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Proto-cooperation: group hunting sailfish improve hunting success by alternating attacks on grouping prey

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We present evidence of a novel form of group hunting. Individual sailfish (*Istiophorus platypterus*) alternate attacks with other group members on their schooling prey (*Sardinella aurita*). While only 24% of attacks result in prey capture, multiple prey are injured in 95% of attacks, resulting in an increase of injured fish in the school with the number of attacks. How quickly prey are captured is positively correlated with the level of injury of the school, suggesting that hunters can benefit from other conspecifics' attacks on the prey. To explore this, we built a mathematical model capturing the dynamics of the hunt. We show that group hunting provides major efficiency gains (prey caught per unit time) for individuals in groups of up to 70 members. We also demonstrate that a free riding strategy, where some individuals wait until the prey are sufficiently injured before attacking, is only beneficial if the cost of attacking is high, and only then when waiting times are short. Our findings provide evidence that cooperative benefits can be realized through the facilitative effects of individuals' hunting actions without spatial coordination of attacks. Such 'proto-cooperation' may be the pre-cursor to more complex group-hunting strategies.

1. Introduction

Group hunting is a fascinating example of social behaviour that can be observed in taxonomic groups including arthropods [1–3], fishes [4–8], birds [9,10] and mammals [11,12]. The level of coordination between individuals during hunts, both within and between these taxa, varies considerably. In its simplest form, group hunting involves hunters attacking prey together with little or no coordination of attacks while the most complex form, collaborative hunting, involves individuals adopting specific hunting roles to herd and catch their prey [13–15].

Explaining the origins and maintenance of group hunting, however, remains unresolved. Despite group hunting allowing some species to catch considerably

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larger prey [13,16] as well as increasing the likelihood of making a kill [16], individuals do not necessarily increase the amount of prey they consume when hunting together (compared with when hunting alone). For example, food intake per individual wolf (*Canis lupus*) can be lower in larger packs compared with smaller hunting groups or lone individuals [17], and lions (*Panthera leo*) do not always hunt in group sizes that optimize the amount of prey they consume [18]. Other reasons, therefore, may explain the existence of group hunting in some taxa. For example, individuals in groups may be better at limiting the access of kleptoparasites to the kill, may travel less distance, and may have a reduced likelihood of being injured during group hunts, compared with when hunting alone [16,19,20].

When hunters attack smaller grouping prey, the reasons for group hunting appear clearer. In some cases, group hunters use their superior speed and coordinated attacks to disrupt and fragment prey groups [4,21,22]. Groups of piscivorous fishes, for example, have a higher probability of breaking up prey schools and capture more prey than single attackers [21]. Groups of humpback whales (*Megaptera novaeangliae*) employ bubble-nets to capture schooling fishes [23,24] and various dolphin species have been described to use cooperative hunting strategies [25]. Raptors have similarly been observed to use spatially coordinated attacks to hunt flocking passerines [9,10]. Spatially coordinated attacks appear to break down the collective defences of grouping prey, thereby increasing consumption rates for group hunters. But how did these more complex coordinated attacks evolve from simpler forms of group hunting?

In their simplest form, apparent group hunts may simply be a by-product of clumped prey distribution, when hunters join others by eavesdropping on the cues produced from hunters finding ephemeral food patches [11]. Cattle egrets (*Bubulcus ibis*), for example, aggregate where prey are highly abundant, with feeding rates and prey density being closely linked [26]. In these cases, it is unclear whether the presence of other hunters benefits individuals' hunting success. In other cases, the presence of other hunters can increase hunting success, even though hunters' attacks are not coordinated in space. Lionfish (*Dendrochirus zebra*) alternate attacks on schooling prey and catch more prey when hunting in pairs than when alone [5]. Group hunting in a weakly electric fish (*Mormyrops anguilloides*) does not appear to be spatially coordinated, and instead hunters may benefit from prey fleeing in their direction when prey escape another hunter's failed attack [27]. Black headed-gulls (*Larus ridibundus*) capture twice as many fishes when hunting in groups of six than when hunting alone, even though attacks are uncoordinated [28]. If individuals can benefit from the hunting actions of others without spatial coordination of attacks, then these group hunts could explain the origins of more complex group hunting strategies. But the mechanisms allowing increased capture rates for individuals with uncoordinated attacks remain unclear. One possibility is that the alternation of attacks gives hunters the opportunity to save energy, while others exhaust and injure the prey. This could allow individuals to benefit from increased capture success during later attacks if it is easier to catch tired, injured prey. Here, we investigate whether such a 'proto-cooperative' strategy could benefit individual hunters in groups. We investigated group hunting sailfish (*Istiophorus platypterus*) that alternate their attacks on schooling sardine prey (*Sardinella aurita*) [29,30]. Attacks by sailfish appear to be uncoordinated in space, and one sailfish will abandon its attack if another individual attacks the school at the same time.

We first used behavioural observations and image analysis to systematically quantify the group hunting strategies of sailfish, which can only be done in the wild. This puts strong constraints on the type and quantity of data we could record. Therefore, to complement our empirical work, we used a mathematical model to test whether the attack-alternation strategy we observed could be effective at allowing predators to increase their capture success beyond that possible for a solitary sailfish. We hypothesized that group hunting would allow individuals to capture more sardines per unit time using this strategy compared with if they hunted alone. Further, we evaluate the predator group sizes where this attack-alternation strategy is beneficial over solo hunting under different hunting conditions. We also investigate whether this form of group hunting is likely to be exploited by free riders, i.e. individuals that wait until the school is sufficiently injured before attacking.

2. Empirical material and methods

Research was conducted 30–70 km offshore Cancun in the Gulf of Mexico (N 21 28.3–41.15, W 86 38.41–41.30). We observed group-hunting sailfish separating smaller schools of sardines from larger ones containing thousands of fish. The sailfish then herded these smaller schools to the surface where the last stage of the hunt occurred. Under snorkel, we used Casio EX-FH100 cameras (operating at 240 fps) to record these smaller sardine schools that were being attacked by the sailfish. We visited this site once a year for 5 years to record the hunting behaviour of sailfish. However, we could only perform the school injury analyses (see below) in videos when sky conditions were overcast (because we required the light to be evenly distributed across the schools). This restricted the amount of data we could use. In total, our analyses are based on 63 min of video from 2012 documenting these interactions. As we did not observe some of the behaviours and could not calculate some of the measures for all schools ($n = 8$ in total), we report the number of schools used in each analysis below.

(a) Attack and capture rates

During an attack, sailfish use their rostra to facilitate prey capture by slashing or tapping the sardines [30]. From the videos, we recorded the number of these attack events ($n = 210$ attacks across all schools) as well as the number of successful prey capture events ($n = 51$ across all videos). By dividing the total number of captures by the length of the video recordings we had recorded of particular schools, we determined a capture rate for each school ($n = 7$ schools; note, we did not observe any attacks on one of the schools we recorded). We recorded the number of sardines that the bill hit during these attacks (taps or slashes). This represents the minimum number of fish hit during these attacks because some hits may not have been visible from the camera angle. In 52 out of the 210 attacks, we could not see how many fish were hit and these events were excluded from analysis. We also determined whether we could see if some of the sardines' scales were removed during the attacks. Scale removal indicates injury to the sardines (movie S1). Sometimes it was not clear whether scales were removed or not during an attack (owing to subsequent obstruction by other fish), and

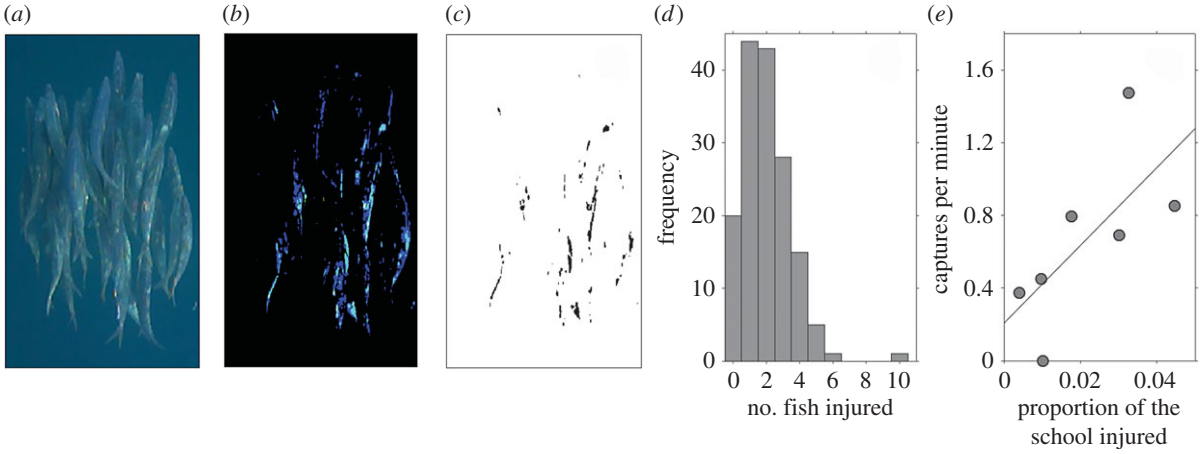

Figure 1. (*a*) Original frame taken from one of the videos showing the white injury marks on the sardines caused by damage from sailfish bills. (*b*) The original image has its contrast and brightness adjusted before binary thresholding (*c*), which reveals the injuries on the sardines. (*d*) The minimum number of sardines that were hit with the bill during a sailfish's attack (determined for 158 attacks). (*e*) Relationship between the proportion of the school that was injured and the sailfish capture success rate on the prey schools. Solid line represents the least-squares regression; $y = 21.4x + 0.21$.

therefore these ambiguous events ($n = 61$ attacks out of 210) were not included when calculating the proportion of fish that were injured during an attack.

(b) Proportion of the school that was injured

We investigated what proportion of each school had injuries. We selected 39 video stills where light contrast across the schools was minimal. For this analysis, we only selected multiple images from the same video if there was at least 1 min between the two frames of interest (see the electronic supplementary material, table S1 for the number of images used for each school). The marks on the sardines caused by injuries from the bill have a distinctive white/pinkish appearance, different from other parts of the fish's bodies or surrounding water (figure 1*a*). This allowed us to use image analysis to determine how injured the fish were in the school. To perform this analysis, we marked a polygon around the edge of the school, and then cleared all pixels from outside the marked polygon (setting their grey-scale intensity to 255). We then adjusted the brightness and contrast of each image so that only the injury marks on the fish became pronounced. By adjusting the brightness and contrast for each image appropriately (figure 1*b*), we could then binary threshold the images to reveal the pixels in each image where the injuries had occurred (figure 1*c*). Note that because the average intensity of each image differed, we had to adjust the brightness and contrasts of each image manually. We imported the binary converted images into MATLAB (2012b). Each image was represented by a matrix where cells equal to zero (black pixels) were injured parts of the school, and cells equal to 255 (white pixels) were uninjured parts of the school. By counting the number of values in the matrix equal to zero, and then by dividing this total by the area of the school calculated by the polygon in IMAGEJ, we determined the proportion of pixels in the school depicting injuries. We determined the mean proportion of injuries of a school if that school had been measured in multiple images (see the electronic supplementary material, table S1). We note that this semi-automated analysis provides information on a general level of injury, which combines both the frequency and severity of injury into one variable.

3. Empirical results

(a) Sailfish group hunting behaviour

Sailfish were observed in groups of approximately 6–40 individuals hunting sardine schools ($n = 8$) that differed in number from approximately 25 to 100–150 fish (electronic supplementary material, S1.1 and figure S1*a*). Owing to observational limitations, we could not determine the exact number of sailfish that were hunting each sardine school. Different sailfish alternated their attacks on the sardine schools (movie S2). Individual identification of all sailfish was not possible, and therefore we could not determine the order in which individual sailfish attacked the prey school. The median time between consecutive approaches by different sailfish was 6.5 s (electronic supplementary material, S1.2 and figure S1*b*). There was no relationship between the time between approaches and the sardine school size (Spearman's correlation; $\rho = 0.11$, $n = 7$, $p = 0.84$). The median length of individuals' attacks was 2.6 s, but again, this was not related to school size (Spearman's correlation; $\rho = -0.21$, $n = 7$, $p = 0.66$). A sailfish's attack was interrupted by another sailfish 19% of the time, after which either one or both sailfish would abandon their attack.

During attacks, sailfish used their bills to 'tap' or 'slash' at the sardines in an attempt to capture individual fish (movie S1) [29]. Only 24% of these attacks resulted in a successful capture and we never observed a sailfish to handle or ingest two or more fish at once. However, both the mean and the median number of sardines that were hit with a sailfish's bill during an attack was 2.0 (figure 1*d*). While the attacks with the bill were very rarely observed to kill the sardines outright, sardines' scales were removed when contact was made between the sailfish's bills and the sardines' bodies in 95% of cases. Because more fish were injured per attack than were caught, this led to many sardines in the schools having pronounced injuries on their bodies, accumulated from past attacks (figure 1*a*). The most heavily damaged fish had over 20% of their body covered in injuries (electronic supplementary material, S1.3 and figure S1*c*).

We observed successful captures ($n = 51$) on six of the eight sardine schools we recorded. Sailfish caught individual sardines at an average rate (across all the schools) of 0.66 ± 0.17

s.e. sardines per minute. By quantifying the proportion of the school that was injured (figure 1*b*,*c*), we found a positive correlation between the school's injury level and the capture rate (Spearman's correlation; $\rho = 0.82$, $n = 7$, $p = 0.03$; figure 1*e*); sardines in more injured schools were captured more quickly. Given the observational constraints, we could not determine whether it was the most injured fish in the shoal that were captured next; however, we often observed injured sardines breaking off from the prey schools that presumably could not keep pace with the school. These individuals were quickly captured by the sailfish (movie S3). There were non-significant negative correlations between capture success rates and school size (Spearman's correlation; $\rho = -0.54$, $p = 0.24$, $n = 7$), and between the proportion of the school that was injured and school size (Spearman's correlation; $\rho = -0.69$, $p = 0.07$, $n = 8$; see the electronic supplementary material, S1.4 and S1.5 for a discussion of these results).

4. Group hunting model

From the empirical information above, it appears that sailfish increase their capture rates as prey become progressively injured from previous attacks. But this does not explain why they hunt in groups, as a solitary hunter could get these benefits by hunting on its own. To better understand why sailfish hunt in groups, therefore, we built a simple mathematical model to capture the dynamics of the hunt. We chose to model group hunting using a non-spatial, individual-based model. On the one hand, this model effectively accounts for the fundamental temporal 'mechanics' of the hunt observed in the field, and on the other hand is open to a full analytical investigation of its dynamics. Our model allows us to systematically investigate the rates at which sailfish catch sardines in different predator group sizes. It also allows us to explore potential differences in the strategies predators could use during the hunt. A general advantage of an individual-based approach is that our model can be easily extended to incorporate more additional features, such as agent heterogeneity or stochastic effects.

We consider a group of $N = const.$ predators (sailfish), hunting a group of initially $S(t = 0) = S_0$ prey (sardines). The number of sailfish observed hunting in groups was $N = 6$–40; however, group sizes exceeding 50 individuals have been previously reported. Therefore, in our model we studied a range of group sizes from solitary hunters $N = 1$ up to a group size $N = 100$. The prey schools from our empirical observations ranged from 25 to 150 sardines. However, we have no information about the number of sardines that were initially separated from the school containing thousands of fish during the initial stages of the hunt. In our model calculations, therefore, we set the initial number of sardines to be larger, but in the same order of magnitude, as the largest groups observed: $S_0 = 200$.

Basic biomechanics predict that small prey (sardine average body length is approximately 19 cm [30]) are more manoeuvrable than larger predators [31,32] (sailfish are approximately 200–250 cm). If the sardines can perform one or more sharp turns, removing a sailfish's potential for attack, then a sailfish is likely to abandon its attack owing to its lower manoeuvrability. Meanwhile, this gives another sailfish an opportunity to initiate its attack sequence. In our model, therefore, each predator needs a finite time to perform an attack, τ_a, and after an attack it requires a finite time, τ_r, to be ready for the next attack. τ_a represents the time where an individual sailfish 'monopolizes' the prey school by performing its approach, manoeuvre and attack. Here, we set it to the median attack time observed for hunting sailfish; $\tau_a = 2.6$ s. τ_r describes the average time required by an individual hunter to prepare for the next attack sequence, i.e. for the sailfish to assume a suitable position at the rear of the prey school. This time is not available from our observations, as it requires repeated observations of a solitary sailfish hunting a sardine school. However, a reasonable timescale can be estimated from qualitative observations of the hunting process and other timescales, as well as from the assumed cooperative benefits of the hunt. Here, we reasonably assume that τ_r is larger than τ_a, and significantly shorter than 1 min. Therefore, we use as a default parameter $\tau_r = 20$ s. Note that while the attack and preparation times may vary, only their average values, τ_a and τ_r, determine the conditions where group hunting is beneficial (see the electronic supplementary material, figure S2 for an exploration of how τ_a and τ_r determine these conditions).

A single predator requires the time $\Delta t_{\text{single}} = \tau_a + \tau_r$ for a full attack cycle: 'perform attack' (τ_a) and 'prepare for next attack' (τ_r). Thus, it attacks on average only once during this time interval and the number of attacks scales linearly with time $n_a(t) = t/\Delta t_{\text{single}}$. If we have more than one predator, the average time interval between two attacks by a focal individual depends on the number of predators N, whereby two cases have to be distinguished: (i) if N is small, then on average all other hunters can perform their attacks within the time required by the focal individual to prepare for the next attack, and the average time interval between initiation of subsequent attacks for the focal individual is simply $\tau_a + \tau_r$. (ii) If N is larger than $1 + \tau_r/\tau_a$, then the focal individual will typically have to wait until other, better prepared individuals have performed their attacks. If we assume that at any time the individual with the longest waiting time will attack next, then typically all other hunters will perform their attacks between two subsequent attacks of the focal individual and the corresponding time interval becomes $N\tau_a$. In summary, therefore, the average waiting time between two attacks for an individual predator can be expressed as

$$\Delta t_{\text{single}}(N) = \begin{cases} \tau_a + \tau_r & \text{for} \quad N\tau_a \leq (\tau_a + \tau_r) \\ N\tau_a & \text{for} \quad N\tau_a > (\tau_a + \tau_r) \end{cases}.$$

Using this we can calculate the average number of attacks $n_{a,s}(T, N)$ an individual predator performs until time T in a group of size N (electronic supplementary material, figure S3). Note that, T, can be interpreted simply as the time available for hunting, and is different from the actual time required to hunt down a school of sardines, T_{tot} (see the electronic supplementary material, figure S4 for an exploration of how T_{tot} changes depending on the hunters' group size). The average number of attacks performed by single hunter at time T in a group of N is given by

$$n_{a,s}(T, N) = \left\lfloor \frac{T}{\Delta t_{\text{single}}(N)} \right\rfloor = \begin{cases} \left\lfloor \dfrac{T}{\tau_a + \tau_r} \right\rfloor & \text{for} \quad N\tau_a \leq (\tau_a + \tau_r) \\ \left\lfloor \dfrac{T}{N\tau_a} \right\rfloor & \text{for} \quad N\tau_a > (\tau_a + \tau_r). \end{cases}$$

Here, $\lfloor \cdot \rfloor$ indicates the floor function as $n_{a,s}(T, N) \in \mathbb{N}$.

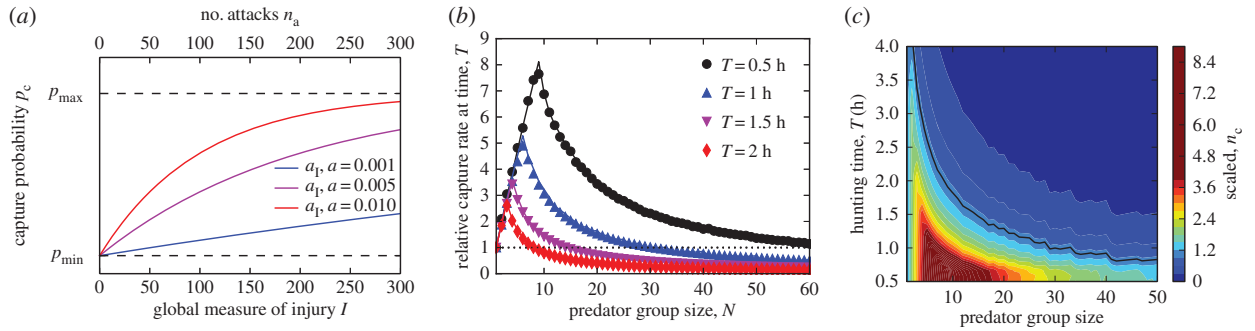

Figure 2. (*a*) Capture probability versus the global measure of injury of the prey school and the number of attacks for different values of the injury growth constants a_l, a (see electronic supplementary material, equations S1 and S2 for details) assuming $\Delta I = 1$. The dashed lines indicate p_{min} and p_{max}. (*b*) Group hunting model: number of prey captured per individual as a function of N scaled by the number of prey captured for a solitary predator (horizontal dotted line). The largest group sizes, which offer an advantage to solitary hunting, are typically observed for short times $T \leq 1$ h and decrease for longer times (or small prey schools). (*c*) Theoretical prediction on number of fish captured per predator versus predator group size for varying hunting times T. Again, n_c is normalized by the number of prey captured by a solitary predator. Solid line shows the contour corresponding to the value of $n_c = 1$ (same as solitary hunter) and represents therefore the border of the region where group hunting is beneficial. Default model parameters in all panels if not varied or otherwise stated: $\tau_a = 2.6$ s, $\tau_a = 20$ s, $a = 5 \times 10^{-4}$, $p_{min} = 0$, $p_{max} = 1$, $S_0 = 200$.

An attacking predator has the probability p_c to catch a single prey. During each attack, there is also a chance that prey are injured. As it is unclear how the injuries are distributed among individuals, we introduce a global measure of injury in the prey school I. In the empirical data, we found a correlation between the level of injury of a school and the capture success rate (see Results). This suggests that the capture probability is a monotonically increasing function of the injury level in the prey school, $p_c = p_c(I)$ (figure 2*a*). The capture probability $p_c(I)$ can never exceed 1, thus it has to approach $p_{max} \leq 1$ for $I \to \infty$. Using this, and assuming that the global injury level increases linearly with the number of attacks, we may rewrite the probability of capture as a function of the number of attacks n_a: $p_c(I) \to p_c(n_a)$ (see figure 2*a*, and the electronic supplementary material, S2.1). We have also checked that a nonlinear dependence of I on n_a does not qualitatively affect our findings (see the electronic supplementary material, S2.2).

During the full cycle of the focal individual ('attack sequence' + 'preparation/waiting time') on average, N attacks take place, which increases the injury of the prey and therefore the capture probability. The number of attacks performed by all hunters can thus be expressed as $n_a = iN$, with i being the number of the attacks by a focal individual and N being the group size. We can calculate the expected number of prey captured by a focal predator at time T by summing over all the capture probabilities $p_c(iN)$ during its subsequent attacks i. Here, we have to take into account that the total school size imposes an upper limit on the possible number of fish caught, which is simply the average number of prey per predator S_0/N. Thus, the expected number of prey captured per predator is

$$\langle n_c \rangle(T, N) = \min\left\{ \sum_{i=0}^{n_{a,s}(T,N)} p_c(iN),\ \frac{S_0}{N} \right\}, \tag{4.1}$$

with $n_{a,s}(T, N)$ being the number of attacks performed by the focal individual in a group of N hunters, up to T (the time available for hunting). We have explored the model's behaviour with different parameters, and whereas quantitative results might differ, the overall results appear surprisingly robust and the qualitative predictions remain unchanged.

(a) Group hunt simulations

In order to test our theoretical predictions, we performed numerical simulations of a simple individual-based model. N hunters perform subsequent attacks on a school of $S(t)$ sardines, with the initial school size being $S(t = 0) = S_0$. The attack sequence of each hunter has a fixed duration τ_a. The attack may lead to a successful capture of a single prey with probability $p_c(n_a)$, which is a function of the number of all previous attacks on the school according to equation S2 in the electronic supplementary material. A simulation run is terminated when all prey are captured $S(t) = 0$. The preparation time for the next attack for each hunter is τ_r. The initial attack order is set randomly. As time progresses, the next attack is performed by the individual with the longest waiting time. For a fixed attack duration τ_a and preparation time τ_r, the initial attack order of the hunters remains unchanged. All results are obtained by averaging 100 independent simulation runs. We confirmed that our results are robust with respect to random attacks and preparation times, which introduces additional stochasticity and randomizes the order of the hunters within a single run (see the electronic supplementary material, S2.3 for details).

(b) Are there benefits for free riders?

This form of group hunting immediately raises questions surrounding the existence of producers and free riders in groups. Producers (hunters that begin attacking from the start of the hunt) generate a public good where higher levels of prey injury leads to higher capture success rates. There is the potential, therefore, for free riders (individuals that delay their attacks for some time until the school is sufficiently injured) to avoid paying the costs of attacking at the beginning of the hunt where the initial capture probability is low, and profit from the higher capture probability at later stages of the hunt.

In order to explore possible fitness trade-offs in terms of the energy expenditure versus energy uptake, we combined the stochastic individual-based model with an energetic balance equation (see the electronic supplementary material, S2.4). We consider an 'optimal' situation of being a single free rider hunting with $N - 1$ producers. The free rider refrains from

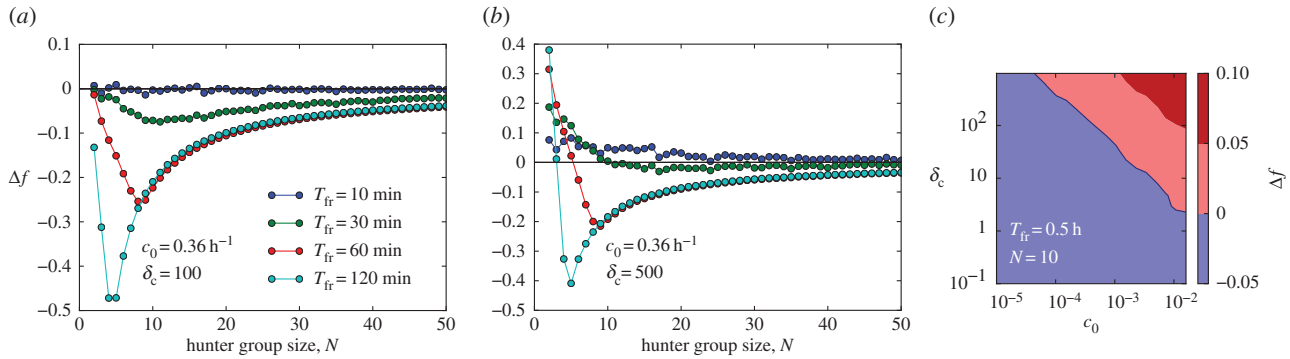

Figure 3. (*a*,*b*) Relative energy payoff difference Δf versus hunter group size N for different attack delay times T_{fr} with $c_0 = 0.0001\ s^{-1} = 0.36\ h^{-1}$ and different values of the relative energetic costs of attacks $\delta_c = 100$ (*a*) and $\delta_c = 500$ (*b*). (*c*) Δf versus c_0 and δ_c for fixed $T_{fr} = 0.5$ h and $N = 10$ (blue region indicates $\Delta f < 0$; i.e. where free riding is not beneficial). All other simulation parameters as in the main text and electronic supplementary material, S2.4.

attacking prey at the beginning of the hunt for a time T_{fr} (attack delay time). Using the energy payoffs an individual receives during the hunt, $\Delta e_{total,i}$, we can calculate the relative energy payoff of an individual f_i within a population:

$$f_i = \frac{\Delta e_{total,i} - \min(\Delta e_{total,i})}{\max(\Delta e_{total,i}) - \min(\Delta e_{total,i})}, \tag{4.2}$$

which scales between 0 for minimal energy payoff and 1 for maximal energy payoff. Here, $\Delta e_{total,i}$ is a function of a sailfish's base energy expenditure (the energy needed to simply remain with the prey school), the energy required to perform attacks, and the energy received by the captures it makes during a hunt (see the electronic supplementary material, S2.4).

In order to assess possible energy benefits of free riders, we calculated the difference between the average relative energy payoff of free riders and producers:

$$\Delta f = \langle f \rangle_{fr} - \langle f \rangle_{prod}. \tag{4.3}$$

Positive values indicate an advantage for the free riding strategy, whereas negative values indicate on average higher energy payoffs for the producers. All results discussed were obtained by simulating 100 independent runs for each group size N and attack delay time T_{fr}.

5. Modelling results

If the time available for hunting $T \to \infty$, the expected number of sardines caught $\langle n_c \rangle$ is always equal to S_0/N, and always has a maximum at $N = 1$. Hence, if time is not a limiting factor, then it is always better for a predator to hunt alone because it would not have to share prey with conspecifics. However, predators may attempt to maximize how many prey they catch per unit time (i.e. the capture rate), and not just the absolute amount of prey they catch (see the electronic supplementary material, S1.6). Under this scenario, it may not be beneficial to hunt alone. By performing numerical simulations of the model, we determined the conditions where group hunting can improve capture rates for individual sailfish. Figure 2*b*,*c* shows the number of fish captured per predator as a function of group size N, scaled by the number of prey a solitary hunter ($N = 1$) would have caught at that time (see the electronic supplementary material, figure S5 for unscaled values). In this way, we can identify the maximum group size N_m, where each individual outperforms a solitary hunter. This depends strongly on the available hunting time. While the optimal group sizes that maximize prey intake rates per hunter are small (10 when hunting times are short ($T = 0.5$ h) to 3 when hunting times are long ($T = 2$ h)), the group sizes where group hunting outweighs hunting alone are typically much larger. For $T = 0.5$ h, we observe $N_m = 70$, which then quickly decreases to $N_m = 30$ for $T = 1$ h and $N_m = 13$ for $T = 1.5$ h. Eventually, for $T \to \infty$, N_m will always converge to 1 owing to the finite size of the school. At short times T, N_m is always larger than $1 + \tau_r/\tau_a$, which is the group size at which the individual hunters start to pay temporal costs of group hunting (electronic supplementary material, figure S3). We checked how changing the initial number of sardines in the prey school, S_0, affected the conditions under which group hunting was beneficial. Smaller (or larger) initial prey group sizes shifted the hunting times so that shorter (or longer) times T made group hunters outperform solitary hunters.

We also investigated whether a free riding strategy could be beneficial for some individuals in groups. One key parameter, δ_c, predominantly controls whether there is an advantage for the free riding strategy with respect to energy payoffs (see the electronic supplementary material, S2.4 for details). δ_c is a dimensionless number that represents the effective increase of the energy expenditure during an attack relative to the base energy expenditure. A value of $\delta_c = 1$, would correspond to a doubling of the energy consumption rate during an attack sequence. An advantage for the free riding strategy can only be observed for very large values of $\delta_c \gg 10$ (figure 3*a*,*b*). Even then, this advantage only becomes significant for small hunter group sizes $N < 10$ or small attack delay times T_{fr} (figure 3*b*). Decreasing values of δ_c and the base energy consumption rate, c_0, make free riding increasingly unlikely for a given group size and hunting time (figure 3*c*). Free riding remains disadvantageous for large regions of parameter space if we allow for nonlinear dependence of the injury level on the number of attacks (electronic supplementary material, S2.2), or if there is the potential for the hunt to be interrupted (electronic supplementary material, S2.5).

6. Discussion

We have proposed a simple mechanism that can explain why sailfish hunt in groups. During a sailfish's attack, more fish are injured than are caught. Injuries can simply result as a by-product of the sailfish attempting to catch sardines, and we do not suggest that the sailfish are attempting to injure but not catch the sardines during attacks. Sailfish bills are covered in small denticles or micro-teeth [29,33], which probably facilitates this injury. Because more fish are injured than

caught per attack, this necessarily leads to more injured fish in the school as the number of attacks increases. We found a positive correlation between the injury level of a school and the rate at which prey in that school were caught. Our modelling approach demonstrated that individuals using an attack-alternation strategy while hunting in groups can achieve increased *per capita* capture rates compared to if hunting alone. This strategy does not require spatial coordination of attacks between hunters. Simply hunting in a group can improve capture success rates, even though individuals do not need to change how they attack prey whether alone, or in groups.

Like other systems [27,28], sailfish do not appear to spatially coordinate their attacks. In fact, sailfish predominantly attack the prey schools when no other individual is doing so (presumably to reduce the risk of individuals injuring themselves during attacks). This suggests that sailfish time their attacks to generally take place after another hunter has departed the prey school. Indeed, temporally coordinated attacks have been observed in other species that hunt grouping prey and have been shown to improve capture success rates [5,34]. Modelling studies have also indicated that temporally coordinated attacks act to improve capture success rates for group hunters [35]. While temporal, and not spatial coordination occurs during individuals' attacks, spatial coordination may occur in other aspects of the hunt. Sailfish herd and chase their prey, which may involve individuals moving to positions around the prey school that are dependent on the positions of other hunters. Alternatively, this herding behaviour may simply be a by-product of predators occupying empty space around the prey school, without direct coordination between predators' movements, unlike other group hunting species [25]. Fine resolution sonar data will be needed to investigate these herding dynamics further. In any case, we have demonstrated that group hunting can benefit individual sailfish without spatially coordinated attacks or individuals adopting specific hunting roles. Our results also highlight that temporal, rather than spatial coordination of attacks, may allow for simpler forms of cooperative behaviour to evolve.

We found a correlation between the level of injury of the prey school and the capture success rates of sailfish. While we interpret this as a causal link, there are other explanations which could lead to this correlation. For example, if some groups of predators are more efficient at catching prey (and as a by-product injure more sardines in the school) than other predator groups, this may lead to higher capture rates on more injured schools. Little is known about the social organization of group-hunting marine fishes [36]. The traditional assumption has been that these predators live in fission–fusion systems with little social cohesion [37]. However, novel tracking technology and interest in social networks have provided a fresh methodological and conceptual approach to this topic, producing some evidence for significant co-occurrence of particular individuals [38–40]. Understanding the social organization of sailfish groups, perhaps by identifying individuals using unique markings or sail patterns would greatly improve our understanding of this system.

More work is needed to determine the causal mechanism between increased capture success and prey injury level. While we observed injured fish breaking off from the shoal that were quickly captured, it may not always be the most injured fish in groups that are captured next. Injured fish may have reduced ability to transfer directional information about a predators' location, which in turn could affect the school's escape manoeuvres [41,42]. This may lead to non-injured fish being at greater risk in injured, versus non-injured prey schools. It is also likely that multiple attacks can have internal physiological effects on prey behaviour. For example, attacks over time are likely to reduce the energy stores in prey, reducing their ability to perform escape manoeuvres or sustain high escape speeds through fatigue. Hence sustained attacks, even without predators actively injuring their prey, could lead to increased capture success rates for group hunters [43,44]. This may explain why in other systems, prey intake rate increases as a function of group size, without predators coordinating their attacks [28]. Indeed, the attack and success rates of other marine predators that attack schooling prey are in the same order of magnitude as our study [45,46]. In theory, our model can be applied to any system where the likelihood of capturing prey increases as a function of the number of attacks of previous predators.

Cooperation through turn-taking strategies has been described in other systems, for example, in predator-inspection behaviour in fishes [47,48]. But the exploration of turn-taking has usually been assessed in dyads and the role of turn-taking is not well understood in larger groups. Indeed, turn-taking strategies in larger groups raise interesting questions regarding the potential for cheating [49]. It has previously been proposed that when hunters attack small grouping prey that cannot be shared, there is no temptation to cheat, as not participating in the hunt returns no payoffs [50]. However, this approach did not consider that it may be easier to catch prey over time as they receive injuries or become exhausted. The increase in injured prey over time can be interpreted as a public good [51], which may be susceptible to exploitation by cheaters that delay the onset of their attacks. In microbial communities with diffusing public goods, the partial monopolization of resources owing to spatial localization may promote cooperation by denying non-producers access to resources [52,53]. While such an explicit spatial effect is likely to be absent in the highly dynamic turn-taking hunting process of sailfish, a direct analogy can be drawn via the intrinsic coupling of the production of the public good and the capture of individual prey. Producers (attackers) have access to the prey school from the onset of the hunt, albeit with low initial capture probabilities. Our investigation of the potential energetic trade-offs during the hunt suggests that individuals who delay their onset of attacks (free riders) would only benefit from such a strategy if the cost of attacking was 10 times higher than simply remaining with the prey school. Future work, with observations on the behaviour of individually identifiable predators, will be needed to determine if this strategy exists. Nevertheless, opportunistic access to the prey school, combined with the by-product of injuring prey during attempted captures, can promote individual hunting success in groups. We regard this form of group hunting, which does not require explicit cooperation, as 'proto-cooperation'.

Our results demonstrate that individuals can benefit from group hunting without specific hunting roles (as in collaborative hunting), higher social organization or complex cognition. While hunting in groups potentially reduces the total amount of prey an individual predator is likely to catch, sailfish can offset this by collectively catching more prey per unit time when hunting together. This facilitative hunting method raises new questions surrounding the evolution of cooperative behaviour in group living animals.

Ethics. All research was conducted in line with the laws and legislation of Secretaría de Medio Ambiente y Recursos Naturales, Mexico.

Authors' contributions. All authors except P.R., D.S. and S.K. collected field data. J.E.H.-R. and D.S. analysed the empirical data and performed statistical analyses. P.R. designed the modelling component of the paper. All authors wrote the paper. All authors gave final approval for publication.

Data accessibility. All data accompanying this paper are available at Dryad Digital Repository http://dx.doi.org/10.5061/dryad.t9m6c [54].

Competing interests. We have no competing interests.

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