Published in Science 327, no 5962, 171, 2010
which should be used for any reference to this work

Punishers Benefit From Third-Party Punishment in Fish

Nichola J. Raihani,[1]* Alexandra S. Grutter,[2] Redouan Bshary[3]

Human studies show that uninvolved bystanders often pay to punish defectors (*1*, *2*). Such behavior has typically been interpreted in terms of group-level benefits (*3*) despite theoretical predictions that third-party punishment can yield individual benefits to the punisher (*4*). Here, we show that male cleaner fish, *Labroides dimidiatus*, punish their female partners if females cheat while inspecting model clients. Punishment promotes female cooperation, yielding direct foraging benefits to the male. This finding demonstrates empirically that third-party punishment can evolve via self-serving tendencies.

When servicing clients, cleaners either cooperate by removing ectoparasites or cheat by taking a bite of mucus. Cleaners prefer to eat mucus (*5*) but risk clients terminating the interaction if they do (*6*). The conflict of interest between cleaner and client is less pronounced during inspections by cleaner pairs than during singleton inspections (*7*). Increased service quality during pair inspections was interpreted as resulting from female cooperation, both under natural conditions and in the laboratory where Plexiglas (acrylic plastic) plates serve as model clients. Larger males regularly chased smaller female partners if females caused clients to leave, particularly in the laboratory (*7*). This male behavior is peculiar because clients, not males, are the victims of biting females. Despite this fact, it is possible that male chasing could cause females to behave more cooperatively in future interactions. If males benefit personally through increased foraging success, then the males' behavior represents third-party punishment that evolves via self-regarding, rather than altruistic, tendencies.

Cleaners were trained to feed off model clients (Plexiglas plates) containing two food types: preferred prawn and less-preferred fish flake (*8*). Eating prawn corresponded to cheating the client by eating mucus, whereas eating flake corresponded to cooperating by removing ectoparasites. Eating prawn resulted in the immediate removal of the plate. We replicated earlier results (*7*) that males more often chased females when the latter's behavior caused plate removal (Wilcoxon signed-rank test, $n = 8$, V (rank sum of positive values of $x = y$) = 21, $P = 0.036$). After being chased, females were less likely to eat prawn again in the second plate presentation 60 s later (Wilcoxon signed-rank test, $n = 8$, $V = 34$, $P = 0.030$; Fig. 1A) and fed against their preference, eating a higher ratio of flake to prawns (Wilcoxon signed-rank test, $n = 8$, $V = 36$, $P = 0.008$; Fig. 1B). This allowed males to increase their food intake in the second presentation (Wilcoxon signed-rank test, $n = 8$, $V = 28$, $P = 0.02$; Fig. 1C). Conversely, when chasing was prevented with a temporary partition, females that cheated in the first presentation were equally likely to cheat in the second one (Wilcoxon signed-rank test, $n = 8$, $V = 11$, $P = 0.67$; Fig. 1A) and did not eat a higher ratio of flake to prawn items (Wilcoxon signed-rank test, $n = 8$, $V = 8$, $P = 0.35$; Fig. 1B), and male foraging efficiency did not improve (Wilcoxon signed-rank test, $n = 8$, $V = 17.5$, $P = 1.0$; Fig. 1C). In nature, male cleaners may benefit if they punish cheating females, even though clients are the primary victims. The establishment of self-serving third-party punishment in response to personal losses may be a key step toward third-party punishment without current involvement as in humans (*2*).

References and Notes

1. E. Fehr, U. Fischbacher, *Evol. Hum. Behav.* **25**, 63 (2004).
2. E. Fehr, S. Gächter, *Nature* **415**, 137 (2002).
3. R. Boyd, H. Gintis, S. Bowles, P. J. Richerson, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 3531 (2003).
4. K. Jaffe, *Acta Biotheor.* **52**, 155 (2004).
5. A. S. Grutter, R. Bshary, *Proc. Biol. Sci.* **270** (suppl. 2), S242 (2003).
6. R. Bshary, A. S. Grutter, *Anim. Behav.* **63**, 547 (2002).
7. R. Bshary, A. S. Grutter, A. S. T. Willener, O. Leimar, *Nature* **455**, 964 (2008).
8. Materials and methods are available as supporting material on *Science* Online.

9. We thank M. Cant, A. Ridley, and A. Thornton for commenting on earlier versions of this manuscript and L. Brun, A. Bshary, A. Pinto, D. Rappaz, and M. Soares for assistance in the field. N.J.R. is funded by the Zoological Society of London, R.B. by the Swiss Science Foundation, and A.S.G. by the University of Queensland.

[1]Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK. [2]Institut de Biologie, Universitè de Neuchâtel, CH-2009 Neuchâtel, Switzerland. [3]School of Biological Sciences, The University of Queensland, Brisbane Qld 4072, Australia.

*To whom correspondence should be addressed. E-mail: nichola.raihani@ioz.ac.uk

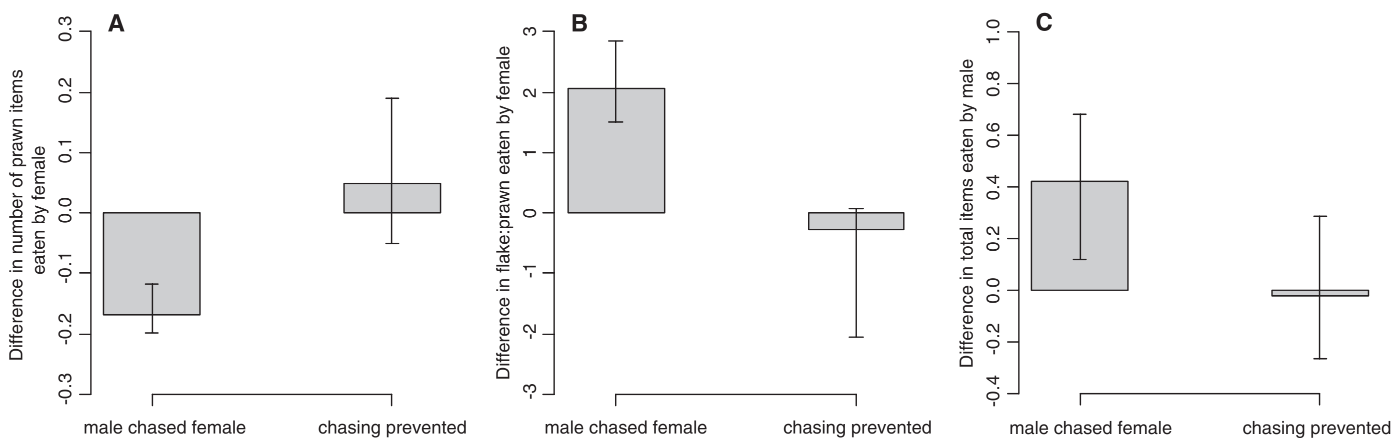

Fig. 1. Median difference according to treatment in (**A**) the number of prawn items eaten by females, (**B**) the ratio of flake to prawn items eaten by females, and (**C**) the total number of food items eaten by the male. For each pair, we first calculated (A) mean number of prawn items female ate, (B) mean ratio of flake to prawn items female ate, and (C) mean number of food items male ate in first and second presentations, respectively. Differences for each pair were calculated by subtracting mean (presentation one) from mean (presentation two). The median of these differences and the interquartile range were then calculated and are presented in the figure (gray boxes and bars, respectively).