

Redouan Bshary - selected references

- 1 Vail, A. L., Manica, A., & Bshary, R. (2014). Fish choose appropriately when and with whom to collaborate. *Current Biology*, 24, R791-R793.
Notes: Collaborative abilities are integral to human society [1] and their evolutionary origins are of great interest. Chimpanzees are capable of determining appropriately when and with whom to collaborate in a rope-pull experiment [2] - the only non-human species known to possess both abilities. Chimpanzees are thought to share these abilities with humans as a result of common ancestry [2]. Here, we show that a fish - the coral trout *Plectropomus leopardus* - has partner-choice abilities comparable to those of chimpanzees in the context of its collaborative hunting relationship with moray eels [3]. Using experiments analogous to those performed on chimpanzees [2], but modified to be ecologically relevant to trout, we showed that trout recruit a moray collaborator more often when the situation requires it and quickly learn to choose the more effective individual collaborator. Thus, these collaborative abilities are not specific to apes and may be more closely linked to ecological need [4] than brain size or relatedness to humans
- 2 Bshary, R. & Brown, C. (2014). Fish cognition. *Current Biology*, 24, R947-R950.
Notes: The central nervous system, and the brain in particular, is one of the most remarkable products of evolution. This system allows an individual to acquire, process, store and act on information gathered from the environment. The resulting flexibility in behavior beyond genetically coded strategies is a prime adaptation in animals. The field of animal cognition examines the underlying processes and mechanisms. Fishes are a particularly interesting group of vertebrates to study cognition for two reasons (Figure 1). First, they occupy a key position in the vertebrate phylogenetic tree: the common ancestor of the tetrapods was a bony fish. Thus, all vertebrates share key genetic features that code for the body structure, including the vertebrate brain. Similarities in brain structure and function are hence likely to be due to common ancestry. A second reason to study fish cognition is that fish have had their own independent evolution/radiation since they split from tetrapods. Bony fishes are by far the most species-rich vertebrate group. As a consequence, they provide the best options for a comparative approach that aims to link the evolution of cognition to a species' ecology. Therefore, the study of fishes may reveal general principles of ecological effects on cognitive abilities in vertebrates
- 3 Bshary, R., Gingins, S., & Vail, A. L. (2014). Social cognition in fishes. *Trends Cogn Sci.*, 18, 465-471.
Notes: Brain evolution has often been correlated with the cognitive demands of social life. Further progress depends on our ability to link cognitive processes to corresponding brain part sizes and structures, and, ultimately, to demonstrate causality. Recent research suggests that fishes are suitable to test general hypotheses about vertebrate social cognition and its evolution: brain structure and physiology are rather conserved among vertebrates, and fish are able to

perform complex decisions in social context. Here, we outline the opportunities for experimentation and comparative studies using fish as model systems, as well as some current shortcomings in fish social cognition research

- 4 Vail, A. L., Manica, A., & Bshary, R. (2013). Referential gestures in fish collaborative hunting. *Nat. Commun.*, 4, 1765.

Notes: In humans, referential gestures intentionally draw the attention of a partner to an object of mutual interest, and are considered a key element in language development. Outside humans, referential gestures have only been attributed to great apes and, most recently, ravens. This was interpreted as further evidence for the comparable cognitive abilities of primates and corvids. Here we describe a signal that coral reef fishes, the grouper *Plectropomus pessuliferus marisrubri* and coral trout *Plectropomus leopardus*, use to indicate hidden prey to cooperative hunting partners, including giant moray eels *Gymnothorax javanicus*, Napoleon wrasses *Chelinus undulatus* and octopuses *Octopus cyanea*. We provide evidence that the signal possesses the five attributes proposed to infer a referential gesture: it is directed towards an object, mechanically ineffective, directed towards a potential recipient, receives a voluntary response and demonstrates hallmarks of intentionality. Thus, referential gesture use is not restricted to large-brained vertebrates

- 5 Gingins, S., Werminghausen, J., Johnstone, R. A., Grutter, A. S., & Bshary, R. (2013). Power and temptation cause shifts between exploitation and cooperation in a cleaner wrasse mutualism. *Proc. Biol. Sci.*, 280, 20130553.

Notes: In many instances of cooperation, only one individual has both the potential and the incentive to 'cheat' and exploit its partner. Under these asymmetric conditions, a simple model predicts that variation in the temptation to cheat and in the potential victim's capacity for partner control leads to shifts between exploitation and cooperation. Here, we show that the threat of early termination of an interaction was sufficient to induce cleaner wrasse *Labroides dimidiatus* to feed selectively against their preference (which corresponds to cooperatively eating client fish ectoparasites), provided that their preference for alternative food was weak. Under opposite conditions, cleaners fed selectively according to their own preference (which corresponds to cheating by eating client mucus). By contrast, a non-cleaning fish species, *Halichoeres melanurus*, failed to adjust its foraging behaviour under these same conditions. Thus, cleaners appear to have evolved the power to strategically adjust their levels of cooperation according to the circumstances

- 6 Salwiczek, L. H., Pretot, L., Demarta, L., Proctor, D., Essler, J., Pinto, A. I. et al. (2012). Adult cleaner wrasse outperform capuchin monkeys, chimpanzees and orang-utans in a complex foraging task derived from cleaner--client reef fish cooperation. *PLoS ONE.*, 7, e49068.

Notes: The insight that animals' cognitive abilities are linked to their evolutionary history, and hence their ecology, provides the framework for the comparative approach. Despite primates renowned dietary complexity and

social cognition, including cooperative abilities, we here demonstrate that cleaner wrasse outperform three primate species, capuchin monkeys, chimpanzees and orang-utans, in a foraging task involving a choice between two actions, both of which yield identical immediate rewards, but only one of which yields an additional delayed reward. The foraging task decisions involve partner choice in cleaners: they must service visiting client reef fish before resident clients to access both; otherwise the former switch to a different cleaner. Wild caught adult, but not juvenile, cleaners learned to solve the task quickly and relearned the task when it was reversed. The majority of primates failed to perform above chance after 100 trials, which is in sharp contrast to previous studies showing that primates easily learn to choose an action that yields immediate double rewards compared to an alternative action. In conclusion, the adult cleaners' ability to choose a superior action with initially neutral consequences is likely due to repeated exposure in nature, which leads to specific learned optimal foraging decision rules

7 Bshary, A. & Bshary, R. (2010). Self-serving punishment of a common enemy creates a public good in reef fishes. *Current Biology*, 20, 2032-2035.

Notes: A key challenge for evolutionary biologists is to determine conditions under which individuals benefit from a contribution to public goods [1, 2]. For humans, it has been observed that punishment of free riders may promote contributions [3, 4], but the conditions that lead to stable cooperation based on punishment remain hotly debated [5-8]. Here we present empirical evidence that public goods may emerge as a by-product of self-serving punishment in interactions between coral reef fishes and parasitic saber-tooth blennies that stealthily attack their fish victims from behind to take a bite [9]. We first show that chasing the blenny functions as punishment [10], because it decreases the probability of future attacks. We then provide evidence that in female scalefin anthias, a shoaling species, punishment creates a public good because it increases the probability that the parasite switches to another species for the next attack. A final experiment suggests that punishment is nevertheless self-serving because blennies appear to be able to discriminate between look-alike punishers and nonpunishers. Thus, individuals that do contribute to the public good may risk being identified by the parasite as easy targets for future attacks

8 Bshary, R., Grutter, A. S., Willener, A. S., & Leimar, O. (2008). Pairs of cooperating cleaner fish provide better service quality than singletons. *Nature*, 455, 964-966.

Notes: Service providers may vary service quality depending on whether they work alone or provide the service simultaneously with a partner. The latter case resembles a prisoner's dilemma, in which one provider may try to reap the benefits of the interaction without providing the service. Here we present a game-theory model based on the marginal value theorem, which predicts that as long as the client determines the duration, and the providers cooperate towards mutual gain, service quality will increase in the pair situation. This

prediction is consistent with field observations and with an experiment on cleaning mutualism, in which stable male-female pairs of the cleaner wrasse *Labroides dimidiatus* repeatedly inspect client fish jointly. Cleaners cooperate by eating ectoparasites off clients but actually prefer to cheat and eat client mucus. Because clients often leave in response to such cheating, the benefits of cheating can be gained by only one cleaner during a pair inspection. In both data sets, the increased service quality during pair inspection was mainly due to the smaller females behaving significantly more cooperatively than their larger male partners. In contrast, during solitary inspections, cleaning behaviour was very similar between the sexes. Our study highlights the importance of incorporating interactions between service providers to make more quantitative predictions about cooperation between species