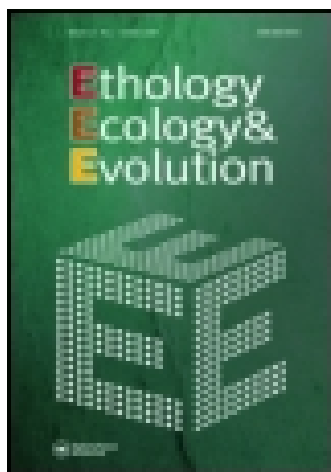


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Apparent coordination and collaboration in cooperatively hunting crocodilians

Vladimir Dinets^a

^a Department of Psychology, University of Tennessee, 1404 Circle Dr., Knoxville, TN 37996-0900, USA

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Forum

Apparent coordination and collaboration in cooperatively hunting crocodilians

What is coordination and collaboration?

Coordinated hunting, in which individual predators relate in time and space to each other's actions, is a complex form of cooperative hunting (BAILEY et al. 2012), considered to be very rare in vertebrates (GAZDA et al. 2005). It is known with certainty only in hominid primates (BOESCH & BOESCH 1989; STINER et al. 2009), a few carnivores (STANDER 1992; CREEL & CREEL 1995; MECH 2007; EATON 2009; BAILEY et al. 2012), bottlenose dolphins (GAZDA et al. 2005), killer whales (SMITH et al. 1981), two species of raptors (BEDNARZ 1988; LEONARDI 1999), two species of corvids (BOWMAN 2003; YOSEF & YOSEF 2010) and two species of fish (BSHARY et al. 2006).

An even more sophisticated and rarely observed hunting behavior is collaboration, defined by BAILEY et al. (2012) as performing different complementary actions focused on the same prey during coordinated hunting. In some cases, individual animals might take on the same role (being, for example, the driver or the ambusher) during multiple hunts, as observed in lions (STANDER 1992). It is, of course, possible that the rarity of these behaviors is overestimated due to the notorious difficulty of observing predation events in the wild.

Coordination and collaboration in crocodilians: anecdotal evidence old and new

One group of predatory animals with very complex behavior is crocodilians (crocodiles, alligators, caimans and gharials). Recent discoveries, often accidental, have shed some light on their spectacular social interactions, well-developed parental care, and multimodal communication systems (see DOODY et al. 2013 for an overview). One aspect of crocodilian behavior that remains particularly little known is hunting techniques. For example, the common notion that crocodilians are almost exclusively aquatic predators has been only recently proven wrong, as it was found that many species regularly hunt on land (DINETS 2011). Use of objects as hunting lures by crocodilians has been demonstrated only very recently as well (DINETS et al. *in press*).

Cooperative hunting is now known to occur in many crocodilian species (KING et al. 1998; DINETS 2010). But are these animals capable of coordination and collaboration? Until recently, the only published observation indicating such a possibility was by MIKLOUKHO-MAKLAY (1892), a Russian anthropologist and biologist with an

immaculate scientific record (GREENOP 1944). In his diary, MIKLOUKHO-MAKLAY described cooperative fishing by estuarine crocodiles (*Crocodylus porosus*), shown to him by a Papuan hunter. A larger crocodile repeatedly chased fish towards the shore with powerful splashes of its tail, while smaller, more agile crocs waited in the shallows, ready to snatch the cornered fish.

Unlike many other of MIKLOUKHO-MAKLAY's discoveries, this report had not been confirmed for more than a century following its publication. The diary containing it has never been fully translated into languages other than Russian, and is now a bibliographical rarity.

In 2012, I conducted an informal survey of crocodile researchers, conservationists and amateur enthusiasts, asking for observations of complex hunting behavior, and received some descriptions strikingly similar to MIKLOUKHO-MAKLAY's account. Alex Mitchell, Supervisor of Reptiles in Cairns Tropical Zoo, Australia, reported the following observation of Johnston's crocodiles (*Crocodylus johnstoni*), made in July 2008 from 22:00 hr onwards in Lakefield National Park, Queensland, Australia:

A group of approximately five crocodiles were sitting in a shallow area of the main river adjacent to a sandy river bank. I witnessed over a period of approximately 1.5–2 hrs two to three crocodiles at a time "herding" small fish which I presume were Rainbow Fish, *Melanotaenia* sp., into the shallows allowing the remaining crocodiles to feed upon them.

Similar observations were made by Chip Campbell, a visitor services contractor for Okefenokee National Wildlife Refuge, Georgia, USA. He reported that in 12 years of observing American alligators (*Alligator mississippiensis*), he had seen cooperative feeding on three occasions, and two of those were "quite evidently coordinated, as a phalanx of 'drivers' pushed schools of fish (entrapped in the shrinking pools) to waiting 'catchers'". He described one observation, made in 2011, as follows:

One morning in early May, we arrived at work to find approximately 60 alligators gathered in our boat basin. This gathering demonstrated the most consistent and seemingly coordinated behavior I have yet observed. The animals appeared to alternate between two strategies: the "driving" phalanx described above and something I called the "purse seine" approach – the phalanx would ease itself into a loose semi-circle and then close in, pushing the fish into the shallows and against the bulkheads. Hunting behavior was almost constant, but at any given time, 1/3–1/2 of the animals seemed to be resting and "waiting their turn". When an alligator captured a fish, it would swim over and join the "resting" gators after swallowing its fish – and one of the previously dormant gators would slide out to join the active hunting group. This continued until about lunch time, at which point most (not all) of the alligators began to break away and disperse. They did it again the following morning – about the same number of alligators and for about the same length of time.

Two more accounts were provided by amateur naturalists. Ernesto Jimenez, a native tour guide working in the Santa Elena area, Venezuela, reported observing a spectacled caiman (*Caiman crocodilus*) as it walked along a lakeshore and flushed frogs so that they jumped into the water and were snatched by another caiman. Peter Chadwick described seeing Nile crocodiles (*Crocodylus niloticus*) behaving in a similar way to alligators in Chip Campbell's report; he made this observation while on a safari tour in Chobe National Park, Botswana. However, the accounts by Jimenez and Chadwick were written many years after the events, and were rather sketchy.

Personal observations

In 2005–2011, I conducted a comparative study of crocodylian signaling behavior. This research project and follow-up studies in 2011–2013 involved over 3000 hr of observations in the wild by me and teams of volunteers. During that time, I observed 17 cooperative hunting events, three of which were indicative of coordination. In one case, a group of mugger crocodiles (*Crocodylus palustris*) in Yala National Park, Sri Lanka, swam in a circular pattern around a shoal of fish and took turns cutting through the center of the gradually shrinking circle, snatching the fish (BRITTON et al. in review). The other two of these three hunting events were more clearly indicative of coordination and suggested also collaboration; these two events are described below.

All observations were conducted opportunistically. Sizes and distances were estimated visually. Details on locations and dates are provided in relevant sections below.

Chasing prey into an ambush by estuarine crocodiles

Estuarine crocodiles were observed on 20–25 August 2009, in mangroves near Sorong, West Papua, Indonesia (1°04'S, 131°14'E). Observations were conducted from a tree growing on the shore of a brackish lagoon inhabited by at least 11 crocodiles. The lagoon, ~ 1 km in diameter and up to 2 m deep at low tide, was crossed by a trail of compacted mud 50–100 cm wide. The trail was completely flooded at high tide, but surrounded by up to 1 m of exposed mudflats on either side at low tide. When not flooded, the trail was frequently used by people and domestic animals, and crocodiles could sometimes be seen stalking the latter. In 6 days of observing the lagoon for 2–4 hr every morning and evening, I saw four predation attempts. In each case, my elevated vantage point allowed me to see fully submerged crocodiles, while prey animals using the trail probably couldn't see them until they were very close.

In two cases, dogs running along the trail at intermediate tide were approached by single crocodiles, 2 m long in one case and 3.5 m long in the other. The predator would remain underwater until it got within ~ 1.5 m of its prey, at which point the water became too shallow for the crocodile to remain submerged. It would then emerge and rush towards the dog, snapping its jaws. Despite the high speed of these sudden attacks, both dogs were able to escape.

In one case, a calf walking along the trail at intermediate tide was approached by a large (4.5–5 m long) crocodile which glided toward the calf with its eyes and nostrils above the water. The calf didn't show any sign of recognizing the danger until the crocodile was less than 5 m away, at which point a teenage boy walking behind the calf noticed the croc and threw a stick at it. The crocodile submerged and disappeared from view.

The fourth predation attempt looked very different. It happened at dusk (~ 20 min after sunset), shortly before the high tide, when the trail was almost covered by water. A pig walking along the trail was approached by a large crocodile (probably the same individual as in the calf predation attempt) moving underwater on the western side of the trail. When the crocodile was 5 m from the pig, and apparently still in deep water, it suddenly erupted from the water with its jaws widely open and its tail splashing. To me, this behavior looked more like a threat display than the sneaky approaches to prey normally used by crocodylians. The pig ran away from the croc, leaving the trail and wading into the water on the eastern side of the trail. At that moment I noticed two

other crocodiles, 3–4 m long, floating just under the water surface east of the trail. One of them seized the pig. The largest crocodile quickly crossed the trail and also seized the pig. All animals moved away from the trail and submerged, apparently drowning their prey.

Assuming complementary roles during fishing by American alligators

American alligators were observed on 26 September 2012, in Bogue Chitto National Wildlife Refuge, Louisiana, USA (30°25'54"N, 89°44'30"E), in a pond measured the next morning to be 70 × 60 m, with depth gradually changing from 30–40 cm near the shore to more than 1 m in the center. The pond is part of an extensive forested wetland, and is connected to Pearl River by a channel opening into its southeastern part. The alligators ($n = 7$) were initially found 1 hr 14 min after sunset in a cooperative fishing gathering (as described in DINETS 2010). At first, the animals were observed by moonlight (full moon 29 September) and by the red light of a headlamp. After about 20 min, the headlamp batteries became almost drained and the moonlight was partially blocked by clouds; the animals could still be followed by their eyeshine, but differentiating them by size became impossible, except for the largest and the smallest alligator present.

When first observed, three mostly larger alligators (2.0, 2.0 and 2.5 m long; called 'Group 1' hereafter) were in the northern part of the pond 5–15 m from the shore, while four mostly smaller ones (1.0, 1.5, 1.5 and 2.0 m long; called 'Group 2' hereafter) were in the same part of the pond 1–4 m from the shore. Once every 2–10 min, Group 1 alligators would quickly move along parallel trajectories (with 1–3 m between them) towards the northern shore. They all moved at roughly the same time, but not in perfect synchronization, starting their movement towards the shore up to 1 sec apart. They had their mouths open and were creating an unusually high wake. Every time, splashes by fish trying to avoid them could be seen near the shore, where Group 2 alligators were actively chasing those fish. Some fish tried to avoid Group 2 animals by moving back into deeper water, and were snatched by Group 1 alligators. After each run towards the shore, Group 1 animals would slowly float back into the deeper part of the pond with their mouths closed. In the first 20 min, four such chases were observed, all of them performed by all Group 1 animals. Numerous successful prey captures by animals from both groups were seen. In some instances, the fish could be identified as catfish, most likely channel catfish (*Ictalurus punctatus*). After ~ 30 min (by which time the flashlight battery was already mostly drained), one of the Group 1 alligators (not the largest animal) joined Group 2. After another 8–10 min, two of the Group 2 alligators (sizes unknown, but not the smallest animal) left the edge of the pond and joined Group 1. Judging by eye movement and splashing sounds, fishing continued in the same way, with rapid runs from the central part of the pond towards the shore every few minutes. It is possible that other movements of animals between groups took place, but were not recorded. ~ 70 min after the start of observations, the headlamp batteries became completely drained and observations were discontinued.

The pond was revisited at sunrise. At that time, only three alligators (1.0, 2.0 and 2.0 m long) were visible, all of them partially submerged near the eastern shore. The following night, 1 hr after sunset, the pond was visited again, and three animals

(possibly the same ones) were still present, but no fishing was seen in 10 min of observation using moonlight and red light from a headlamp.

What does it all mean?

A major problem in evaluating opportunistic observations of coordination and collaboration during hunting is that the intentions of the participating animals can virtually never be known with certainty. Did they intentionally drive the prey towards the ambushers, or was it just a coincidence? Did other hunters anticipate the prey's movement and position themselves so as to intercept it, or did they just happen to be in the right place in the right time? Was it really mutual cooperation, or were some animals simply snatching prey that was being pursued by others?

The only way to convincingly demonstrate coordination and collaboration is to make numerous observations, showing that the observed patterns are too regular to be artefacts. In the case of crocodylians, this is extremely difficult to do. They do not spend as much time hunting as do mammals or birds, they are predominantly nocturnal and much of their hunting is conducted underwater, often in murky waters. In addition, cooperative hunting appears to be used only rarely, and only a fraction of cooperative hunts involves coordination and collaboration. Of 17 cooperative hunts by crocodylians I have observed to date (see DINETS 2010; BRITTON et al. in review), only two (described here) apparently involved collaboration.

By itself, each of the observations presented here is open to alternative explanations. However, the similarity between some of the accounts by independent observers is striking, and strongly suggests that the observers' interpretation of the animals' behavior might be correct. If all these accounts are accurate, it would mean that coordination and collaboration occur in at least five crocodylian species representing two different families – the first case of such ability in reptiles. It would also mean that crocodylians can use more than one method of coordinated hunting.

The case of the estuarine crocodiles hunting the pig is particularly interesting, because the chaser was separated from the ambushers by the trail and could not see them. However, the chaser apparently tried to drive the pig towards the ambushers instead of attempting to snatch it, which suggests that it had correctly guessed their positions.

The only way to prove beyond doubt that crocodylians are capable of such complex behavior is to accumulate more observations. Every such record is a fortunate event for a field researcher, and should not remain unpublished.

Many animals exhibiting coordinated and collaborative hunting do so in family groups or are otherwise related. However, there are many exceptions and even one case of interspecific coordination (BSHARY et al. 2006), showing that relatedness of animals is not a necessary prerequisite for these behaviors. There is no reason to think that in the cases described above, the participating crocodylians were closely related. It is more likely that such complicated techniques are directly beneficial for all participating animals, as they maximize every crocodylian's chances of catching small prey, and large prey is divided between all participants of the hunt, as is common among crocodylians (NEILL 1971).

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VLADIMIR DINETS, Department of Psychology, University of Tennessee, 1404 Circle Dr., Knoxville, TN 37996-0900, USA (E-mail: dinets@gmail.com).