 2013; Stankowich & Blumstein, 2005). As a result, escape behaviours involve the complex integration of biotic, abiotic and locomotor variables that should optimize the ratio of benefits to costs of remaining versus fleeing (Cooper & Frederick, 2007, 2010; Domenici, 2010; Lima & Dill, 1990; Stankowich & Blumstein, 2005; Ydenberg & Dill, 1986). Consequently, even slight changes in an organism's ability to react to, evade or outrun a predator can alter individual risk perception and decisions about when to flee an approaching threat.

Parasitic infection can dramatically affect host behaviour and physiology (Barber, Hoare, & Krause, 2000). Several studies have

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linked impaired escape responses (decreased reactivity or locomotor abilities) to parasitism in a range of animals (e.g. Barber, Walker, & Svensson, 2004; Goodman & Johnson, 2011; Libersat & Moore, 2000; Møller, 2008; Perrot-Minnot, Kaldonski, & Cézilly, 2007; Seppälä, Karvonen, & Tellervo Valtonen, 2004). However, these studies generally focus on the effects of endoparasites, many of which have complex life cycles and rely on transmission from prey to predator for their own success (Barber et al., 2000; Poulin, 2010). Consequently, there is a conflict of interest between hosts and parasites regarding predation-relevant behaviours (i.e. parasite increased trophic transmission hypothesis; Barber et al., 2000; Lafferty, 1999; Poulin, 2010, 2013). Conversely, the fitness of directly transmitted parasites, including many externally attached ectoparasites, is enhanced if the host can successfully flee from a predator. As a result, these parasites should be selected to minimize any negative effects on host predation risk (Barber et al., 2000), and hosts should make decisions that will optimize their energy expenditure and chance of escape during a predator encounter. However, ectoparasites may impose additional costs on hosts due to their relatively large size (e.g. Fogelman, Kuris, & Grutter, 2009; Grutter et al., 2011). This may be particularly true in aquatic species given the challenges of moving through relatively dense water (Vogel, 1994). Various studies have found that ectoparasites negatively affect the swimming performance of fish in part by increasing drag, suggesting that the ability to escape an approaching predator may be severely impaired (Grutter et al., 2011; Ostlund-Nilsson, Curis, Nilsson, & Grutter, 2005; Wagner, McKinley, Bjorn, & Finstad, 2003).

The predicted response of parasitized hosts to predator attacks is not necessarily obvious. Flight initiation distance (FID) is the distance at which an organism begins to flee an approaching predator and provides a reliable estimate of an animal's perception of fear or risk (Stankowich & Blumstein, 2005). On the one hand, parasitized fish may be slower than uninfected fish, and thus more vulnerable to predation. One prediction of the economic hypothesis proposed by Ydenberg and Dill (1986) is that FID should increase with higher predation risk. If parasitized fish are less able to outswim a predator once a chase is initiated, we might predict that parasitized individuals will initiate their escape response earlier in an attempt to put more distance between themselves and a predator. On the other hand, the physiological burden imposed by parasites on their hosts means that the energetic and opportunity costs of initiating an escape are much greater relative to unparasitized individuals (Binning, Roche, & Layton, 2013; Godin & Sproul, 1988; Ostlund-Nilsson et al., 2005). The economic hypothesis also predicts that FID should decrease when the costs of fleeing are high (Ydenberg & Dill, 1986). As such, parasitized individuals should only engage in costly flight when a predator approaches close and the threat is high (see Godin & Sproul, 1988; Møller, 2008; Ydenberg & Dill, 1986).

Parasitized or heavily parasitized fish are often smaller than similarly aged uninfected or moderately infected hosts, and previous studies on FID in fishes suggest that size is an important predictor of FID, with small fish generally fleeing at a closer distance to a threat (smaller FID) than larger individuals (Gotanda, Turgeon, & Kramer, 2009; Januchowski-Hartley et al., 2011; Miller et al., 2011). This phenomenon has been largely attributed to the asset protection hypothesis, which predicts that as reproductive value increases, individuals should engage in less risky behaviours in order to protect their reproductive assets (Clark, 1994; Cooper & Frederick, 2007). In fishes, reproductive value typically increases with size (Reinhardt, 2002; Rogers & Sargent, 2001). Thus large fish should increase their FID compared with smaller, less fertile individuals. Consequently, parasites may indirectly decrease host FID through interactions with fish size. Parasites can also directly

decrease host reproductive value independent of size by physically castrating hosts (e.g. Fogelman et al., 2009; Lafferty & Kuris, 2009). Based on this logic, we would predict that parasitized individuals should wait longer before fleeing from a threat.

On the Great Barrier Reef, the cymothoid isopod *Anilocra nemipteri* parasitizes the bridled monocle bream, *Scolopsis bilineata*, with up to 30% of fish infected at some sites (Grutter, 1994; Roche, Strong, & Binning, 2013). This species is directly transmitted to its host, although postlarval juveniles (mancae) of some *Anilocra* species may use optional intermediate hosts before settling on a definitive host where they grow into adults (Fogelman & Grutter, 2008). A single isopod typically attaches to a fixed location on one side of the host's head where it breeds repeatedly and can live for several years (Brusca, 1981; Roche, Strong, et al., 2013; Fig. 1). Parasites can grow to 30% of the fish's total length and reduce host growth (Roche, Strong, et al., 2013). *Anilocra nemipteri* does not exhibit any side bias in attachment preference on either the left or right side of the host's body (Roche, Strong, et al., 2013). However, parasitized fish are more highly lateralized (i.e. have a stronger side preference) than unparasitized individuals (Roche, Binning, Strong, Davies, & Jennions, 2013), a behaviour that may enhance escape responses by decreasing reaction time (Dadda, Koolhaas, & Domenici, 2010). These parasites also impair the swimming

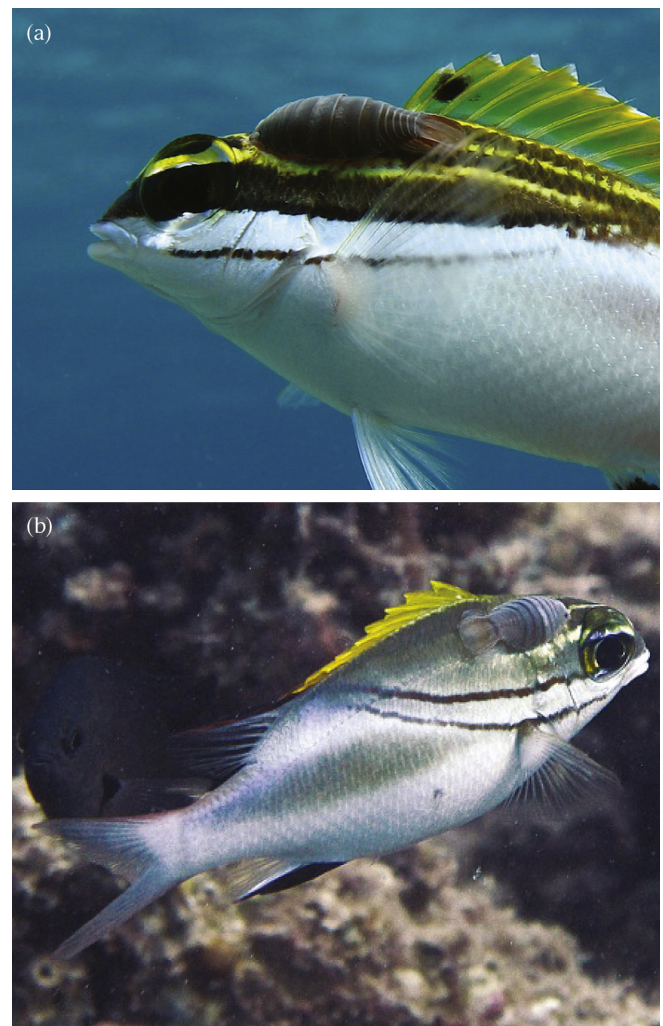


Figure 1. Bridled monocle bream, *Scolopsis bilineata*, with a cymothoid ectoparasite, *Anilocra nemipteri*, attached above the eye. Parasites can attach on either the (a) left or (b) right side of the host. Photo credits: (a) D. Roche and (b) S. Gingins.

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