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The cleaner wrasse outperforms other labrids in ecologically relevant contexts, but not in spatial discrimination

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The ecological approach to cognition provides a clear prediction regarding cognitive performance: performance should be higher in contexts that are ecologically valid than in invalid contexts. Here, we tested this prediction by comparing juvenile and adult cleaner wrasse, *Labroides dimidiatus*, with juveniles and adults of five related labrid species. Only the former fully depend on interactions with a large variety of so-called 'client reef fish' for their diet, which involves feeding largely on ectoparasites rather than on preferred client mucus. Our results show that cleaners outperform the other species tested in two contexts that are tightly linked to cognitive challenges during cleaning interactions: the willingness to explore novel objects and the ability to feed against preference in order to increase energy intake. In contrast, all species performed similarly in a spatial discrimination task, which was chosen for its limited ecological relevance to any of the species tested. In conclusion, the cognitive abilities of cleaners seem to be tightly linked to the domain-specific challenges they face in nature. We found no support for the alternative hypothesis that selection for social competence in cleaning interactions leads to domain-general cognitive abilities that also enhance performance in unrelated contexts.

Broadly defined, cognition refers to the mechanisms by which animals acquire, process, store and act on information from the environment (Shettleworth, 2010). The ecological approach to cognition emphasizes ecological validity as a main predictor of a species' performance in a given task, independent of the underlying cognitive mechanism (Shettleworth, 2010). This approach is particularly suitable for explaining why various complex behaviours and cognitive traits such as tool use, self-recognition and many of the features associated with the demands of social living appear to have evolved independently in distant clades. Furthermore, it explains why species with less complex central nervous systems may perform better than species with more complex central nervous systems, including humans, given tasks that are ecologically relevant only to the former. For instance, it has been shown that bees are capable of quicker conceptual learning than primates and infants (Avarguès-Weber, Dyer, & Giurfa, 2011; Chittka & Jensen, 2011), that pigeons, *Columba livia*, outperformed humans in a probability puzzle (Herbranson & Schroeder, 2010) and that the bluestreak cleaner wrasse, *Labroides dimidiatus*, outperformed primates in a foraging task relevant only to the cleaners' ecology (Salwiczek et al., 2012). Unsurprisingly, an increasing number of studies suggest that phylogenetic relatedness is often a poor predictor of related abilities when it comes to cognition. For example, food hoarding in birds correlates with hippocampal volume better than phylogenetic relationships do (Krebs, Sherry, Healy, Perry, & Vaccarino, 1989; Sherry, Vaccarino, Buckenham, & Herz, 1989), although the exact nature of the relationship is still debated (Healy, de Kort, & Clayton, 2005). In primates too, social ecology appears to explain the evolution of brain size better than phylogeny (Barton, 1996; Dunbar & Shultz, 2007). Furthermore, it was recently proposed that high general intelligence has independently evolved at least four times within primates alone (Reader, Hager, & Laland, 2011). Cognitive skills thus appear to emerge in order to respond to challenges present in nature, and cannot be predicted from phylogenetic relationships alone (Bolhuis & Wynne, 2009).

The ecological approach has been highly successful in yielding examples of high performance linked to ecological pressures in various taxa, such as in birds (Kamil & Balda, 1990), mammals (Gaulin & Fitzgerald, 1989) or fish (White & Brown, 2015). However, it has so far contributed little to the long-standing question of the degree to which cognition is domain specific (modular) or driven by

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a general-purpose machine (Healy et al., 2005; Heyes, 2003; Krause, 2015; MacLean et al., 2012; Magphail & Bolhuis, 2001; Samuels, 1998; van Schaik, Isler, & Burkart, 2012). It has often been argued that forms of general intelligence (i.e. intelligence in which performance correlates across very different cognitive domains) require the presence of a large brain, while domain-specific abilities can be wired in small brains, and may be based on 'simpler' cognitive processes (van Schaik et al., 2012). A key control in this context is to test species not only in a context in which the ecological approach predicts high performance but also in a context where the ecological approach predicts 'low' or 'average' performance (Shettleworth, 2010). To assess whether a particular aspect of a species' ecology relates to its cognitive performance, it is crucial to compare species that are similar on as many levels as possible (e.g. habitat, ancestry, size, diet), yet differ for the trait of interest. The best and most studied example supporting the ecological approach is the link between spatial memory abilities and food caching in birds. In this system, the ecology of the species (dependency on food caching) appears to be a very good predictor of performance in spatial memory tasks in the laboratory (Balda & Kamil, 1989; Kamil & Balda, 1990; Kamil, Balda, & Olson, 1994), and also appears to correlate with hippocampus size (Sherry et al., 1989). To our knowledge, only a few studies have explicitly tested a control condition in the form of a task for which high performance would not be predicted by the ecology of the species, and thus allow us to distinguish between general and specific cognitive abilities (Olson, Kamil, Balda, & Nims, 1995; Pravosudov & Clayton, 2002). Thus, we see a need to expand proper testing of the ecological approach to other taxa and other contexts. Here, we used a comparative approach to investigate the degree to which the cleaner wrasse, a fish that is renowned for demonstrating complex decision-making skills in social interactions, may excel compared to closely related species in either ecologically relevant or irrelevant tasks.

The bluestreak cleaner wrasse (hereafter 'cleaner') is a small coral reef fish that interacts with dozens of other species (called 'clients'), including predatory fishes, having more than 2000 interactions per day in which it removes ectoparasites from the clients (Grutter, 1996). Conflicts of interest between cleaner and client arise because cleaners prefer to eat the protective client mucus over ectoparasites, where consumption of the former constitutes cheating (Grutter & Bshary, 2003). As a consequence, clients use various partner control mechanisms such as partner switching, punishment, premature termination and image scoring in order to promote cooperative behaviour in cleaners (i.e. feed against their preference and focus on ectoparasites as opposed to mucus; Bshary, 2011). In response to these client control mechanisms, cleaners have evolved the ability to fine-tune service quality to the specific dynamics of each interaction: the quality of a client as a food patch (i.e. the potential benefits of interacting with it), the client's strategic options, the presence of bystanders, and the co-inspection with partners as well as internal states are all taken into consideration when cleaners determine whether to cheat or not (Bshary, 2011; Gingins, Werminghausen, Johnstone, Grutter, & Bshary, 2013; Pinto, Oates, Grutter, & Bshary, 2011; Raihani, Grutter, & Bshary, 2012; Soares, Cardoso, Grutter, Oliveira, & Bshary, 2014). While food acquisition in cleaners leads to a sophisticated interspecific social life, it does not require environmental cognitive abilities such as advanced spatial memory. This is because the cleaners' food patches actively visit them when they are replenished with ectoparasites. We thus expect cleaners to face the same spatial memory challenges as other fishes that share the same habitat (i.e. navigating within their territory on the reef). Three of the five other wrasse species tested here are facultative cleaners. As facultative cleaners do not rely solely on cleaning for their nutritive intake, only some individuals engage in cleaning behaviour, and those that do evidence less sophisticated strategies than obligate cleaners such as *L. dimidiatus* (Barbu, Guinand, Bergmüller, Alvarez, & Bshary, 2011; Côté, 2000). Whether facultative cleaners prefer mucus like *L. dimidiatus* (Grutter & Bshary, 2003) or ectoparasites like Caribbean cleaning gobies is unknown (Soares, Côté, Cardoso, Oliveira, & Bshary, 2010). However, field observations from the Red Sea support the idea that they may prefer ectoparasites: client jolt rate, a correlate of cleaner cheating (Bshary & Grutter, 2002) is lower in interactions with facultative cleaners than with the obligate cleaner *L. dimidiatus* (Barbu et al., 2011). These results, together with the fact that facultative cleaners mainly feed on prey other than ectoparasites, suggest that feeding against preference is of little or no ecological relevance for facultative cleaners. We expect feeding against preference to be of no ecological relevance for noncleaning wrasse species.

Based on the specific aspects of *L. dimidiatus* ecology, we decided to test their performance relative to other wrasses in three different paradigms. First, we investigated whether their high levels of interactions with many client species, including predators, select for increased levels of exploration. While exploration is not as such a cognitive trait, it has been documented repeatedly that exploration or neophobia may have an important impact on cognitive performance especially within species (Boogert, Reader, & Laland, 2006; Carazo, Noble, Chandrasoma, & Whiting, 2014; Dugatkin & Alfieri, 2003; Guillette, Reddon, Hurd, & Sturdy, 2009; Sneddon, 2003; Trompf & Brown, 2014), and also between species (Day, Coe, Kendal, & Laland, 2003; Webster & Lefebvre, 2001). Second, we investigated whether, due to the conflict of interest with clients, cleaners are more able to feed against their preference than other wrasses that do not face this problem in their foraging behaviour. This experiment expands on a previous study that compared cleaners with one other wrasse species which suggested that feeding against preference represents a major challenge for noncleaner and facultative cleaner species alike (Gingins et al., 2013). On the cognitive level, this task has all the features of a self-control task, in which the subject has to choose between two options and can access the more valuable reward for a certain cost such as a time delay or larger effort (Beran, 2015). Finally, we tested all our study species in a spatial discrimination task, which does not appear to be of particular ecological relevance to any of them. Rather than calculating correlations of individual performances across tasks as is often done in within-species comparisons (Isden, Panayi, Dingle, & Madden, 2013; Shaw, Boogert, Clayton, & Burns, 2015), we asked whether performance differed between species in some tasks but not in others. More specifically, if the cognitive abilities of cleaner wrasse are domain specific and tightly linked to their ecological needs, we expected that they should not learn to solve the spatial discrimination task faster than the other species. In contrast, if the interactions with clients have led to the evolution of more domain-general cognitive abilities, then we expected that cleaners would learn faster than the other species even in this ecologically nonrelevant task. Domain-general abilities could, for example, indicate a general ability to learn faster based on associations, or a more general understanding of the existence of food patch variation could allow cleaners to readily use location as an alternative cue to client identity. For the comparison between facultative cleaners and noncleaners, we were interested in whether our data would support the notion that cleaning interactions per se may enhance cognitive performance, or whether facultative cleaning is not important enough to drive the acquisition of specific cognitive skills. For the former hypothesis we expected facultative cleaners to show levels of performance that are intermediate between the noncleaners and the obligate cleaner. Alternatively, we predicted that facultative cleaners should not