Title
In Sync or Vocal? How Bottlenose Dolphins Coordinate in a Cooperative Task

Journal
Proceedings of the Annual Meeting of the Cognitive Science Society, 43(43)

ISSN
1069-7977

Authors
Jaakkola, Kelly
Guarino, Emily
Donegan, Katy
et al.

Publication Date
2021

Peer reviewed

In Sync or Vocal? How Bottlenose Dolphins Coordinate in a Cooperative Task

Kelly Jaakkola (kelly@dolphins.org), Emily Guarino (emily@dolphins.org), Katy Donegan(katy@dolphins.org), Christina McMullen (christina.mcmullen@dolphins.org)
Dolphin Research Center, 58901 Overseas Highway
Grassy Key, FL 33050, USA

Stephanie L. King (stephanie.king@bristol.ac.uk)
School of Biological Sciences, University of Bristol
Bristol, BS8 1TQ, UK

Abstract

Cooperation experiments have long been used to explore the cognition underlying animals' coordination towards a shared goal. While the ability to understand the need for a partner has been demonstrated in a number of species, far fewer studies have explored the behavioral strategies animals use to coordinate their behavior in such tasks. Here, we investigate the strategies two dolphin dyads used to coordinate their behavior during a cooperative button-pressing task that required precise behavioral synchronization. Both dyads were more likely to succeed if they used whistles prior to pressing their buttons, but the results showed that they adopted different strategies. Specifically, one dyad favored physical synchrony, waiting nearby for their partner and swimming together to approach the buttons. The other dyad was much more vocal, and more likely to swim independently before coordinating at the buttons. Only for this second dyad did increased whistling lead to more success. Our results suggest that bottlenose dolphins have the behavioral flexibility to employ either vocal signals or physical synchrony to coordinate their cooperative efforts.

Keywords: cooperation; communication; synchrony; dolphins; comparative cognition

Introduction

Cooperative behavior is ubiquitous across the animal kingdom. In species after species, one can find examples of animals working together to hunt, fight, raise young, build shelter, and so forth (e.g., Bugnyar & Massen, 2017; Mitani, 2009; Smith et al., 2012). However, while cooperative behavior is ubiquitous, the cognitive and behavioral mechanisms underlying such cooperation are quite varied (Duguid & Melis, 2020; Noë, 2006). These may range from situations in which two or more animals pursue the same goal simultaneously but individually, to situations in which two or more animals intentionally work together to achieve a shared goal and adjust their behavior accordingly.

To date, the most common method for exploring the cognitive mechanisms underlying animal cooperation has been the rope-pulling task (also known as the loose-string task) (Hirata & Fuwa, 2007; Melis, Hare, & Tomasello, 2006). In this task, a rope or string is threaded around an out-of-reach board that is baited with food. If two animals each pull one end of the rope, the board moves toward them and they can retrieve the food. If just one side of the rope is pulled, however, then the rope unthreads and the food stays out of reach. In the critical condition, one animal is allowed access to the apparatus first, to test if it will wait or even open a door for a partner before pulling, thus demonstrating that it understands the cooperative nature of the task.

Such studies, including adaptations using coordinated handle-pulling or button-pressing, have suggested that some animals such as chimpanzees, elephants, wolves, dolphins, and keas, understand the need for a partner (e.g., Heaney, Gray, & Taylor, 2017; Jaakkola et al., 2018; Marshall-Pescini et al, 2017; Melis et al., 2006; Plotnik et al., 2011), whereas others, including otters, rooks, ravens, dogs, and the African Grey parrot, do not (Massen, Ritter, & Bugnyar, 2015; Marshall-Pescini et al., 2017; Péron et al., 2011; Schmelz et al., 2017; Seed, Clayton, & Emery, 2008). The behavioral strategies animals use to coordinate their behavior in such tasks, however, has so far remained largely unexplored.

One of the animals that has demonstrated this kind of understanding of cooperation is the bottlenose dolphin (Jaakkola et al., 2018), who also show striking cases of cooperative behavior in the wild, including feeding strategies that require coordinated action (e.g., Duffy-Echevarria, Connor, & St. Aubin, 2008; Gazda et al., 2005) and nested alliances where male dolphins engage in joint action to herd single females and steal or defend them from rival alliances (Connor& Krützen, 2015). There are at least two possible strategies dolphins could use to coordinate their cooperative behavior. One possibility is visually-mediated behavioral coordination, a precise form of which has been demonstrated repeatedly in bottlenose dolphins, as shown by synchronous breathing between mothers and calves (Mann & Smuts, 1999) and in synchronous displays by allied males (Connor, Smolker, & Bejder, 2006). A second possibility is vocal communication, which has been posited to play a key role in the evolution of cooperative abilities in humans (e.g., Smith, 2010). Indeed, human children, unlike chimpanzees, have been shown to use vocal communication to coordinate their behavior during difficult cooperative tasks (e.g., Duguid et al., 2014). While vocal communication appears to play a prominent role when allied male dolphins work together to herd single estrus females (King et al., 2019), our knowledge of the role vocal communication plays in facilitating cooperation in dolphins and other non-human animals remains limited.

In the current study, we investigate the strategies two dolphin dyads used to coordinate their behavior during a cooperative task. Rather than the rope-pulling paradigm, we used a cooperative button-pressing task in which the dolphins were required to swim across a lagoon and each press their own underwater button simultaneously (within a 1 s time window), whether sent at the same time or with a delay between partners. The tight behavioral coordination required for this task eliminates the possibility that success could be achieved by responding to an environmental cue such as partner presence or tension in the rope (Jaakkola et al., 2018; Duguid & Melis, 2020). We recorded the vocal and motor behaviors of the dyads to determine whether the dolphins used vocal signals and/or physical synchrony when working together. If the dolphins use vocal signals to coordinate their cooperative behavior, then we would expect that they would cooperate more successfully when they whistle, and that the timing of those whistles would be related to the timing of their button presses. If they use physical synchrony, then we would expect the first dolphin sent to wait for their partner before swimming side-by-side to the buttons.

Methods

Four common bottlenose dolphins at Dolphin Research Center (DRC) in Grassy Key, Florida participated in this study: Aleta and Calusa (females, age 33 and 17 years) formed dyad 1; Delta and Reese (males, age 9 and 7 years) formed dyad 2. All four dolphins were born at DRC and lived in natural seawater lagoons. The members of each dyad had lived together at various points throughout their lives and lived together during the study.

The apparatus consisted of two underwater push buttons positioned off the front of a dock, 53 cm below the water's surface and 2.6 m apart (see Figure 1), connected via a custom-made computer that was also attached to an underwater speaker. Each trial began with both dolphins and their respective trainers located at the opposite side of the lagoon from the apparatus (approx. 11 m away). During a trial, each trainer gave their respective dolphins a hand signal to "press the button", separated by a delay of 0 – 20 seconds between signals. To succeed, both members of the dyad needed to swim across the lagoon and each press their own button simultaneously (within a 1 s time window), regardless of the difference in their start times. If the buttons were pressed within this 1 s time interval, the computer automatically played a 'success' sound (i.e., a trainer's whistle) and the dolphins returned to the trainers for positive reinforcement of fish and social interaction. If there was more than a 1 s delay between the dolphins' button presses, the computer played a 'failure' sound, and no reinforcement was given. For each trial only the first press of each button was relevant, and it was impossible for dolphins to succeed by repeatedly pushing their buttons.

Figure 1: Aerial view of the cooperative task apparatus.

Because this task included no perceptible causality by which the dolphins could deduce the need to work together, we employed a series of trial phases through which each dolphin dyad learned the task and then demonstrated that they understood its cooperative nature (Table 1).

Throughout the study, the computer automatically recorded time between button presses (accurate to 0.01 s), which button was pressed first, and whether the trial outcome was a success or failure. Dolphins' vocalizations were recorded via a rectangular 4-element hydrophone array in the lagoon. The dolphins' behavior was recorded with a video camera positioned across the lagoon and a GoPro positioned above the apparatus; the video data was later coded using the event logging software BORIS (Friard & Gamba, 2016). Specifically, *waiting* was coded when a dolphin stopped moving forward for at least 2 s, and *swim together* was coded when both dolphins swam together in the same orientation within one body length of each other.

Table 1: Summary of trial phases.

Phase	Trial type	Criterion to pass
0	Simultaneous release	8/10 (80%) over two sessions
1	Incremental delays (1-5s)	3 in a row at each delay
2	Randomized delays (0-5s)	16/20 (80%) in a single session
3	Incremental delays (8-20s)	3 in a row at each delay
4	Randomized delays (1-20s)	Test (20 trials per dolphin)
5	Buttons moved; simultaneous release from different places	3 in a row at each location configuration

Our previous paper reported on the dolphins' learning of this task, showing that they were able to work together even when they had to wait for their partner, thus demonstrating that they understood the cooperative nature of the task (Jaakkola et al., 2018). To examine their behavioral strategies for coordinating that cooperation in the current study, we examined only those trials in which both animals in the dyad pressed their buttons, as a conservative way of ensuring that both were participating in the task.

Results

Vocal Behavior

There was a significant difference between dolphin dyads in the number of whistles produced [Welch's t-test: t(345) = 16.41, $p < 0.0001$], with dyad 1 averaging 0.4 whistles per trial, and dyad 2 averaging 2.3 whistles per trial. We examined the effect of these whistles in two ways: first assessing whether the presence of whistles influenced trial success; and then, for those trials with whistles, whether the number of whistles affected trial success.

For both dyads, the presence of whistles led to a higher rate of success [dyad 1: $\chi2$ (1, 396) = 13.14, $p < .001$; dyad 2: $\chi2$ (1, 294) = 18.32, $p < .0001$)] (See Figure 2). That is, both dyads were more successful on trials in which they whistled than on trials in which they did not.

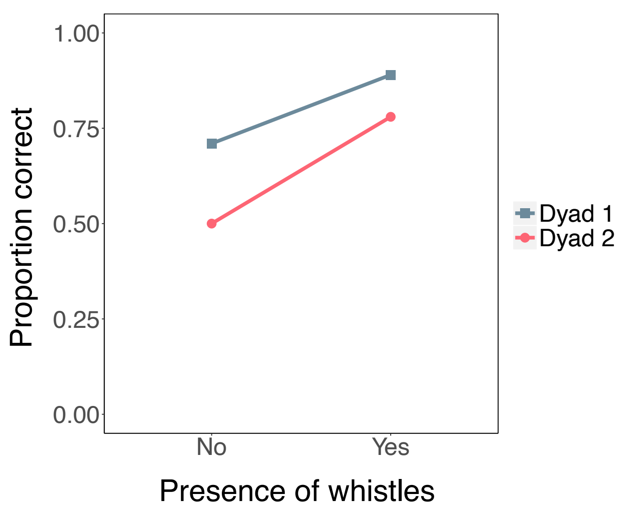

Figure 2: The proportion of correct trials for each dyad as a function of whether any whistling occurred.

However, within the trials that included whistles, only in dyad 2 did the dolphins whistle more during successful trials than during unsuccessful trials, $t(232)=2.50$, $p < .02$ (See Figure 3).

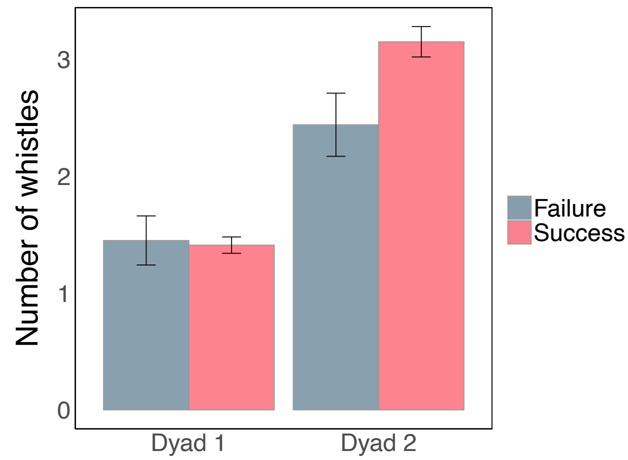

Figure 3: For trials with whistles, the average number of whistles (+/- SEM) each dyad produced during unsuccessful and successful trials.

Next, we examined the relationship between the timing of the whistles and button presses. For both dyads, whistles tended to occur near the end of the trial (See Figure 4).

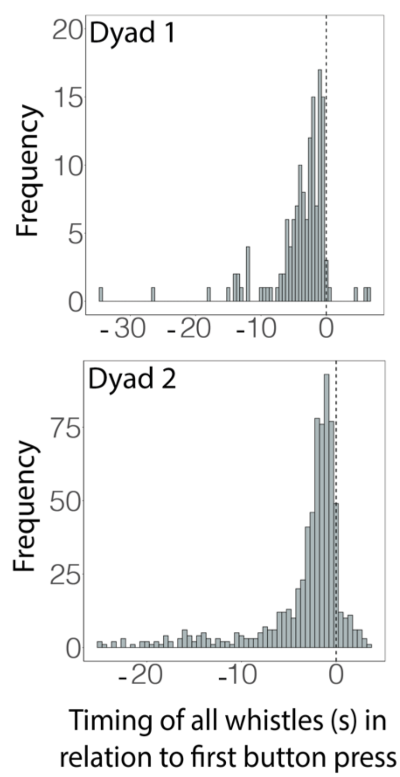

Figure 4: The timing of all whistles for each dyad in relation to their first button press.

To further explore the specific relation between whistle timing and success, Figure 5 shows the time between each dyad's last whistle and their first button press for both successful and unsuccessful trials.

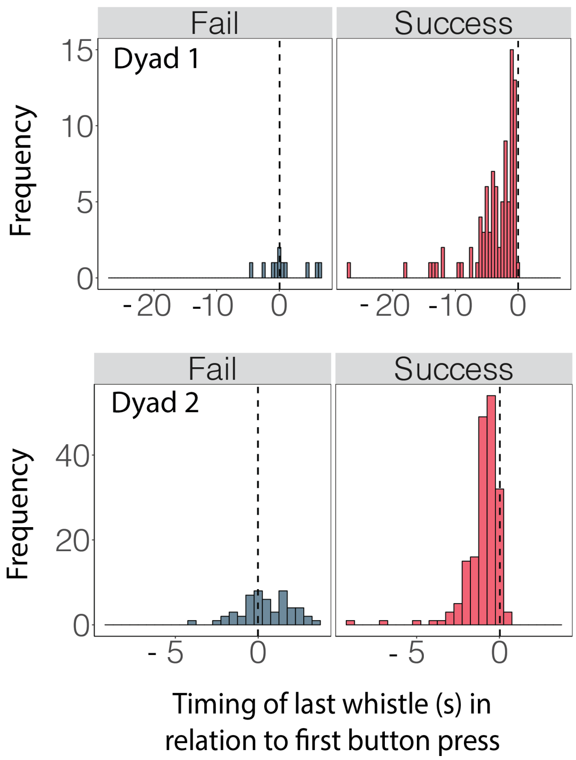

Figure 5: The timing of the last whistle of the trial in relation to the first button press, for both unsuccessful and successful trials.

There were two patterns of note: First, the timing of the last whistle differed between successful and unsuccessful trials for both dyads (two-tailed Fisher exact, *p*'s $< .0001$). Specifically, the first button press was more likely to occur after the last whistle in successful than in unsuccessful trials. In fact, for both dyads almost all of their whistles occurred before the button press in successful trials. Second, however, the timing of the final whistle was significantly different for dyad 1 versus dyad 2, whether looking at all trials [$M = -3.8$ vs -1.0, $t(271) = -8.38$, $p < .0001$)] or only successful trials [$M = -3.3$ vs -0.7, $t(344) = -8.25$, $p < .0001$)]. Specifically, dyad 2's final whistles occurred closer to the button presses than dyad 1's final whistles.

Motor Behavior

In addition to differences in vocal behavior, the dyads also showed differences in their motor behavior, suggesting different behavioral strategies for coordinating with their partner. Specifically, dyad 1 spent a significantly greater proportion of their time waiting in place for their partner than did dyad 2 (Welch's t-test: $t(766) = 6.5$, $p < .0001$) and a significantly greater proportion of their time swimming together when approaching the buttons (Welch's t-test: $t(766)= -3.2$, $p < .002$) (See Figure 6). Dyad 2, in contrast, tended to explore other areas of the lagoon until their partner was released, meeting up at the buttons prior to pressing.

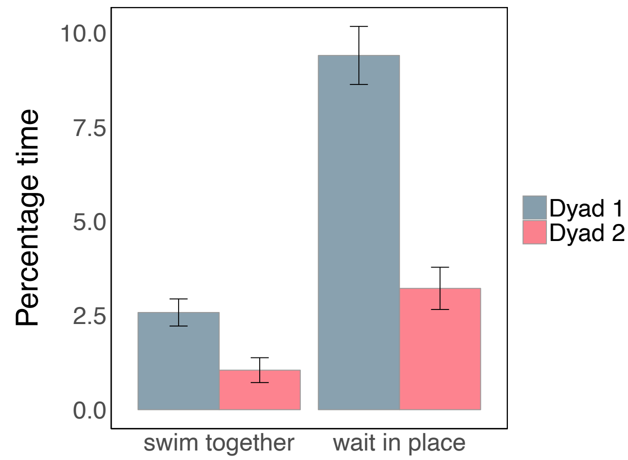

Figure 6: The average percentage of time (+/- SEM) each dyad spent waiting in place and swimming together during a trial.

Discussion

Our results show that dolphins can use both physical synchrony and vocal communication to coordinate their behavior in a cooperative task, and may adopt different strategies to achieve that coordination. While both dyads were more likely to succeed if they whistled during a trial, dyad 1 tended to favor physical synchrony, i.e., waiting nearby for their partner and swimming together when approaching the buttons, and their whistle rates tended to be lower. Given their proximity to each other, whistles were unlikely to be needed to signal general location but could be used to facilitate coordinated behavior. Members of dyad 2, on the other hand, tended to move away to other areas of the lagoon until their partner was released and then coordinate at the buttons. This may explain why their whistle rates were higher, particularly towards the end of the trials when they were coordinating at the buttons, and why more whistling was associated with greater success. By producing more whistles, uncertainty regarding their current locations in the lagoon was reduced, allowing them to locate each other and then coordinate their button presses.

One might question whether the dolphins' whistling could be a result of their success rather than a causal factor, perhaps due to increased excitement during successful trials. The timing of the whistles suggests otherwise, however, given that both dyads were significantly more likely to succeed if they pushed their buttons after their final whistle. Instead, it seems far more likely that they were using their whistles to coordinate behavior, either to facilitate coming together and swimming synchronously, and/or coordinating the final press.

The different strategies exhibited by the dyads could theoretically be explained by a number of factors including sex (dyad 1 is female; dyad 2 is male), age (dyad 1 is older), and/or individual differences in behavior. That said, it may be worth noting that acoustic coordination plays an important role when allied male dolphins cooperatively herd estrus females (King et al., 2019; Moore et al., 2020). Males may therefore have a propensity for using vocal signals to coordinate their behaviour in a cooperative context. Physical synchrony is thought to promote coordination and cooperation both between male alliance partners (King et al., 2018) and between female dolphins and their calves (Mann & Smuts, 1999). Thus, the sex differences we saw in our limited sample are consistent with the mechanisms posited to explain coordinated behaviors in the wild.

Acknowledgments

This work was supported by a research grant from Jim and Marjorie Sanger to Dolphin Research Center. S.L.K. was supported by The Branco Weiss Fellowship – Society in Science. We wish to thank Jesse Fox, Ted Due, Mandy Rodriguez and Jane Hecksher for apparatus design, creation, and troubleshooting. A special thanks to the staff and dolphins of DRC for their cooperation and patience, especially Aleta, Calusa, Delta, and Reese.

References

Bugnyar, T., & Massen, J. J. M. (2017). Avian social relations, social cognition and cooperation. In C. ten Cate & S. D. Healy (Eds.), *Avian cognition.* Cambridge: Cambridge University Press.

Connor, R. C. & Krützen, M. (2015). Male dolphin alliances in Shark Bay: Changing perspectives in a 30-year study. *Animal Behaviour, 103*, 223–235.

Connor, R. C., Smolker, R., & Bejder, L. (2006). Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Animal Behaviour, 72*, 1371–1378.

Duffy-Echevarria, E. E., Connor, R. C., & St. Aubin, D. J. (2008). Observations of strand-feeding behavior by bottlenose dolphins (*Tursiops truncatus*) in Bull Creek, South Carolina. *Marine Mammal Science, 24*, 202–206.

Duguid, S., & Melis, A. P. (2020). How animals collaborate: Underlying proximate mechanisms. *Wiley Interdisciplinary Reviews: Cognitive Science*, *11*, e1529.

Duguid, S., Wyman, E., Bullinger, A. F., Herfurth-Majstorovic, K., & Tomasello, M. (2014). Coordination strategies of chimpanzees and human children in a Stag Hunt game. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20141973.

Friard, O., & Gamba. M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution,* 7, 1325–1330.

Gazda, S. K., Connor, R. C., Edgar, R. K., & Cox, F. (2005). A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proceedings of the Royal Society of London B, 272*, 135–140.

Heaney, M., Gray, R. D., & Taylor, A. H. (2017). Keas perform similarly to chimpanzees and elephants when solving collaborative tasks. *PLoS One, 12*, 1–13.

Hirata, S., & Fuwa, K. (2007). Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. *Primates, 48*, 13–21.

Jaakkola, K., Guarino, E., Donegan, K., & King, S. L. (2018). Bottlenose dolphins can understand their partner's role in a cooperative task. *Proceedings of the Royal Society B, 285,* 20180948.

King, S. L., Allen, S. J., Krützen, M., & Connor, R. C. (2019). Vocal behaviour of allied male dolphins during cooperative mate guarding. *Animal Cognition*, *22*, 991–1000.

King, S. L., Friedman, W. R., Allen, S. J., Gerber, L., Jensen, F. H., Wittwer, S., ... & Krützen, M. (2018). Bottlenose dolphins retain individual vocal labels in multi-level alliances. *Current Biology*, *28*, 1993–1999.

Mann, J., & Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour, 136*, 529–566.

Marshall-Pescini, S., Schwarz, J. F. L., Kostelnik, I., Virányi, Z., & Range, F. (2017). Importance of a species' socioecology: Wolves outperform dogs in a conspecific cooperation task. *Proceedings of the National Academy of Sciences, 114*, 201709027.

Massen, J. J. M., Ritter, C., & Bugnyar, T. (2015). Tolerance and reward equity predict cooperation in ravens (*Corvus corax*). *Scientific Reports, 5*, 1–11.

Melis, A. P., Hare, B., & Tomasello, M. (2006). Chimpanzees recruit the best collaborators. *Science, 311*, 1297–1300.

Mitani, J. C. (2009). Cooperation and competition in chimpanzees: Current understanding and future challenges. *Evolutionary Anthropology, 18,* 215–227.

Moore, B. L., Connor, R. C., Allen, S. J., Krützen, M., & King, S. L. (2020). Acoustic coordination by allied male dolphins in a cooperative context. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20192944.

Noë, R. (2006). Cooperation experiments: Coordination through communication versus acting apart together. *Animal Behaviour*, *71*, 1–18.

Péron, F., Rat-Fischer, L., Lalot, M., Nagle, L., & Bovet, D. (2011). Cooperative problem solving in African grey parrots (*Psittacus erithacus*). *Animal Cognition, 14*, 545–553.

Plotnik, J. M., Lair, R., Suphachoksahakun, W., & de Waal, F. B. M. (2011). Elephants know when they need a helping trunk in a cooperative task. *Proceedings of the National Academy of Sciences, 108*, 5116–5121.

Schmelz, M., Duguid, S., Bohn, M., & Völter, C. J. (2017). Cooperative problem solving in giant otters (*Pteronura*

brasiliensis) and Asian small-clawed otters (*Aonyx cinerea*). *Animal Cognition, 20*, 1107–1114.
Seed, A. M., Clayton, N. S., & Emery, N. J. (2008). Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society B: Biological Sciences, 275*, 1421–1429.
Smith, E. A. (2010). Communication and collective action: Language and the evolution of human cooperation. *Evolution and Human Behavior*, *31*, 231–245.
Smith, J. E., Swanson, E. M., Reed, D., & Holekamp, K. E. (2012). Evolution of cooperation among mammalian carnivores and its relevance to hominin evolution. *Current Anthropology, 53,* S436–S452.