

pathogens, so far they have been insufficiently exploited as targets of antibacterial therapy. Nevertheless, inhibitors of secretion and molecules blocking the expression of T3SS genes have been identified *in vitro*. Furthermore, vaccines comprising injectosome-derived antigens are under evaluation. Unlike antibiotics, T3SS-targeting anti-virulence drugs do not put pressure for survival on microorganisms (as bacteria are viable without T3SS) and are potentially more specific, which reduces the risk of widespread resistance. However, since our knowledge of the T3SS in symbiotic, commensal and environmental prokaryotes is poor, the possible impact of T3SS-targeting drugs on microbial communities is difficult to evaluate.

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Fish choose appropriately when and with whom to collaborate

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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.

Humans frequently decide on whether and with whom to collaborate [1]. Of the collaborative abilities experimentally demonstrated in chimpanzees, amongst the most sophisticated are the abilities to choose appropriately when and with whom to collaborate. In a collaborative rope-pulling paradigm chimpanzees recruit a partner more often when collaboration is necessary to retrieve a baited food platform than when it can be retrieved alone. They also choose the more effective of two collaborative partners after a few trials [2]. The abilities of chimpanzees are consistent with a close link between a species' ecology and its cognitive abilities [4]. Chimpanzees hunt in groups more often in dense forest where solo hunting may be less effective, and make alliances for territorial defense potentially based

on previous experience with various partners [2]. Other large-brained species have since been tested for their ability to determine when cooperation is possible (albeit without the necessity to recruit a partner), with elephants succeeding [5] and rooks failing [6]. Here, we test for the abilities to determine when and with whom to collaborate in a species for which these abilities should be ecologically relevant.

We studied the coral trout (hereafter 'trout'): a fish of the genus *Plectropomus*, which use gestural communication to initiate collaborative hunts with moray eels on coral reefs [3, 7]. This relationship relies on naturally complementary hunting tactics, that, when combined, reduce the prey's escape options and benefit both partners. Plectropomids are fast to chase prey fish above the reef, while morays have a sinuous body to access prey hidden in crevices. Therefore, collaboration with a moray should only be useful to the plectropomid if the prey is inaccessible in a crevice. Regarding partner-choice, field observations suggest that individual morays differ consistently in their willingness to collaborate, and trout should benefit from preferentially recruiting these individuals.

To determine if trout can determine when to collaborate, we presented them with a situation (experiment 1) where prey was either in a crevice (collaborative condition) or in the open (solo condition; Figure 1A). The correct choices (respectively) were to recruit a nearby model moray that would flush the prey out into the open or attack alone, after which the trout was fed a reward to simulate a successful hunt (Supplemental information; Movie S1). For both experiments, the number of trials and subjects was designed to match that for chimpanzees [2]. In experiment 1, eight trout participated in up to four trials per condition per day for six days (one testing period per day), with solo and collaborative trials alternated within testing periods. Chimpanzees undertook the same maximum number of trials (48 total) but these were divided between two sessions of unspecified duration [2], making days 1–3 and 4–6 for trout equivalent to sessions 1 and 2 for chimpanzees.

Trout were similarly proficient to chimpanzees at determining when to collaborate. Trout recruited the moray significantly more often in the

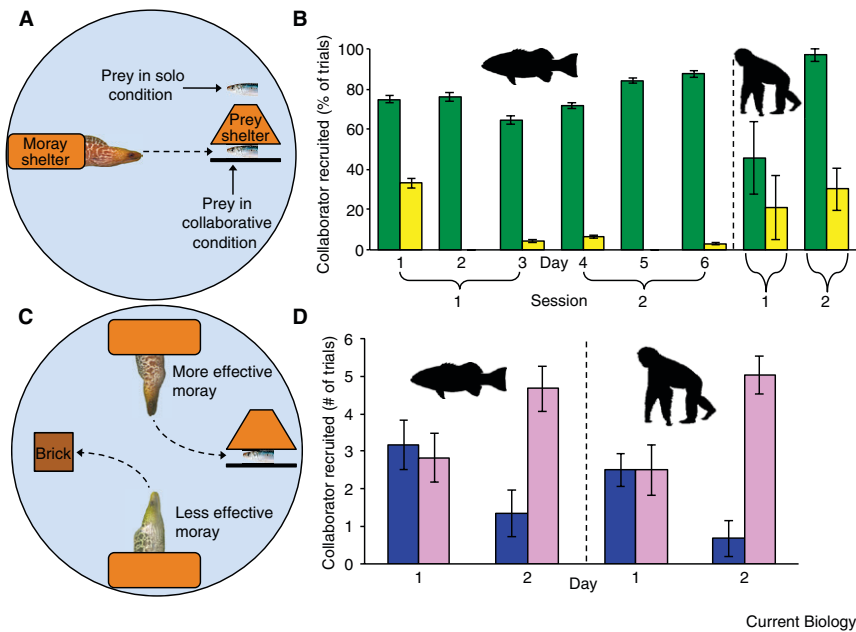


Figure 1. Trout can choose appropriately when and with whom to collaborate. Results from chimpanzees are also presented (for which the data are obtained from [2]) to allow for a qualitative comparison between the species (given important methodological differences between the studies). (A) Bird's eye view (morays and shelters shown side-on for clarity) of the aquaria setup and (B) results of experiment 1 (dark green bars represent collaborative trials and light yellow bars represent solo trials; a dotted line separates the trout and chimpanzee results, as for experiment 2). (C) Setup and (D) results of experiment 2 (dark blue bars represent the less effective collaborator and light pink bars represent the more effective collaborator). All values are means \pm S.E. (See also Supplemental information; Movie S1 and S2.)

collaborative than solo condition on all six testing days (binomial GLMs for each day, blocked by individual: $\chi^2_{1,7} \geq 11.12$; $p < 0.001$; Figure 1B). Chimpanzees also recruited more often in the collaborative than solo condition in both test sessions but only to a modest level in the first session, improving their performance in the collaborative (but not solo) trials in the second session. Learning effects were also apparent for trout. Over the six days of testing they increased their propensity to recruit in the collaborative condition (GLM: $\chi^2_1 = 4.45$; $p = 0.035$) and reduced their propensity to recruit in the solo condition (GLM: $\chi^2_1 = 20.93$; $p < 0.001$). They also reduced their time to decision in the collaborative (time log transformed: $F_{1,7} = 36.0$; $p < 0.001$) and solo trials ($F_{1,7} = 53.5$; $p < 0.001$) over the six days of testing.

To test whether trout could quickly learn to choose the more effective moray collaborator, we presented them with two model morays and a prey positioned in a crevice (experiment 2). If recruited, the more effective collaborator swam to the prey and flushed it out, allowing the trout to be

rewarded, whereas the less effective collaborator swam away from the prey, making a successful hunt impossible (Figure 1C; Supplemental movie S2). For trout and chimpanzees [2], six subjects participated in six trials per day for two days.

The trout's performance was nearly identical to that of chimpanzees (Figure 1D). On day one trout chose the more and less effective collaborator at a ratio that did not significantly differ from 1:1 (a binomial GLM with an intercept deviating from 1:1 did not explain the data significantly better than a model with a 1:1 intercept; $\chi^2_1 = 0.1$; $p = 0.739$). They increased their preference for the more effective collaborator from day one to day two (GLM: $\chi^2_1 = 9.5$; $p = 0.002$) and on day two chose the more effective collaborator significantly more often than the less effective collaborator (a GLM with an intercept deviating from 1:1 explained the data significantly better; $\chi^2_1 = 11.8$; $p < 0.001$).

Our results show that, like chimpanzees, trout determine appropriately when a situation requires a collaborator and

quickly learn to choose the more effective collaborator. Our study thus strengthens the case that a relatively small brain (compared to warm-blooded species) does not preclude at least some fish species from possessing cognitive abilities that compare to or surpass those of apes, provided that the situation is ecologically relevant to them [7,8]. However, the processes that underlie superficially similar cognitive abilities may vary widely among taxa [4]. We currently do not know what processes underlie trout or chimpanzee partner-choice abilities. As we set our experiments in an ecological context, the 'when to collaborate' paradigm should have been relatively familiar to our wild-caught trout, and hence learned or unlearned stimulus-response reactions could explain their success from day one. However, the fact that the trout decreased their propensity to (incorrectly) recruit the moray in the solo treatment over time strongly suggests that their performance was not simply driven by a predisposition to attack the prey in the open, and that the accessibility of the prey was being assessed. Furthermore, given recent demonstrations of intentional communication by plectropomids [7], we would not exclude an explanation of the trout's abilities that invokes an understanding of the collaborator's role. The chimpanzees' ability to recruit a collaborator more often when required has often been interpreted as representing an understanding of the task. This is certainly a possibility, but further investigation of the underlying processes is required to disentangle this possibility from alternatives such as the chaining of behaviors [9] learned during training sessions in components of the task [2]. Fast associative learning could account for the performances of chimpanzees and trout in choosing the best collaborator and choosing when to collaborate. Regarding the former, a unique cue that could have facilitated learning was associated with the more effective collaborator for each species: individual collaborator locations remained constant for each trout, while the more effective chimpanzee collaborator more often sat in front of and shook its cage door. Elucidating the processes underlying collaborative partner-choice in humans, chimpanzees, and

trout would aid in determining whether the shared abilities of the former two species are due to common ancestry or convergence. Convergence has been suggested as the reason for other superficially similar ape and human abilities [10] and is most likely the reason why trout have superficially similar partner-choice abilities to humans and chimpanzees.

Supplemental Information

Supplemental Information including experimental procedures can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.07.033>.

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Pollinator-induced twisting of flowers sidesteps floral architecture constraints

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Specific pollen placement by zygomorphic flowers on pollinators is one of the key innovations of angiosperm evolution [1]. In most phylogenetic lineages that have evolved zygomorphic flowers, reproductive organs are positioned either in the lower or upper part of the flower. Although these specific positions largely enhance pollen economy, they also represent architectural constraints such that flowers are able to place pollen only on the dorsal or ventral part of pollinators’ bodies [2]. Such constraints can lead to interspecific pollen placement in situations where phylogenetically related species with the same floral architecture share pollinators [3].

Here, we present a simple but ingenious adaptation of *Impatiens frithii*, a bird-pollinated plant that shares its main pollinator with four other *Impatiens* species on Mt. Cameroon. In contrast to other species of the genus, the nectar spur of *I. frithii* is not curved downwards, but slightly upwards. This apparently small modification significantly affects how pollen is placed on birds’ bodies. When a bird forages on nectar, the flower twists as the spur conforms to the shape of the bird’s bill. As a consequence, pollen is placed in an unusual location on the bird’s body – the ventral surface of its bill or head. Our observations demonstrate that a minute change in floral morphology can effectively overcome constraints resulting from the basal floral architecture early in the group’s evolution. We assume that such adaptations can not only help the plants avoid interspecific competition, but as the adaptations create strong reproductive barriers, they may also contribute to plant speciation.

The origin of pre-pollination reproductive barriers has been one

of the central topics of evolutionary biology since Darwin’s time, and remains rather mysterious in situations where phylogenetically related species grow in sympatry and share the same pollinators. In these situations, one way to separate gene flow is to place pollen on different parts of pollinators’ bodies [4]. Extremely precise placement that leads to reproductive isolation can be found particularly in orchids [5], which achieve this precision by producing pollinia. Plants with free granular pollen, however, cannot in this way achieve mechanical isolation, as has been well documented, for example, in members of the genera *Pedicularis* and *Stylidium* [6,7]. In these cases, the only possible way of creating a sufficiently strong reproductive barrier is to place and pick up pollen sufficiently far apart [6,7]. The evolutionary process that can lead to this situation is nevertheless almost always related to gradual changes in traits (e.g. gradual changes in the reward–stigma distance and/or the reward–anther distance), which result in overlapping pollen placement on pollinators’ bodies by different plant species [8]. Such processes, therefore, cannot lead to effective reproductive isolation [6]. In some cases, architectural constraints can be overcome if a pollinator alters its foraging position, as has been demonstrated in insects collecting pollen on *Pedicularis* [6] or in perching sunbirds foraging for nectar on *Aloe* [9].

The endemic species *Impatiens frithii* has only relatively recently been described from the Bakossi Mountains and Mt. Etinde in western Cameroon [10]. Its floral properties correspond to the bird-pollination syndrome. The epiphytic *I. frithii* grows on smaller trees or lower tree branches, and its long-peduncled red flowers protrude out of the foliage. We observed *I. frithii* flowering on the slopes of Mt. Cameroon at elevations of 879–1340 m above sea level during the wet season of 2013 (July 24–September 2). To identify its main pollinators we observed seven individuals of *I. frithii* using remote video systems (163.3 hours of observations). We recorded eighteen arrivals of *Cyanomitra oritis*, and this sunbird