

game. The secret is [to sharpen your] game [theory], set [your controllers optimally] and match [your sensory processing to the task].

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# The shadow of the future affects cooperation in a cleaner fish

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Humans show great flexibility in adjusting their levels of cooperation to account for current and future circumstances. For example, levels of cooperation are higher if there is more competition at the level of the whole population than with interacting partners [1] and when individuals are likely to gain social prestige [2]. Humans also show the capacity to increase current levels of cooperation to account for future payoffs if it is likely that repeated interactions will occur with the same partner (known as 'the Shadow of the Future') [3]. Here, we provide the first evidence for this capacity in a non-human animal, the cleaner fish *Labroides bicolor*. *L. bicolor* individuals show uneven frequency of use of different areas within a large home range, which should in turn affect the delay between repeated interactions with individual reef fish 'clients'. In areas where the frequency of clients encountering cleaners is higher, cleaners are more likely to experience future costs of cheating, so future payoffs are of more concern for current decisions. In line with this, we found a negative correlation between cheating and the frequency of clients encountering cleaners in *L. bicolor* home ranges.

In contrast to the well-studied cleaner fish *Labroides dimidiatus*, which has small cleaning stations, the closely related *L. bicolor* roves over much larger areas [4]. Roving is predicted to destabilize cooperative behaviour [5] because it would reduce the frequency of repeated interactions between cleaners and clients. This would undermine the effectiveness of punishment and partner switching [6], which are used by clients of *L. dimidiatus* to ensure that cleaners do not cheat by feeding on their preferred mucus, but instead cooperate by feeding on client ectoparasites [7]. Accordingly, it has

been found that *L. bicolor* individuals cheat clients more frequently than sympatric *L. dimidiatus* individuals [4].

Here, we make use of the fact that *L. bicolor* individuals show uneven frequency of use of different areas within their large home ranges. Therefore, they are likely to encounter clients within their preferred areas more frequently. Where frequent repeated interactions occur, cheating is likely to cause future costs due to clients switching to other cleaners or cleaners investing in reconciliation following client punishment [6], in addition to the immediate costs for cleaners. Therefore, an individual *L. bicolor* could increase its overall benefits if it were able to adjust cooperative levels depending on location. If cleaners were able to make such adjustments, we predicted that we would observe a negative correlation between cheating and the frequency of clients encountering cleaners.

In a field study on Moorea Island in French Polynesia, we measured home range usage in *L. bicolor* and compared client jolt rates as a correlate of cheating behaviour [6] across the home range (see Supplemental Information). Ten adult *L. bicolor* were observed for eight 30 minute sessions, and the following observations were recorded on an underwater slate: species of client; size of client; duration of interaction in seconds; number of jolts by client and whether or not the client terminated the interaction in response to cheating by chasing or swimming off. The observer remained directly above, or immediately adjacent to, the focal cleaner and recorded the position of cleaning interactions using a global positioning system unit on the surface.

To show patterns of usage of the home range, we used home range analysis to create isopleths from the cleaning interaction position data for each individual *L. bicolor* (see Supplemental Information). The 5% isopleth is the smallest area to contain 5% of the cleaning interactions, indicating the most heavily used area of the home range. If cleaners used their home ranges homogeneously, isopleths would be relatively similar in size. In contrast, we found that *L. bicolor* mainly used small central areas of the home range and only occasionally interacted with clients in the periphery (Figure 1A). Across all

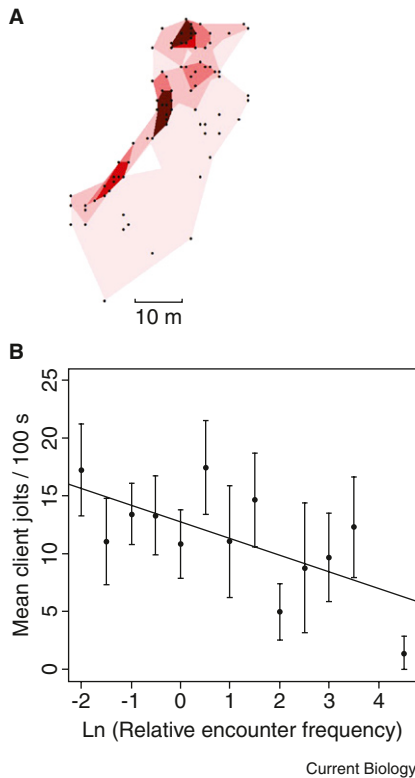


Figure 1. Intensity of home range area use and client jolt rate.

(A) Map of home range isopleths for an individual *L. bicolor*, showing isopleth areas grouped into 20% intervals, with more heavily used areas shown in darker colours. The darkest colour shows the 20% isopleth, which is the smallest area to contain 20% of the cleaning interaction coordinates. (B) Mean client jolts per 100 s  $\pm$  SEM against the relative encounter frequency (ln transformed) for focal cleaners (see also Table S1).

the cleaners, the 50% isopleth covered on average 11% ( $\pm 2\%$ ) of the total home range area (100% isopleth). We used the area of isopleths to estimate the 'relative encounter frequency' for each isopleth of each cleaner, which represents the relative rate at which a client is likely to encounter a cleaner. This enabled us to compare the rates for clients encountering cleaners in different areas of the home range of individual cleaners with varying home range sizes (see Supplemental Information for details). We assigned each cleaning interaction to the corresponding relative encounter frequency for the focal cleaners and found that client jolt rate significantly decreased in areas of home ranges where encounter frequency was high (GLMM,  $p = 0.010$ ,  $\chi^2 = 6.58$ ,  $df = 1$ ; Figure 1B, see also Table S1). In order to test the possibility that

the difference in jolt rate is caused by clients responding directly to how frequently they encounter cleaners rather than cheating rates, we used the fact that home ranges of cleaners overlap. Including a client's frequency of encounters with other cleaners did not improve our model (GLMM,  $p = 0.370$ ,  $\chi^2 = 0.80$ ,  $df = 1$ ; see also Table S1). The model also controlled for the possibility that the correlation could be due to differences in client composition or client size (see Supplemental Information). Furthermore, it does not appear that clients are less likely to terminate interactions in response to cheating in rarely used locations, and cleaners respond to this by cheating more often: there was no significant correlation between relative encounter frequency and the proportion of interactions which clients terminated in response to cheating (GLMM,  $p = 0.686$ ,  $\chi^2 = 0.16$ ,  $df = 1$ ; see also Table S2).

Taken together, our results suggest that *L. bicolor* individuals adjust current levels of cooperation depending on the potential delay of future interactions, not just because of immediate payoff considerations. In contrast, clients do not appear to adjust chasing and swimming off to the likely future benefits. This absence of specific behavioural adjustment could be because clients may not distinguish between individual cleaners, where *L. bicolor* home ranges overlap. Alternatively, it is possible that client responses are adapted to interactions with the more abundant cleaner fish *L. dimidiatus*, and therefore mismatched in interactions with *L. bicolor*.

Other studies have shown that animals are able to adjust levels of cooperation to current situations; for example, lycaenid butterfly larvae produce more attractants if the current number of protecting ants is low and therefore the larvae's security is impaired [8]. In addition, animals and bacteria may adjust levels of cooperation to life history stages and/or population parameters [9,10]. However, our results provide the first evidence supporting the notion that animals may have the ability to flexibly adjust levels of cooperation with individual partners to account for future payoffs, which depend on how likely it is that repeated interactions will occur with each partner. Irrespective of the cues

actually used for such adjustment, *L. bicolor* appears to respond to 'the Shadow of the Future' in the same way as humans, by increasing cooperation in situations which have a greater probability of future repeated interactions.

#### Supplemental Information

Supplemental Information is available at [http://www.cell.com/current-biology/supplemental/S0960-9822\(10\)00460-4](http://www.cell.com/current-biology/supplemental/S0960-9822(10)00460-4).

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