

# The behavioural ecology of marine cleaning mutualisms

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## ABSTRACT

Cleaning interactions, in which a small ‘cleaner’ organism removes and often consumes material from a larger ‘client’, are some of the most enigmatic and intriguing of interspecies interactions. Early research on cleaning interactions canonized the view that they are mutualistic, with clients benefiting from parasite removal and cleaners benefiting from a meal, but subsequent decades of research have revealed that the dynamics of these interactions can be highly complex. Despite decades of research on marine cleaning interactions (the best studied cleaning systems), key questions remain, including how the outcome of an individual cleaning interaction depends on ecological, behavioural, and social context, how such interactions arise, and how they remain stable over time. Recently, studies of marine parasites, long-term data from coral reef communities with and without cleaners, increased behavioural observations recorded using remote video, and a focus on a larger numbers of cleaning species have helped bring about key conceptual advances in our understanding of cleaning interactions. In particular, evidence now suggests that the ecological, behavioural, and social contexts of a given cleaning interaction can result in the outcome ranging from mutualistic to parasitic, and that cleaning interactions are mediated by signals that can also vary with context. Signals are an important means by which animals extract information about one another, and thus represent a mechanism by which interspecific partners can determine when, how, and with whom to interact. Here, I review our understanding of the behavioural ecology of marine cleaning interactions. In particular, I argue that signals provide a useful framework for advancing our understanding of several important outstanding questions. I discuss the costs and benefits of cleaning interactions, review how cleaners and clients recognize and assess one another using signals, and discuss how signal reliability, or ‘honesty’, may be maintained in cleaning systems. Lastly, I discuss the sensory ecology of both cleaners and clients to highlight what marine cleaning systems can tell us about signalling behaviour, signal form, and signal evolution in a system where signals are aimed at multiple receiver species. Overall, I argue that future research on cleaning interactions has much to gain by continuing to shift the research focus toward examining the variable outcomes of cleaning interactions in relation to the broader behavioural, social, and ecological contexts.

*Key words:* cleaner fish, cleaner shrimp, mutualism, interspecific signalling, signal reliability

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## I. INTRODUCTION

Cleaning interactions – in which a ‘cleaner’ organism removes and usually consumes materials from an often larger ‘client’ – are among the most enigmatic and intriguing interspecies interactions. Studies of cleaning interactions have primarily focused on marine systems, where cleaners are small fishes or shrimp that live at ‘cleaning stations’ (Youngbluth, 1968) and remove material such as ectoparasites from clients (Grutter, 2005), which are usually larger fish. The first published record of a marine cleaning interaction dates to 1928, when the naturalist William Beebe noted several small wrasses cleaning a parrotfish on a reef in Haiti (Beebe, 1928). Several decades then passed before Conrad Limbaugh and Howard Feder published observational works (Limbaugh, Pederson & Chace, 1961; Feder, 1966) that framed cleaning interactions as cooperative interactions, in which cleaners benefit from receiving a meal and clients benefit from the removal of harmful parasites. This view was then canonized, and cleaning interactions became a textbook example of mutualism (e.g. Trivers, 1971). Shortly thereafter, however, the purely mutualistic view of cleaning was called into question for several reasons. First, studies demonstrated that cleaners have only limited impacts on client parasite load in the short term (Gorlick, Atkins & Losey, 1987; Grutter, 1996*b*). Second, an early study reporting hugely detrimental impacts of cleaner removal on the health and abundance of reef fish (Limbaugh, 1961) could not be replicated (Youngbluth, 1968; Losey, 1972; Gorlick *et al.*, 1987; Grutter, 1996*b*, 1997*a*). Third, it was found that cleaner fish would sometimes act non-mutualistically, eating scales or mucus instead of ectoparasites (e.g. Randall, 1958; Gorlick, 1980; Grutter, 1997*b*).

Recent research has broadened the scope and scale of our understanding of cleaning interactions, through long-term studies of reefs with and without cleaners, increased study of the dynamics of ectoparasite populations, *in situ* behavioural observations collected *via* remote video recording, and an expansion in diversity of cleaner taxa under study, in particular increased research on cleaner shrimp. This new literature has increased our understanding of the steps by which cleaning interactions are initiated, the behaviour of each party during an interaction, and the broader ecological and environmental context of interactions. One important area of increased research has focused on the signals that mediate cleaning interactions (e.g. Becker, Curtis & Grutter, 2005; Lettieri *et al.*, 2009; Chapuis & Bshary, 2009, 2010; Cheney *et al.*, 2009*a*; Caves, Green & Johnsen, 2018; Caves, Chen & Johnsen, 2019). Signals are

one of the primary means by which animals can access information about one another, and thus signals represent a mechanism by which mutualistic partners can determine when, how, and with whom to interact. Additionally, the traits by which cleaners and clients signal to one another can serve as strong arbiters of fitness, highlighting the important role they play in these interactions.

Here, I focus on recent literature and discuss our current understanding of the behavioural ecology of cleaning interactions. Although other reviews of cleaning interactions exist [which, for example, evaluate the taxonomic diversity of cleaning interactions (Vaughan *et al.*, 2017) or explore cleaning interactions in a game theoretical context, e.g. Bshary (2001)], my focus is both to update a seminal review on the ecology and evolution of cleaning interactions (Côté, 2000), and to provide the first review that highlights the role of signalling in mediating cleaning interactions. In particular, I argue that studying signals can shed light on several important outstanding questions in the study of cleaning interactions, including the balance of costs and benefits in individual cleaning interactions, and how they arise and remain stable over evolutionary time.

First, I discuss the costs and benefits of cleaning interactions. Elucidating costs and benefits is key to understanding both whether or not a given interaction is mutualistic, but also the dynamics of a signalling system, which involves quantifying costs incurred and benefits accrued throughout an interaction: from bearing a signalling trait and producing a signal, to assessment of the sender by the receiver, to the outcome of the interaction.

Second, I summarize the literature regarding how cleaners and clients use signals to assess one another and choose to interact, synthesizing literature from signal theory and other interspecific signalling systems to discuss how signal reliability, or honesty, may be maintained in cleaning interactions. Large bodies of theoretical and empirical work have identified several mechanisms by which signals can remain reliable, or honest, over time. Key to this idea is that receivers can extract information about senders from a signal, and thus evaluate the potential costs and benefits of participating in any given interaction. That signallers may modulate their signalling traits or behaviours (and thus the information conveyed), and that receivers may adjust their responses in turn, can contribute to the stability of these interactions.

Third, I combine information on the ‘diffuse’ nature of cleaning interactions, in which multiple species of cleaners and clients interact, with our understanding of cleaner and client sensory ecology, to discuss the implications for the

evolution of signals that mediate cleaning interactions. Thinking of cleaning interactions as signal-mediated provides an evolutionary framework that may shed light on the steps by which such systems arise. In particular, signal theory makes predictions about the form of signalling traits relative to the environment and the receiver's sensory system, and the evolution of signalling traits and receiver responses. Overall, I argue that studies of cleaning interactions can be used to inform our understanding of the dynamics of inter-specific signalling, partner choice, and the stability of mutualistic interactions more generally.

## II. CLEANING INTERACTIONS

Cleaning interactions are widespread both geographically and taxonomically (Vaughan *et al.*, 2017). Crustaceans, insects, birds, fishes, mammals, and reptiles have been recorded serving as cleaners (Overall, 1980; Perry, 1990; Van Tassell, Brito & Bortone, 1994), and cephalopods, reptiles, mammals, and fish have been recorded acting as clients (Hobson, 1969; Vogt, 1979; Swartz, 1981; Johnson & Chase, 1982; Losey, Balazs & Privitera, 1994; Krawchuk, Koper & Brooks, 1997). Although some species serve as cleaners at various life stages or in captivity [see Côté (2000) and Vaughan *et al.* (2017)], here I focus on marine fishes and shrimp that clean as adults and that appear to acquire the majority of their food from cleaning, because these species exhibit behaviours and morphologies that have likely evolved to facilitate cleaning. These are in large part tropical species, including wrasses in the family Labridae, gobies in the genus *Elacatinus*, and decapod shrimps in the families Palaemonidae and Hippolytidae.

Cleaning systems can involve frequent cleaner–client interactions: each day, an individual bluestreak cleaner wrasse (*Labroides dimidiatus*) may engage in more than 2000 cleaning interactions, spending a daily average of 256 min inspecting clients and feeding on up to 1200 ectoparasites (Grutter, 1996a). For their part, clients have been recorded visiting cleaners up to 144 times and experiencing up to 32 min of cleaning each day (Grutter, 1995). Cleaner fish can affect the dynamics of parasite infestation (Gorlick *et al.*, 1987; Grutter & Lester, 2002) and lower parasite infestation rates (Grutter *et al.*, 2019). *Via* their effects on parasites, cleaners can impact coral reef communities. In particular, they can impact reef fish diversity, abundance, and size (e.g. Bshary, 2003; Grutter, Murphy & Choat, 2003; Clague *et al.*, 2011), and alter the recruitment of juvenile reef fish (Sun *et al.*, 2015). It can, however, take years for these effects to become ecologically significant (e.g. Grutter, 1997a; Clague *et al.*, 2011; Grutter *et al.*, 2018) and the effects are not the same for all reef fish species (Grutter *et al.*, 2003).

One reason for the widespread impact of cleaners on reef ecosystems is that cleaning interactions are ‘diffuse’, involving two multi-species partner classes that interact in a loosely associated network (Cushman & Beattie, 1991). In particular,

a core of cleaner species interacts with numerous client species. In a meta-analysis of data from six geographic sites (Guimaraes *et al.*, 2007), client species richness was sevenfold higher than that of cleaners, and many cleaners have been observed interacting with clients from dozens of genera (see Darcy, Maisel & Ogden, 1974; Criales & Corredor, 1977; Criales, 1979; Wicksten, 1995; Wirtz, 1997; Bansemer, Grutter & Poulin, 2002; Chapuis & Bshary, 2009; Huebner & Chadwick, 2012). Multiple cleaner species usually exist sympatrically on a reef (Guimaraes *et al.*, 2007), and there is often overlap in their clients [e.g. Johnson & Ruben (1988) and Wicksten (1995) in the Caribbean; Chapuis & Bshary (2009) in the Red Sea]. However, the cleaning services offered by different cleaner species may differ. For example, sympatric cleaner species may differ in which client species they clean most frequently (Barbu *et al.*, 2011), the time of day during which they clean (Bonaldo *et al.*, 2015; Titus, Daly & Exton, 2015), and in the frequency and duration of cleaning interactions (Chapuis & Bshary, 2009). Some evidence suggests that cleaner shrimp preferentially consume smaller parasites (McCammon, Sikkil & Nemeth, 2010) while cleaner fish target larger parasites (Gorlick *et al.*, 1987; Grutter, 1997b). However, these differences may be context dependent. For example, in one study, cleaner fish only targeted larger parasites when parasite abundance was high (Grutter, 1997b).

## III. SIGNALS, BENEFITS, AND COSTS IN CLEANING INTERACTIONS

### (I) Behaviours that serve as signals during cleaning interactions

Key to understanding the dynamics of cleaning interactions is understanding how cleaners and clients locate and recognize one another and assess whether to interact. It has long been noted that species-specific stereotyped behaviours occur during cleaning interactions. For example, both cleaner wrasses and gobies perform stereotyped ‘dances’ in the presence of clients (Wickler, 1963, 1964; Feder, 1966; Youngbluth, 1968; Darcy *et al.*, 1974). Among cleaner shrimps, some species rock their bodies [*Urocaridella* sp. C (Becker & Grutter, 2005; Becker *et al.*, 2005)], clap their chelae (*Ancylomenes longicarpus*; Chapuis & Bshary, 2009), whip their antennae (*Ancylomenes pedersoni*), or sway their front legs (*Lysmata amboinensis*; Caves *et al.*, 2019) in the presence of clients. Clients also exhibit stereotyped behaviours during cleaning interactions, adopting certain poses (e.g. Côté, Arnal & Reynolds, 1998; Caves *et al.*, 2018), changing colour (Caves *et al.*, 2018), or jolting (Feder, 1966; Wickler, 1968; Losey, 1971).

Only recently, however, has it been demonstrated that certain behaviours (Becker & Grutter, 2005; Becker *et al.*, 2005; Chapuis & Bshary, 2010; Caves *et al.*, 2018, 2019) or traits [e.g. colour patterns (Cheney *et al.*, 2009a; Lettieri *et al.*, 2009)] actually are signals. A signal is any act or

structure which “alters the behaviour of other organisms, which evolved because of that effect, and which is effective because the receiver’s response has also evolved” (Maynard Smith & Harper, 2003, p. 3). Additionally, signals must on average (i) result in a net (fitness) benefit to both sender and receiver, and (ii) be reliable or ‘honest’ (Johnstone & Grafen, 1993; Kokko, 1997; Searcy & Nowicki, 2005) in the information they convey. From these definitions, it can be seen that whether or not an act or structure is a signal has important implications for the evolutionary dynamics of an interaction, since signals provide one avenue by which parties can place selection pressure on one another’s traits. Additionally, because receivers can extract information about senders from signals, studying signalling can increase our understanding of how and when parties decide to interact.

## (2) Benefits of cleaning interactions

Because the outcome of a signalling interaction must, on average, benefit both parties, understanding the costs and benefits incurred by each party in an interaction is key to elucidating the dynamics of signalling. For cleaners, when signalling leads to cleaning, the primary benefit is in gaining a meal in the form of ectoparasites or other material from the client, and both cleaner fish and shrimp have been shown to consume parasites (Bunkley-Williams & Williams, 1998; Grutter, 1999; Becker & Grutter, 2004; McCammon *et al.*, 2010). Experiments with captive *L. dimidiatus* show that cleaner wrasses do not simply forage at random across the body of a client, but rather seek out parasites to consume (Bshary & Grutter, 2002*b*), and *Elacatinus* gobies spend longer cleaning large clients (Arnal *et al.*, 2000) which likely harbour more parasites. The wrasse *L. dimidiatus* may gain all of its daily energetic requirements from cleaning (Grutter, 1996*a*).

For clients, the primary benefit of a successful signalling interaction that leads to cleaning is likely parasite removal (e.g. Grutter, 2001). Cleaners can be highly effective parasite removers: the cleaner shrimp *Ancylomenes pedersoni* removed 100% of parasitic isopods from clients in each of 10 laboratory trials (Bunkley-Williams & Williams, 1998), and *A. holthuisi* reduced parasite loads on captive surgeonfish by 74.5% relative to controls across 12 48-h trials (Becker & Grutter, 2004). Recent studies have demonstrated that the negative impacts of marine parasites on fish are numerous, including physiological effects like increased oxygen consumption (Grutter *et al.*, 2011), increased cortisol levels in fish (Triki *et al.*, 2016; Allan *et al.*, 2020), and reduced haematocrit (Jones & Grutter, 2005), as well as behavioural effects such as changes to swimming behaviour (Allan *et al.*, 2020), and even increased mortality (Hayes *et al.*, 2011). By removing parasites, cleaners may help mitigate these effects. As discussed above, when parasite load is high, cleaner fish feed selectively on large parasites (Gorlick *et al.*, 1987; Grutter, 1997*b*), reducing perhaps the most detrimental effects on client health (Paperna & Por, 1977). Clients that have cleaner goby stations in their territory harbour fewer parasites than those

that do not (Cheney & Côté, 2001), and access to cleaner wrasse *L. dimidiatus* or the cleaner shrimp *A. pedersoni* results in a fourfold reduction in parasites on clients compared to clients without access (Grutter, 1999; McCammon *et al.*, 2010).

The benefits to clients of being cleaned may also include stress reduction. In the field, cleaner access reduced the short-term stress response in clients in one experiment (Bshary *et al.*, 2007), but in another, did not correlate with several indicators of stress response (Ros *et al.*, 2011). Clients without cleaner access did, however, have higher antibody responses than those with cleaner access. This suggests that regular visits to a cleaner might decrease the need for active immunity and thus release resources to be allocated to other bodily functions (Ros *et al.*, 2011). In another study, Demairé *et al.* (2020) found that clients deprived of access to cleaners showed no changes in cortisol, but did exhibit lower haematocrit, testosterone, and lymphocyte levels compared to fish with cleaner access. Thus, overall, determining how cleaner access or deprivation affects client physiology is complex, and best practice may be for studies to examine a suite of physiological measures. It is also unknown whether effects on client physiology are the direct result of parasite removal, or result from the physical contact (‘tactile stimulation’) delivered by cleaners during cleaning; in one study, lower client stress levels were induced by simulating cleaner contact with a paintbrush (Soares *et al.*, 2011). Cleaners may also benefit clients by assisting with wound healing, by reducing inflammatory responses and thus perhaps the incidence of opportunistic infection (Vaughan *et al.*, 2018).

Recently, long-term studies that manipulate the presence or absence of the cleaner *L. dimidiatus* on reefs have begun to demonstrate how repeated, frequent interactions with cleaners can have long-term benefits to clients. For example, Waldie *et al.* (2011) found that two damselfish species were larger on control reefs compared to those from which *L. dimidiatus* had been removed for 8.5 years. After 13 years of cleaner removal, body condition in four species of damselfish was lower on reefs without cleaners compared to those with cleaners (Ros *et al.*, 2020). Thus, over the long term, parasite removal by cleaners may free up energy and resources (e.g. Ros *et al.*, 2011) that clients can then channel towards critical processes such as maintaining body condition (e.g. Ros *et al.*, 2020) and growth (e.g. Waldie *et al.*, 2011). Future research should examine the long-term effects that other cleaner species, such as cleaner gobies and shrimps, have on their clients, to increase our understanding of the long-term benefits of cleaning to clients.

## (3) Costs of cleaning interactions

As well as benefits, there are potential costs to both parties associated with signalling (and subsequently cleaning). The primary cost that cleaners may face is predation by clients (predatory fish that do not serve as clients may also of course pose a risk to cleaners). In laboratory experiments, both Caribbean cleaner gobies (*Elacatinus evelynae* and *E. prochilos*) and wrasses (*Thalassoma bifasciatum*) were eaten by piscivorous

clients (Darcy *et al.*, 1974), and three *L. dimidiatus* cleaners were consumed by the coral trout *Plectropomus leopardus* within 8 min of the start of trials (Grutter, 2004). Reports of predation on cleaners by clients in nature are extremely rare, but several exist (Côté, 2000). Importantly, predation on cleaners by clients has only been observed away from cleaning stations, suggesting that context – in this case, location – may be important in protecting cleaners from predation. Indeed, evidence from laboratory studies shows that piscivorous clients act overall less aggressively in the presence of *L. dimidiatus*, including towards other clients (Cheney, Bshary & Grutter, 2008), suggesting that cleaning stations may act as ‘safe havens’. Interestingly, the potential for clients to act as predators likely differs substantially between cleaner fish and cleaner shrimp, although no studies have yet directly addressed this difference.

There is evidence that cleaners can strategically minimize risks from clients. Some cleaners adjust various behaviours in the presence of predatory *versus* non-predatory clients in ways that mitigate potential risks, for example by increasing signalling (Chapuis & Bshary, 2009; Caves *et al.*, 2019). Other studies, however, have found no differences in the treatment of predatory *versus* non-predatory clients, for example in time spent cleaning (Arnal & Côté, 1998) or frequency of client ‘jolting’, a behaviour thought to indicate a painful bite or pinch by the cleaner (Caves *et al.*, 2019; Titus *et al.*, 2019).

For clients, the costs associated with cleaning can be time costs, since being cleaned represents a trade-off with time spent feeding and reproducing (e.g. Sikkil, Herzlieb & Kramer, 2005), or predation costs, since travelling to a cleaning station may increase predation risk (Côté *et al.*, 1998). Such costs may be distance dependent and thus vary from client to client, depending on how far an individual travels to seek cleaning (e.g. Arnal & Côté, 1998; Cheney & Côté, 2001). One study found that client fish would tolerate closer approaches from a human snorkeler while they were being cleaned compared to when they were not, suggesting that clients may modify their assessment of risks while being cleaned (Giglio *et al.*, 2020), potentially experiencing higher predation risk as a result. Clients may also pay a cost when cleaners feed on materials that are not ectoparasites, such as mucus (Grutter & Bshary, 2003) or healthy scales (Randall, 1958; Gorlick, 1980; Grutter, 1997*b*; Whiteman & Côté, 2002). Propensity of cleaners to feed on ectoparasites rather than other materials, however, varies with environmental context. For example, the wrasse *L. dimidiatus* had a higher proportion of parasites in its gut on Lizard Island, where parasite abundance was higher, than on Heron Island (Grutter, 1994, 1997*b*). In *Elacatinus* gobies, cleaners conferred greater reductions in parasite load upon their damselfish clients, and consumed less mucus and scales, in areas with high, compared to low, parasite abundance (Cheney & Côté, 2005).

An additional potential cost to both cleaners and clients is that contact with the other party may result in the transmission of parasites (reviewed in Narvaez *et al.*, 2021). Cleaning by definition necessitates close physical contact between

cleaner and client, during which time parasites may be transmitted from cleaner to client, or *vice versa*. Cleaning stations may themselves be parasite ‘hotspots’, where clients waiting to be cleaned could be inadvertently infected (see Narvaez *et al.*, 2021). Thus, although the overall benefits of cleaning seem most pronounced when parasite load is high, high parasite loads may also result in increased transmission of parasites between cleaners and clients, negating some of the benefits of cleaning or being cleaned under such conditions.

Thus, existing evidence points to the important effect that several factors – including client parasite load, cleaning station location, physiological state of the client, whether or not the client is a potential predator, and the transmission dynamics of parasites – have on whether or not the outcome of a given cleaning interaction is strongly mutualistic, weakly mutualistic, neutral, or even parasitic. Overall, the costs and benefits of cleaning vary by location and ecological conditions, and cleaning seems to be most beneficial when parasite load is high.

#### IV. SIGNAL RELIABILITY

Related to the cost–benefit dynamics of a signalling interaction is whether a signal is, on average, reliable or ‘honest’ in the information it conveys. Here, I adopt the definition of Searcy & Nowicki (2005), who state that a signal is reliable (i.e. honest) if: (i) there is a correlation between some characteristic of the signal and some attribute of the signaller or its environment (the signal’s ‘information content’); and (ii) that correlation is strong enough that the receiver on average benefits from assessing the signal.

In cleaners and clients, for example, dishonest signalling could occur if a cleaner displays a signal that conveys it will clean mutualistically (eat parasites), but that cleaner instead acts non-mutualistically (for example, by eating scales or mucus). In such cases, signalling dishonestly can be beneficial to the cleaner, sometimes at a cost to the client. For example, in a population where cleaners signal their service quality (e.g. number of parasites they can remove), a dishonest signaller could attract more clients by dishonestly signalling better service quality than it can actually provide. What maintains signal honesty when signalling dishonestly can be beneficial? I discuss this in greater detail below, but briefly, costs associated with signalling are thought to be fundamental to maintaining honesty. One view holds that fitness costs that increase with some aspect of signal production maintain honesty (Searcy & Nowicki, 2005; but see Penn & Számadó, 2020). However, it may not be necessary for *honest* signallers to pay costs in order to maintain signal honesty if signalling *dishonesty* is costly, for example because signalling dishonestly provokes a costly receiver response (e.g. Johnstone & Bshary, 2002). While dishonest signalling is limited by such costs, it is not fully prevented, because trade-offs between the benefits of eliciting certain responses from receivers and the potential costs of signalling dishonestly

can allow some level of dishonest signalling to persist. However, as long as, on average, most signallers are honest, the signalling system can persist (Johnstone & Grafen, 1993; Kokko, 1997; Searcy & Nowicki, 2005).

Overall, signal reliability is tied to the information in a signal, or how a signal reduces the receiver's uncertainty about the state of the signaller or its environment. What information the receiver extracts from a signal is important, since receivers are expected to continue responding to signals only if they can extract, on average, sufficiently valuable information to make responding to the signal adaptive (see Searcy & Nowicki, 2005). Once studies elucidate the information content of a signal, the correlation between the signal and the attribute of interest – the signal's reliability – can be measured, paving the way for studies of how reliability is maintained.

What (reliable) information might clients extract about cleaners from signals? It seems reasonable to predict that signals allow clients to (i) identify or recognize cleaners, and/or (ii) discriminate between individuals that are more or less willing to clean, that deliver cleaning services of differing quality, that are more or less likely to act non-mutualistically, or that may remove more parasites. Of note is that different types of signalling traits may indicate different types of information, such as information that varies over different time-scales (as discussed in Candolin, 2003). For example, signals of identity as a cleaner are likely to be fixed traits that remain stable throughout an individual's lifetime, such as a morphological feature or colour pattern [in 'dedicated' cleaners specifically, since some fish that clean only as juveniles exhibit different colour morphs as juveniles *versus* adults; see Vaughan *et al.* (2017) for a list of species that clean as juveniles]. By contrast, conveying aspects of the sender's state that change over time, such as condition or motivation, is likely achieved dynamically, for example by modulating signalling traits or behaviours. For each type of signal – fixed or dynamic – the processes by which reliability is maintained will be different, as discussed below.

### (1) The information content of cleaner signals

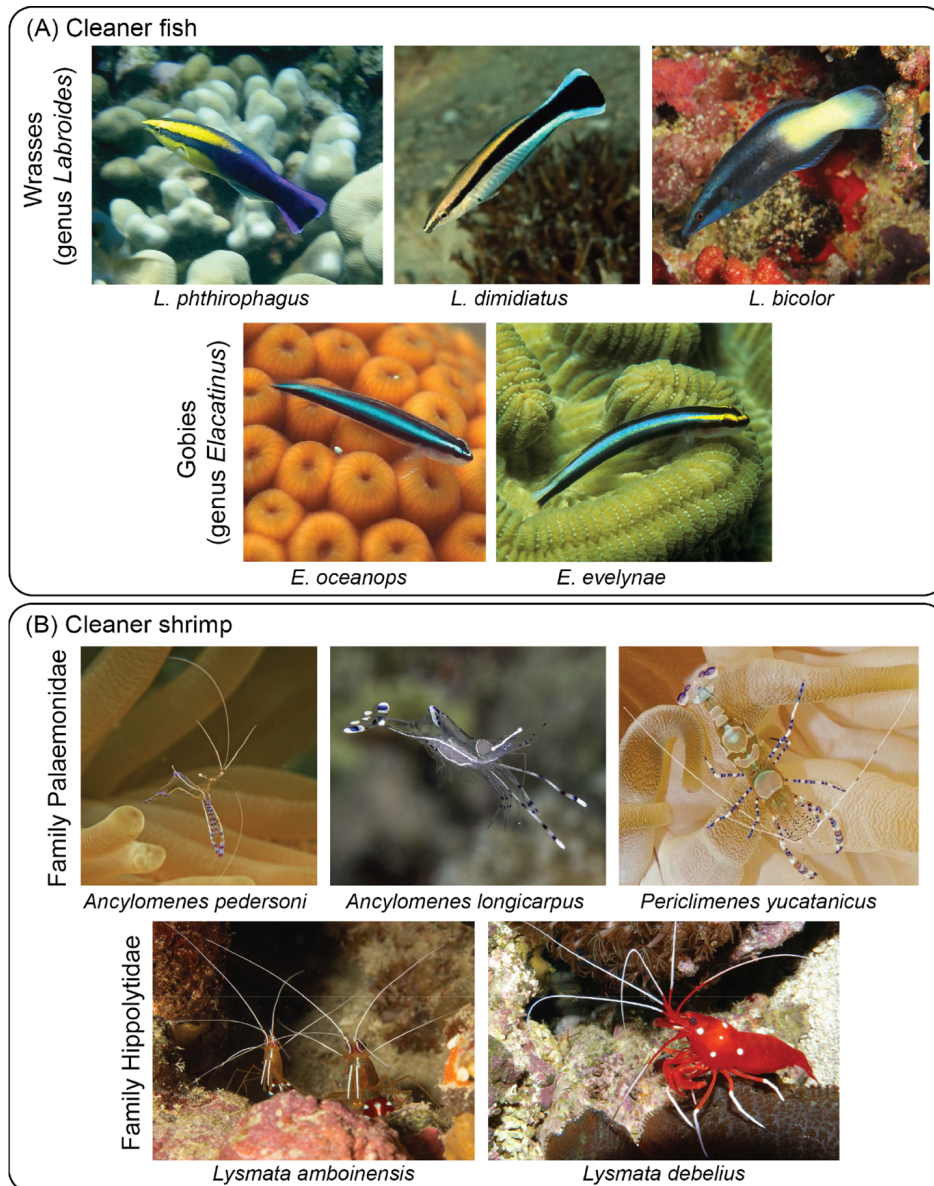
In line with the prediction that cleaner signals may convey information that identifies them as cleaners, studies have long noted that cleaner fish appear to display guild colouration that distinguishes them from non-cleaners (Eibl-Eibesfeldt, 1955; Wickler, 1963; Potts, 1973) (Fig. 1). Recent studies have combined cleaner and client sensory biology with phylogenetic comparative methods to examine the evolution of colour patterns in cleaners. Among gobies, for example, many species display green or yellow stripes, but blue stripes are observed only in species that clean, and are significantly associated with a morphological change in mouth position that may be adaptive to cleaning (Taylor & Hellberg, 2005; Lettieri *et al.*, 2009). In both wrasses and gobies, cleaners are more likely to display a combination of blue and yellow colouration compared to non-cleaning species (Cheney *et al.*, 2009a). Patterns may also be important signals; for example, in cleaner wrasses, there is an

evolutionary correlation between displaying a dark lateral stripe and cleaning behaviour (Arnal, Verneau & Desdevises, 2006).

Not only do cleaners display certain colours and patterns, clients respond to them as well, indicating that clients extract reliable recognition information about cleaners from colour patterns, supporting a signal function. For example, field experiments using model gobies have shown that the presence of lateral stripes is sufficient to elicit posing and deter attack by clients (Lettieri & Strelman, 2010), and model cleaner wrasse attracted more clients if they were painted with blue colouration and/or a dark lateral stripe (Stummer *et al.*, 2004; Cheney *et al.*, 2009a). Thus, in fish, blue colouration and dark lateral stripes may be signals that, on average, reliably identify cleaners. Among cleaner shrimps, several authors have noted the preponderance of white body parts among cleaners from different families (e.g. Wicksten, 2009; Fig. 1), although no studies have yet examined whether this may be guild colouration.

Related to this idea, cleaner signals may provide cleaners with protection from predation (see Lettieri & Strelman, 2010; Cheney, 2013). Many anti-predator signals identify an individual as toxic or distasteful, although there is little evidence to this effect in cleaners (*Elacatinus* cleaner gobies are noxious to predatory fishes, but not as noxious as related non-cleaning gobies; Lettieri & Strelman, 2010). Other anti-predator signals advertise to a predator that it has been seen, or convey information about the prey (Caro, 1995). Some cleaner signals occur either almost exclusively in the presence of potential predators (leg rocking by the cleaner shrimp *Lysmata amboinensis*; Caves *et al.*, 2019) or at an increased rate to predators [chela-clapping by the shrimp *Ancylomenes longicarpus* (Chapuis & Bshary, 2009), or tactile stimulation by the wrasse *L. dimidiatus* (Bshary, 2001)], which could indicate to a predator that it has been seen or convey that the cleaner is a beneficial partner rather than a food item.

Signals of identity can be exploited by mimic species, effectively resulting in low levels of dishonest signalling. For example, the bluestriped fangblenny *Plagiotremus rhinorhynchos* can facultatively adjust its colouration to mimic juvenile *L. dimidiatus* cleaner wrasse (Cheney *et al.*, 2009b). The benefits to *P. rhinorhynchos* of mimicking juvenile cleaner wrasse include: increased access to clients, whom they then attack to obtain food; reduced chasing and punishment from clients; and reduced risk of predation (Côté & Cheney, 2007; Cheney *et al.*, 2009b; Cheney, 2013). Given the costs that clients may pay by mistaking an aggressive mimic for a cleaner wrasse, one might predict that clients should stop using guild colouration to identify cleaners, so how is it able to persist? First, clients rarely adopt cleaning solicitation poses for mimic *P. rhinorhynchos* (Côté & Cheney, 2007), suggesting that clients can (especially at close viewing distances) discriminate mimic from model. Second, mimicry is most effective when mimic and model occur in close proximity (Côté & Cheney, 2004). Lastly, the frequency with which mimics actually attack clients varies spatially and temporally. For



**Fig 1.** Examples of signal colouration in (A) cleaner fish and (B) cleaner shrimp. In cleaner fish, a dark lateral stripe and a combination of blue and yellow colouration seems to represent convergence on a cleaner guild colouration. Among cleaner shrimps, many cleaner shrimps display white body parts (e.g. antennae, chelae, and front legs) which function as signalling traits in several species (*Ancylomenes pedersoni*, *Ancylomenes longicarpus*, and *Lysmata amboinensis*). Images from Wikimedia commons except that of *Periclimenes yucatanicus* (credit: Laura Bagge) and *Lysmata amboinensis* (credit: Frank Gradyan).

example, another mimic of *L. dimidiatus*, the sabre-toothed blenny *Aspidontus taeniatus*, sometimes bites the fins of potential clients. The frequency of fin-biting, however, varies geographically and with environmental conditions (Cheney, Grutter & Bshary, 2014), such as the availability of alternative food sources (Fujisawa, Sakai & Kuwamura, 2020). Thus, the spatial and temporal variation in both the effectiveness of mimicry, and in paying the costs of being duped by mimics, likely allow signals of cleaner identity to remain, on average, honest.

By contrast with signals of identity, some signals indicate aspects of the sender's state that vary over time, and thus

are dynamic, such as willingness to clean at a given time. Approaching and posing at a cleaning station does not guarantee that a client will be cleaned – for example, the cleaner shrimp *A. pedersoni* does not signal to approximately 20% of clients that pose at cleaning stations, and some clients then leave without being cleaned (Caves *et al.*, 2018). In the cleaner shrimp *Lysmata amboinensis*, 44% of predatory clients that pose do not get cleaned (Caves *et al.*, 2019). Therefore, signalling to clients that have already posed at a cleaning station may serve to indicate that a cleaner is willing to clean.

This willingness may be closely tied to state or motivation at a given moment – for example how hungry the cleaner is – which may be communicated by modulating signalling behaviour. In support of this, hungry cleaner shrimps (*Urocaridella* sp. C) spend more time signalling, signal in closer proximity to clients, and clean clients more frequently than do satiated cleaners (Becker & Grutter, 2005; Becker *et al.*, 2005). When given a choice, clients prefer hungry, signalling cleaners to satiated cleaners (Becker *et al.*, 2005). Similarly, the cleaner shrimp *A. longicarpus* claps its chelae more often when food-deprived than when satiated, and hungry shrimps are more likely to approach and clean a human hand (Chapuis & Bshary, 2009). Thus, the hungrier a cleaner is, the more likely it may be actually to engage in cleaning. One reason that clients may benefit from having this information is that hungry cleaners may be less able to afford a client terminating an interaction early in response to non-mutualistic behaviour (i.e. taking a painful bite of scales or mucus), meaning they tend to act more mutualistically, but this remains unstudied.

Cleaner signals may also indicate something about the quality of service a cleaner can provide at that time. For example, oxidative stress can influence the appearance of condition-dependent colour signals, such as the vivid blue colour displayed by *L. dimidiatus*. Cleaner wrasse whose diet had been oxidized exhibited a decrease in the saturation of blue body colouration compared to control fish, and they also decreased the amount of physical contact, using either their fins or their mouths, that they made with clients during cleaning (Trigo *et al.*, 2020). The authors interpreted these behavioural changes as resulting in decreased quality of the cleaning service, a decrease which is reflected in the change in colour patch saturation. Thus, clients could benefit from evaluating cleaner colouration to determine which individuals offer the best cleaning services.

## (2) What maintains signal reliability?

A variety of mechanisms have been identified that maintain signal reliability in systems where the sender and receiver are the same species, including relatedness, differential costs, differential benefits, and receiver-dependent costs (Guilford & Dawkins, 1995; Vehrencamp, 2000; Searcy & Nowicki, 2005). In relation to interspecific systems, I explore each of these possibilities in turn, and discuss how differential benefits and receiver-dependent costs are most likely to explain signal reliability in cleaning interactions.

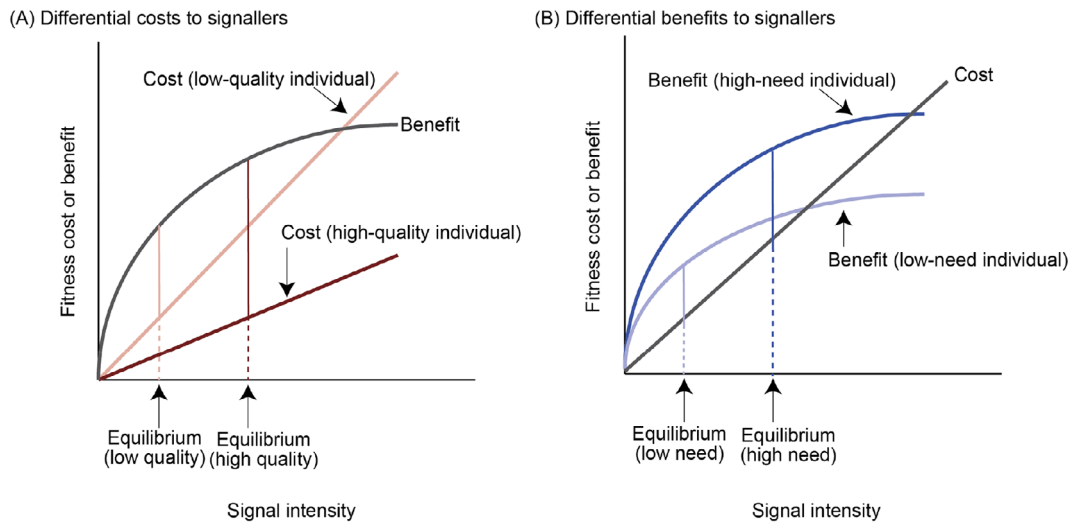
First, in intraspecific systems, signal reliability can be maintained if the sender and receiver are closely genetically related. Although this cannot be the case with interspecific signals, the same predictions are made if there is no conflict of interest between the sender and receiver (see Searcy & Nowicki, 2005). One might predict that this is the case if cleaning is mutualistic, since both parties benefit from the interaction. However, as discussed above, whether an individual cleaning interaction is mutualistic or not is context dependent. Additionally, several studies have demonstrated

a conflict of interest between cleaner fish and their clients. Specifically, laboratory studies of *L. dimidiatus* and *Elacatinus* gobies have demonstrated that, when offered the choice, cleaners prefer to eat client mucus over parasitic gnathiid isopods and copepods (Grutter & Bshary, 2003; Soares *et al.*, 2010). One field study found that mucus comprised almost half of the gut contents in the wrasse *Labroides bicolor* (Oates *et al.*, 2012). This sets up a conflict of interest between cleaner and client, in that the client would benefit most from parasites being eaten, while cleaners prefer to eat mucus. The intensity of these conflicts of interest varies across client species that harbour different parasite communities (Grutter, 1994), as well as across cleaner species (e.g. Oates, Manica & Bshary, 2010; Barbu *et al.*, 2011; Côté & Mills, 2020).

When the interests of the sender and receiver do not precisely align, costs, benefits, and discrimination among individual senders may all contribute to signal reliability. The handicap principle (Zahavi, 1975; Grafen, 1990; Johnstone, 1997) provides one explanation for signal reliability based on the costs associated with signalling. For handicaps to function, the relationship between costs and signal intensity must differ for high- versus low-quality signallers, and thus the optimal signalling level – the value of signal intensity at which the difference between signal benefits and costs is maximized – will be higher for high-quality signallers than low-quality signallers (Fig. 2A) (Grafen, 1990; Johnstone, 1997). Handicaps are robust against cheating because any signallers that signal at an intensity beyond their optimal level will pay higher costs relative to the benefits they receive. Among cleaner shrimp, many signalling structures are exaggerated body parts (long antennae, elongated chelae, etc.), and among cleaner fish bright colours are important signals. The development, maintenance, or display of signalling traits may impose costs that only high-quality signallers can bear. However, as yet no studies have quantified the costs associated with producing, maintaining, and bearing these signals in any cleaning system [but see Trigo *et al.* (2020) who show that oxidative stress alters colour pattern saturation in *L. dimidiatus*]. Whether links exist between signal form and some aspect of signaller quality that is important for clients to assess is underexplored.

The handicap principle, however, is not the only explanation for signal reliability, since the relationship between signal intensity and benefit – rather than cost – can make signalling honest (Fig. 2B) (Grafen, 1990; Johnstone, 1997). If different categories of signallers experience differential benefits from signalling, then, as with handicaps, different signallers will have different optimal signalling levels. An example of such a system is the begging of avian chicks, in which some chicks are hungrier than others and parents must decide which chicks to feed. For a hungrier chick, which is of higher need, the benefit curve rises very steeply, because receiving a certain amount food will have a greater impact on the chick's fitness as opposed to a satiated chick, for which the benefit curve rises less steeply (see Searcy & Nowicki, 2005). Thus, the equilibrium signalling level will





**Fig 2.** The graphical signalling models proposed by Johnstone (1997) and illustrated by Searcy & Nowicki (2005). In A the signal conveys quality. Cost curves for signallers of high and low quality differ, so the equilibrium signalling level (the value of signal intensity at which the difference between signal benefits and costs is maximized) for the high-quality signaller is greater than the equilibrium for the low-quality signaller. In B the signal conveys need. The benefit curves for signallers of high and low need differ such that the benefits received by high-need signallers are greater than low-need signallers at any particular signalling level, and equilibrium signalling levels for each signaller predict that high-need signallers will signal at greater intensity.

be higher for the hungry chick than the satiated chick, and in this type of signalling system, one would predict greater signal intensity from signallers of high need than signallers of low need. Cleaners of different hunger levels modulate their signalling (Becker & Grutter, 2005; Chapuis & Bshary, 2009), and differential benefits experienced by individual cleaners may be what creates the predicted relationship between signaller attributes (hunger level) and signal intensity.

Another way that signals may be reliable is if signalling dishonestly is disadvantageous because of the way that receivers respond. For example, models have shown that cooperation can persist even in the face of non-mutualistic behaviour by some individuals, as long as the partner that is vulnerable to being cheated has control over when to terminate the interaction (Johnstone & Bshary, 2002). In the cleaner wrasse *L. dimidiatus*, individuals can act non-mutualistically by eating healthy scales or mucus instead of ectoparasites, to which clients respond by ‘jolting’ as if in response to a painful bite (Bshary, 2001). Field studies show that clients that have access to more than one *L. dimidiatus* cleaning station swim away when a cleaner acts non-mutualistically (Bshary & Grutter, 2002a). Thus, a cleaner signalling dishonestly that it can provide high-quality cleaning services, but subsequently acting non-mutualistically, can be costly if the client terminates the interaction early.

When repeated interactions between individual cleaners and clients occur, receivers may also remember particular cleaners and discriminate against dishonest individuals in the future. In essence, an individual’s reputation can serve as a kind of receiver-dependent cost. For example, clients that experience non-mutualistic behaviour from a cleaner

and have access to more than one *L. dimidiatus* cleaning station are more likely to visit a different station next than if the interaction had ended positively (Bshary & Schäffer, 2002). Individual *L. dimidiatus* also vary in the frequency with which they consume healthy tissue. Cleaners that do so more frequently are avoided by clients more often as compared to cooperative cleaners (Bshary, 2002). Thus, clients seem able to remember the quality of cleaning services they received at different stations and to avoid low-quality partners in the future. However, repeated interactions between individual cleaners and clients do not occur in all cleaner species. For example, the cleaner *L. bicolor*, rather than occupying a fixed cleaning station, roves over large areas, thus decreasing the frequency of repeated interactions. Oates *et al.* (2010) found that the home range size of individual *L. bicolor* is positively correlated with client jolt rate. Those cleaners with the largest home ranges presumably have the lowest frequency of repeat interactions with individual clients, so the ability of a given client to punish non-mutualistic behaviour by avoiding future interactions is lower. Thus, cleaners with larger home ranges suffer lower costs when they act non-mutualistically towards a given client.

The negative consequences that cleaners experience from acting non-mutualistically can also be imposed by parties other than the client being cleaned. Sometimes, multiple clients are present at a cleaning station at once, allowing bystander clients directly to observe cleaner signals and subsequent quality of service provided by the cleaner. Laboratory experiments show that cleaners increase their levels of cooperation (i.e. jolts decrease in the client being cleaned) in the presence of a bystander client (Pinto *et al.*, 2011), bystanders spend more time associating with cleaners that

appear to feed mutualistically (i.e. do not cause jolting in their clients; Bshary & Grutter, 2006), and bystanders that observe non-mutualistic behaviour avoid that cleaner in the future (Pinto *et al.*, 2011). In some cases, however, cleaners can fool bystander clients. Specifically, cleaner wrasse often administer tactile stimulation to clients using their pelvic and pectoral fins, which reduces client stress (Soares *et al.*, 2011). Some cleaners strategically administer tactile stimulation to small, resident clients in the presence of large bystander clients; however, when those large clients then pose for cleaning, cleaners act non-mutualistically, feeding on client tissue or mucus (Bshary, 2002). Interestingly, whether cleaners switch from apparent cooperation to non-mutualistic behaviour varies with the cleaner's physiological state (Soares *et al.*, 2014) and the richness and diversity of the client community (Binning *et al.*, 2017).

Cleaners can also punish one another for cheating when they clean in groups. In *L. dimidiatus* that clean in male–female pairs, male cleaners sometimes punish female cleaners for acting non-mutualistically (Raihani, Grutter & Bshary, 2010). In the laboratory, females that were punished by males then increased their mutualistic behaviour in the next interaction, allowing the male to increase his own foraging success in that interaction (Raihani *et al.*, 2010), since cleaning interactions last longer when both parties act mutualistically.

## V. CLIENT SIGNALLING

Although I have so far discussed signals produced by cleaners, there is some evidence that clients signal as well. For example, upon arrival at cleaning stations, clients adopt characteristic ‘cleaning solicitation poses’ – highly stereotyped immobile postures (Feder, 1966; Losey, 1971; Côté *et al.*, 1998) – which play an important role in eliciting cleaning. In one study, Côté *et al.* (1998) found that the probability of being cleaned by *Elacatinus* gobies doubles upon posing. Similar patterns were found in a study of the shrimp *Ancylomenes pedersoni*: clients posed in 93% of interactions, and posing almost always preceded cleaning (Caves *et al.*, 2018). It has been noted that there is variation among client species in specific posing position, for example posing with the tail up or down, or with the opercula and fins flared out or not (e.g. Côté *et al.*, 1998), meaning that there is the potential for posing to signal species identity.

Other client behaviours may serve as signals as well. Some have suggested that jolting is an indication that a client is about to terminate an interaction (Feder, 1966; Wickler, 1968; Losey, 1971), although jolting may instead be a response to a painful bite or pinch (e.g. Soares *et al.*, 2008). Rapid colour change may also serve a signalling function, since some clients adopt a darker colouration while visiting a cleaning station (Randall, 1958, 1962; Limbaugh, 1961; Feder, 1966; Caves *et al.*, 2018) (Fig. 3). In support of this, a recent study found that, if a cleaner

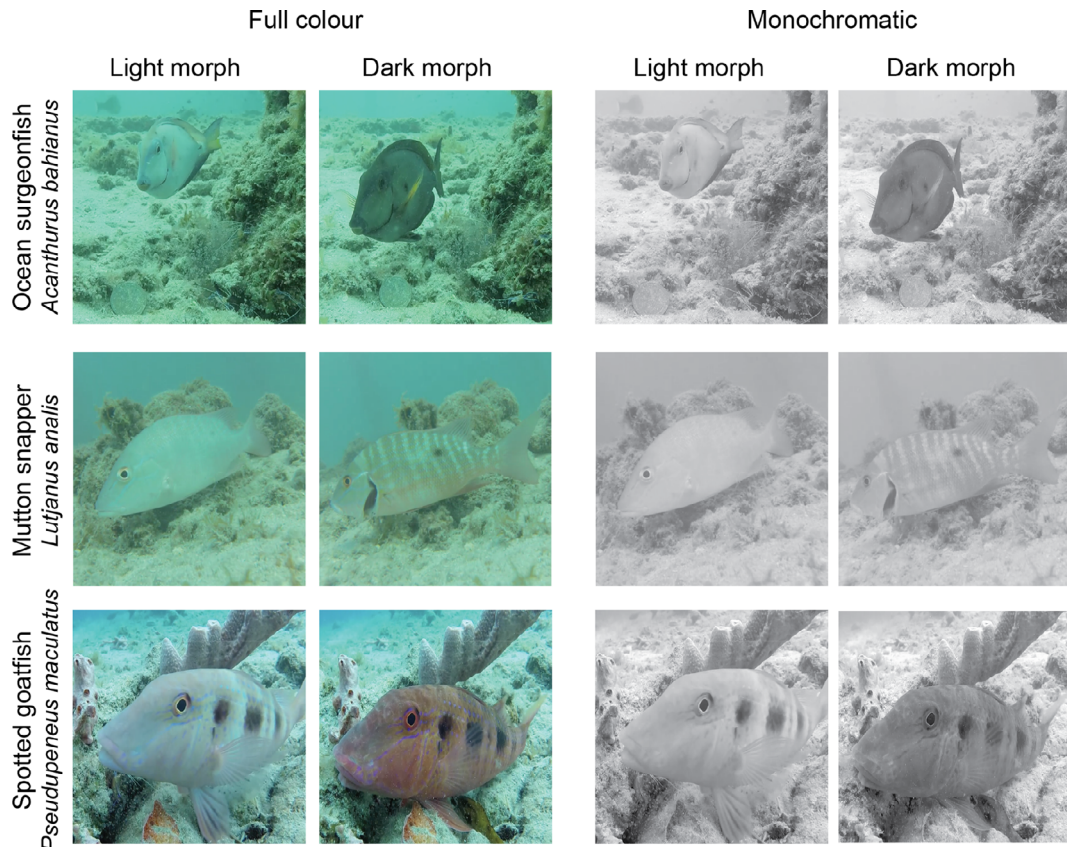
shrimp (*Ancylomenes pedersoni*) did not first signal to a client, a client that changed to a darker colour morph tripled the likelihood it would then be cleaned. This finding suggests that, in the absence of signalling by cleaners, clients have their own signal that can induce cleaning (Caves *et al.*, 2018).

What information might cleaners extract from client signals? First, cleaners may assess something about parasite load, perhaps through posing. Clients with higher parasite load pose more frequently than those with lower parasite load (Grutter, 2004). Cleaners may also assess predation risk – a variety of cleaner species alter their behaviour when interacting with potentially predatory clients versus those that are not (e.g. Darcy *et al.*, 1974; Soares, Cardoso & Côté, 2007; Chapuis & Bshary, 2009; Caves *et al.*, 2019). However, the mechanism by which cleaners might assess predation risk is unknown. Additionally, cleaners could assess information about clients through cues, rather than signals. Cues are similar to signals in that they also allow a receiver to extract information, but differ from signals in not having evolved for the purpose of conveying that information (Searcy & Nowicki, 2019). For example, cleaners may assess parasite load (Arnal *et al.*, 2000) or predation risk (as in Caves *et al.*, 2019) using client body size, perhaps a reliable indicator but not one that evolved to inform cleaners about parasites or predation risk.

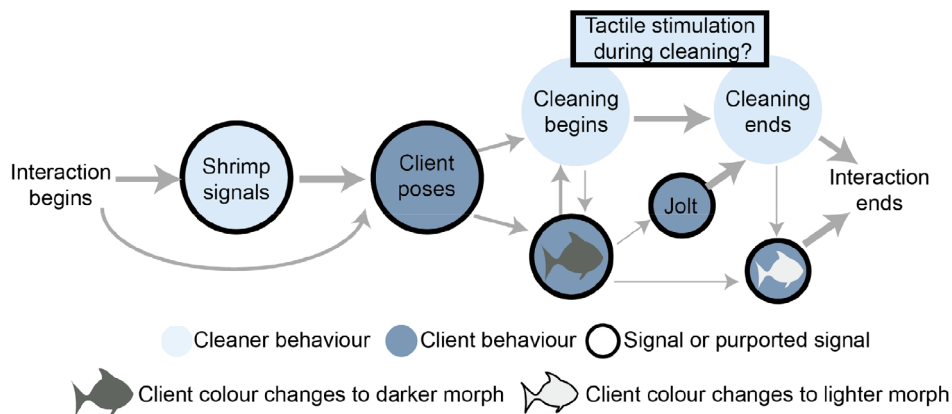
Some evidence suggests that cleaner–client interactions are a network of behaviours in which the cleaner and client can each play the role of signal sender and receiver (e.g. Sargent & Wagenbach, 1975; Caves *et al.*, 2018; Fig. 4), i.e. that cleaners and clients exhibit reciprocal communication. Testing the hypothesis that reciprocal communication exists between cleaners and clients would allow one to probe whether the emergence of stable, cross-species communication systems requires the kind of advanced cognitive skills that are not often attributed to fish and shrimp (e.g. Westrip & Bell, 2015). Thus, examining communication between cleaners and clients may increase our understanding of the diversity of communication systems.

## VI. THE PROBLEM OF SIGNALLING TO MULTIPLE SPECIES OF RECEIVER

Understanding the evolution of cleaner or client signals requires additional insights from sensory ecology. In particular, each party's sensory capabilities likely impose key selective pressures on the signalling traits that mediate an interaction, so it is crucial to know how the intended receiver(s) perceive a signal. Interactions between species that are distantly related and that differ significantly in body size are a particularly promising area for exploring how organisms with different sensory capabilities interact and place selection pressures on one another, because partners likely have very different sensory capabilities. Additionally, because cleaning interactions involve multiple sympatric cleaner species supporting diverse client communities



**Fig 3.** Client fish change from light to dark colour morphs while posing at cleaning stations of the cleaner shrimp *Ancylomenes pedersoni* in Curaçao, Netherlands Antilles. Images are displayed in colour (left) or as they may appear to a viewer with a monochromatic visual system (right), such as that of *A. pedersoni* (Caves, Frank & Johnsen, 2016). The monochromatic images were created by extracting and displaying only the green colour channel from each image. Each pair of photographs come from the same cleaning interaction and are taken within 5 s of each other, illustrating the rapid nature of client colour change. Photographs taken by the author.



**Fig 4.** An example interaction network from 199 interactions between the cleaner shrimp *Ancylomenes pedersoni* and its client fish. The interaction proceeds from left to right, with behaviours (circles) connected by arrows. Circle size is scaled to represent the number of times a given behaviour was observed across all interactions, and arrow size is scaled to illustrate the frequency with which a given behavioural transition occurred. Behaviours with potential or demonstrated signal function are outlined in black. Redrawn from Caves *et al.* (2018).

(Guimaraes *et al.*, 2007), they can help inform our understanding of how signals evolve under selection from multiple receiver species.

Given that the majority of evidence suggests that cleaners and clients attend to visual information during cleaning interactions (e.g. Losey, 1971; Caves *et al.*, 2018; Wismer

*et al.*, 2019), I focus here on visual signalling, although other modalities deserve further attention. In marine cleaning interactions, cleaner signals must be perceptible by the visual systems of a variety of client species, which is non-trivial given that reef fish have famously diverse visual capabilities, both in terms of colour vision (reviewed in Marshall *et al.*, 2019) and visual acuity, the ability to perceive detail (Caves, Sutton & Johnsen, 2017).

### (1) Signal form in a diffuse interaction

Signal theory predicts that if signals communicate similar messages to similar audiences, they should be under selection to be similar across species or even to converge in form [as in alarm calls (e.g. Marler, 1957; Jurisevic & Sanderson, 1998) and convergent floral syndromes (Schiestl & Johnson, 2013)]. Convergence in signal form has been suggested to be a force underlying the asymmetry seen in many mutualistic networks (i.e. the fact that a few species of cleaner support diverse client communities), since convergence allows new species to attach to a network as it evolves (Thompson, 2005). This could indicate a key ecological role for convergence in signalling traits, which could allow new cleaner species to join a cleaning network once it is established (Bascompte, Jordano & Olesen, 2006).

One reason signals might converge on a certain form is if that form is particularly conspicuous to the intended receiver in the signalling environment (e.g. Marler, 1957; Stankowich, Caro & Cox, 2011; Stevens & Ruxton, 2011). Several studies have found evidence that cleaner fish guild colouration represents evolutionary convergence on a signal form that is maximally conspicuous in reef environments, to a variety of relevant viewers. For example, as discussed above, many cleaner fish display blue colouration (often in combination with yellow), along with a dark lateral stripe (Fig. 1A). Cheney *et al.* (2009a) used theoretical models of colour discrimination to show that, to several different reef fish viewers, ‘cleaner blue’ is the most spectrally contrasting colour against a coral reef-coloured background, whereas yellow is the most spectrally contrasting colour against either a blue water background or a black lateral stripe. In Caribbean gobies, the phylogenetic distribution of stripe colour suggests that the ancestral phenotype is either a yellow or a green stripe, but many cleaners display blue stripes, which are, on average, more contrasting with different microhabitat backgrounds than yellow or green stripes (Lettieri *et al.*, 2009). Thus, the combination of colours and patterns displayed by cleaner fish allows them to be highly conspicuous to potential clients no matter what the viewing background (although because different wavelengths of light attenuate with depth, how discriminable colour morphs are from various backgrounds also depends upon depth, e.g. Lettieri *et al.*, 2009).

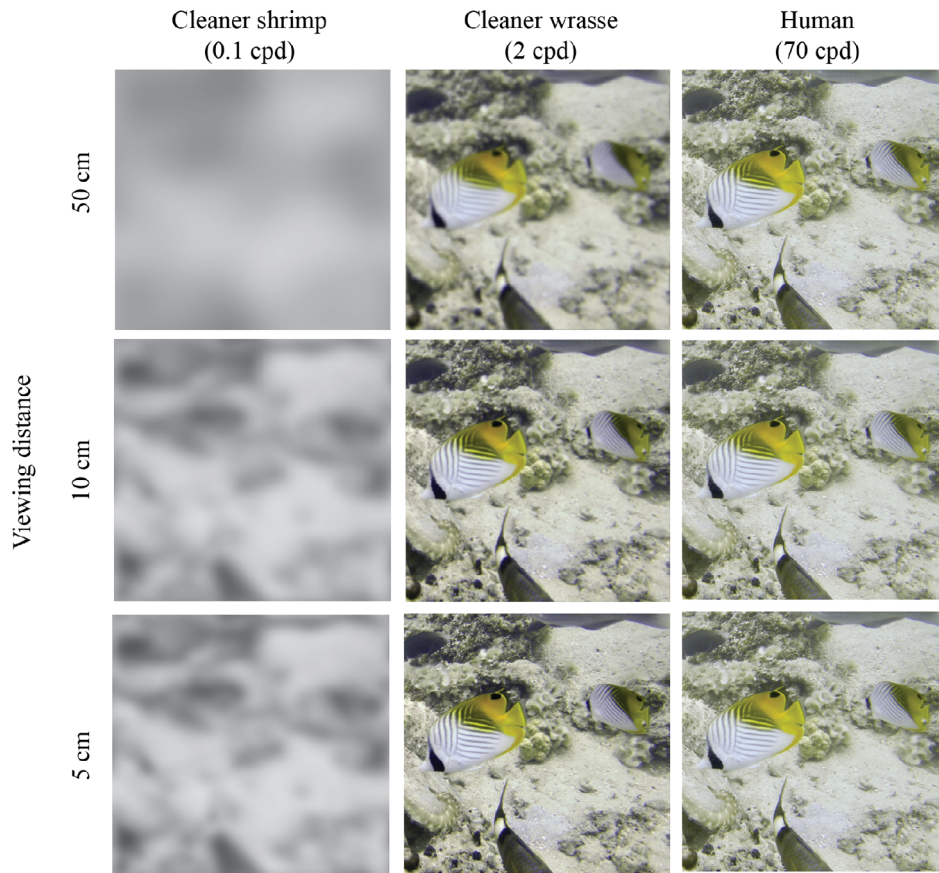
Pressures aside from conspicuousness can also influence signal form. Certain signal forms can be selectively advantageous if they are easier for receivers to learn and remember. Losey (1971, p. 72) predicted that cleaner signals should show a great “dependency on learning mechanisms”, but this

aspect of signalling in cleaner–client systems is underexplored. The impact of receiver learning and preferences, however, has been demonstrated in plant–pollinator signalling [see Schiestl & Johnson (2013) for a review], which may exhibit some parallels with cleaner–client signalling. Some signals are easy to learn to associate with rewards, as in hummingbirds, which despite lacking an innate preference for the colour red can quickly learn to associate it with a reward (e.g. Meléndez-Ackerman, Campbell & Waser, 1997). Associative learning can shift receiver preferences as they learn to prefer the signal associated with the highest reward. Aside from being learnable, signals may exploit pre-existing biases in receivers. For example, honeybees (*Apis mellifera*) show preferences for patterns – radiating stripes, dark centres, and peripheral dots – which are found on many flowers, but those preferences likely evolved in the context of burrow-finding or aggregation behaviour (Biesmeijer *et al.*, 2005). If cleaner signals similarly exploit pre-existing receiver preferences, one might predict that they will not exploit preferences that arose due to species-specific pressures (for example mate-seeking), given the large number of client species whose preferences would have to be exploited.

In considering how cleaners and clients might place pressure on one another’s signals, a major open question is whether or not selection pressure from all signal receivers is equal. One meta-analysis found that the majority of cleaning interactions are dominated by a subset of abundant client species, most of which are gregarious, mid-water, and planktivorous (Floeter, Vázquez & Grutter, 2007), although whether these common species exert particular selection pressure on signals is unknown. Cheney *et al.* (2009a) found that cleaner fish blue colouration was equally contrasting with both blue water and coral reef backgrounds to the piscivorous barracuda (*Sphyraena helleri*) and an herbivorous surgeonfish (*Ctenochaetus strigosus*), suggesting equal conspicuousness to a variety of viewers. Lettieri *et al.* (2009), however, found that amongst cleaner gobies, yellow and blue stripes were the most conspicuous to piscivorous clients, and they suggest that signals are under selection to be most conspicuous to clients that impose the greatest risk.

### (2) Cleaner sensory capabilities and client signals

Despite large overlap in the communities of clients that they serve, sympatric species of cleaner shrimp and cleaner fish are likely to impose different selective pressures on client signals due to differences in their perceptual capabilities (Fig. 5). Caves *et al.* (2016) examined visual capability in three species of cleaner shrimp, and in all three species, they found evidence for only a single spectral sensitivity peak (maximally sensitive at 520–530 nm), implying that cleaner shrimp have monochromatic vision and thus cannot discriminate colour. Additionally, visual acuity across all three species was very low, meaning it is unlikely that they can perceive fine details. By contrast, cleaner wrasse likely have the ability to perceive colour, and a published regression between body size and



**Fig 5.** Differences in visual capability between cleaner shrimp (left) and cleaner wrasse (middle) mean that they likely perceive client fish very differently. Human vision is shown in the righthand column for reference. Acuity in cycles per degree (cpd) is shown in parentheses at the top of each column. Cycles per degree represents the number of black and white stripe pairs that an organism can discriminate in a single degree of visual angle; thus, higher numbers indicate finer vision. Images are shown at three different viewing distances because acuity is distance dependent – for a given visual system, smaller details are resolvable from closer distances. Shrimp vision data were taken from (Caves *et al.*, 2016). Because cleaner shrimp have monochromatic colour vision, we have displayed only the green channel from the image. For the middle column, we assume the acuity of cleaner wrasse is approximately 2 cpd based on a regression between body size and acuity in ray-finned fishes (Caves *et al.*, 2017), and assume trichromatic colour vision. To create images that reflect the acuity of a given viewer, we used the R package *AcuityView* (Caves & Johnsen, 2017). Note that in the case of compound eyes, like those of a cleaner shrimp, depth of field is very large, meaning they are capable of focusing on objects at extremely close distances (Land & Nilsson, 2002). In these images, however, the apparent ‘fuzziness’ is not due to inability to focus on an object from a given distance, but rather reflects that the viewer’s optical system cannot resolve details below a given size. Image taken by the author.

visual acuity in fishes (Caves *et al.*, 2017) suggests that cleaner fish likely possess acuity that is at least an order of magnitude higher than that of a cleaner shrimp.

Considering perceptual capabilities can inform exactly what aspects of a signal may be relevant to a given receiver. For example, although many client fish do change colour at cleaning stations, which appears to serve as a signal (Caves *et al.*, 2018), the monochromatic, low-resolution visual systems of cleaner shrimp are unlikely to be able to perceive the colour change as such. However, it is notable that clients consistently change from a light morph to a dark morph. Thus, what we as humans perceive as a colour change is likely perceived as a brightness change by cleaner shrimp (Fig. 3). Additionally, these colour changes are viewed over very short

distances and do not involve fine-scale spatial stimuli, suggesting they are likely visible to their intended receiver. It is currently unknown, however, whether client fish direct different signals to cleaner fish *versus* shrimp, and whether these signals may be adapted to the visual capabilities of the cleaner.

## VII. OPEN QUESTIONS

At the conclusion of her review, Côté (2000) stated that a central unanswered question in the study of cleaning interactions was whether or not they are always mutualistic. She posited

that this lack of certainty may have arisen because “the nature of the cleaning interaction may be variable, changing spatially and temporally with the environmental context” (Côté, 2000, p. 345). The idea that the outcome of a given interaction is context dependent, and can range from parasitism to mutualism (e.g. Chamberlain, Bronstein & Rudgers, 2014), is well established, and is a concept that we now know applies to cleaning interactions.

Parasite load is one of the key factors that has been shown to influence the outcome of a cleaning interaction, but as I detail here, the broader behavioural and social contexts are important as well. Progress in this regard has been facilitated by the advent of remote video technologies that allow detailed observations to be made of *in situ* cleaner–client interactions in the absence of human observers. As a result, relatively detailed information on the sequence of behaviours, including signalling behaviours, by which cleaning interactions are initiated and by which they proceed is now available for several species of cleaner fish and shrimp. Future work should expand such studies to more cleaner species, to broaden our understanding of the dynamics of both cleaning and interspecific signalling. For example, studying signalling in different cleaner species can help shed light on whether unrelated cleaners have converged on similar signal forms and signalling behaviours.

Studies on cleaner wrasse in the genus *Labroides* and gobies in the genus *Elacatinus* have demonstrated that conflicts of interest, in which cleaners prefer to eat client fish mucus instead of ectoparasites, exist in many cleaner systems. The strength of this conflict of interest differs across cleaning systems, in turn influencing the dynamics of partner choice and partner retribution. However, increased study regarding conflicts of interest or the dynamics of partner retribution in a greater number of cleaning systems, especially in cleaner shrimp systems, is needed. An open question is whether cleaner shrimp, for example, act non-mutualistically (and whether client jolting indicates non-mutualistic behaviour in cleaner shrimp, as it does in cleaner wrasse), and if so what magnitude of cost it imposes on a client.

Another poorly studied topic is the information content of cleaner signals. This is key to understanding how signals remain reliable, as the correlation between signal and information represents reliability. For example, some cleaners alter their signalling behaviour based on hunger level, but do these differences in signals then indicate something about the cleaning services they provide? Very little is currently known about exactly what cleaners are signalling about their own state or future behaviour, and how clients adjust their response. Additionally, the costs of developing and bearing signalling traits, or of producing signals, are understudied; thus, whether some signalling traits are handicaps that can only be borne by high-quality signalers is unknown. A first step in any of these studies will be to determine which behaviours serve as signals; for this, we require *in situ* observations of cleaner–client interactions, as well as demonstrations of how purported signalling behaviours both impact the

client’s behaviour and correlate with some aspect of the cleaner’s state or future behaviour (see Caves *et al.*, 2018). Once signalling traits are identified, one can examine information content [by measuring the correlation between signal characteristic(s) and characteristic(s) of the signaller or environment] and signal reliability (by quantifying the strength of that correlation).

Thanks to long-term studies of reefs from which *L. dimidiatus* cleaners are periodically removed, we now have a good understanding of the long-term negative health effects of bearing parasites and how the presence or absence of cleaner wrasse on reefs may alter the dynamics of reef fish populations over time. However, in species other than *L. dimidiatus*, demonstrations of how cleaners impact client fitness – and an understanding of the time span and the magnitude of these benefits – are still lacking.

The impacts of anthropogenic changes on cleaners also deserve study. For example, the bleaching of corals and anemones will change the visual backgrounds against which many cleaners signal (e.g. Marshall *et al.*, 2019), and climate change-induced shifts in depth ranges may alter how cleaner and client signals appear, given that different wavelengths of light attenuate differently with depth (Caves & Johnsen, 2021). Thus, anthropogenic impacts may affect cleaning interactions. Cleaners that are stressed are less predisposed to interact with clients (de Abreu *et al.*, 2020), but how stressors like rising temperatures and other changes to marine environments will impact cleaning interactions is unstudied.

Finally, despite significant strides in understanding cleaning interactions in marine systems, non-marine cleaning systems have remained poorly studied. Future studies should focus on additional cleaning systems, such as mammal and bird cleaners, because together these systems represent a natural experiment with which to explore the evolutionary trajectories followed by multiple distantly related groups in which the same intriguing behaviour has arisen independently.

## VIII. CONCLUSIONS

- (1) Cleaning mutualisms are a distinctive kind of interaction. They are different from the coevolved relationships that occur between many mutualistic species pairs [for example figs and fig wasps or yucca plants and yucca moths (Janzen, 1979, 1980; Pellmyr & Huth, 1994)], and instead are a relatively loose, yet frequent, association between large numbers of client species and small numbers of cleaner species. Although they bear some similarity to plant–pollinator mutualisms, there are (almost) no situations under which a flower poses a predation risk to its pollinator, and yet many cleaners regularly interact with clients that represent significant risk, highlighting the strong pressures operating in cleaning interactions.

- (2) The outcome of a given signalling, and subsequent cleaning, interaction is not always mutualistic, and factors ranging from parasite load, to the presence of bystander clients, to which individual cleaners comprise a group, can influence the outcome of a cleaning interaction. How abiotic and/or biotic contextual factors affect interaction outcomes, however, is understudied in cleaning interactions relative to many other interspecies interactions (see Hoeksema & Bruna, 2015). Thus, increased research effort should be given to understanding how variation in the ecological, social, behavioural, and even genetic context of a cleaning interaction affects the balance of costs and benefits.
- (3) Signals have been shown to mediate cleaning interactions in both cleaner fish and several species of cleaner shrimp. At least in marine cleaning interactions, signals appear to be widespread across taxa, and increasing evidence shows that these signalling behaviours and traits are key to allowing partners to determine where, when, and with whom to interact. However, increased attention should be given to understanding the information content of signals, as well as how signals vary with context and how clients respond to that variation.
- (4) Cleaning interactions provide an excellent system in which to examine how selection pressures imposed by different receivers with different sensory capabilities can impact the evolution of signal form. For example, among cleaner wrasses and gobies, convergent evolution has resulted in signals that are conspicuous to a diverse array of clients. However, our understanding of how receiver sensory ecology and cognition affect the evolution of signal form in a diffuse system like cleaning will be greatly improved by additional data on signal form and signalling dynamics in a larger number of cleaning systems, whether marine, freshwater, or terrestrial. Additionally, signals may provide a means by which to categorise species as obligate, dedicated cleaners *versus* facultative, incidental cleaners (see Vaughan *et al.*, 2017), which is basic yet fundamental information about any cleaning system. Thus, as we expand studies of cleaning to include other species, signals may provide a useful framework with which to examine patterns of cleaning in a broad, comparative manner.

## IX. ACKNOWLEDGEMENTS

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