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Birds versus bats: attack strategies of bat-hunting hawks, and the dilution effect of swarming

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Abstract

Aggregation is often thought to reduce predation risk, whether through dilution, confusion, or vigilance effects. Such effects are challenging to measure under natural conditions, involving strong interactions between the behaviours of predators and prey. Here we study aerial predation on massive swarms of Brazilian free-tailed bats *Tadarida brasiliensis* by diurnal raptors, to test how the behavioural strategies of predators and prey influence catch success and predation risk. The Swainson's hawks *Buteo swainsoni* that we observed achieved high (31%) catch success without any morphological specializations for bat-hunting, but showed clear evidence of adaptive behaviour: the odds of catching a bat were increased threefold when executing a stoop or rolling grab manoeuvre, one or both of which were observed in three-quarters of all attacks. Catch success was several times higher against the column than against lone bats, so we found no evidence for any vigilance or confusion effect. Attacks on lone bats were infrequent (~10%), but were >50 times more common than the lone bats themselves. Because of their preferential targeting, the overall risk of predation was >20 times higher for lone bats. Dilution is therefore both necessary and sufficient to explain the higher survival rates of bats flying in column formation.

1. Background

Flocking, shoaling, and swarming behaviours can all serve to reduce an individual's predation risk, by shifting the burden of predation onto others, or by decreasing a predator's hunting efficiency [1-3]. The first of these mechanisms is usually called dilution, but is not merely the result of a predator sampling prey from a larger population: in fact, the relative risk of predation will only be diluted among individuals if a predator's attack rate increases less than proportionally with group size or density [1]. This might occur for a variety of reasons: for example, an itinerant hunter may be just as likely to encounter a lone individual as a group; alternatively, if predation occurs at a site where prey regularly congregate, then the risk of predation within the swarm may be diluted through marginal predation, or preferential targeting of smaller groups or lone individuals [1-3]. The second mechanism, involving a reduction in hunting efficiency, is often attributed to the confusion effect occurring when the presence of multiple prey makes it harder for a predator to catch any one individual [1, 3]. This

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may well occur in a directed chase, but a predator lunging or plunging into a dense prey aggregation need not be targeting any one individual. In such cases, hunting may be more – not less – efficient against a denser group, as is certainly the case for large pelagic predators that exploit the shoaling of their prey during engulfment [4]. It follows that flocking, shoaling, and swarming can all affect predation risk in different ways, depending on the ecological circumstances of the behaviour. Observational studies under natural conditions are therefore essential to understanding the ecology and evolution of behavioural interactions between predators and their aggregated prey.

Research on the predation of three-dimensional prey aggregations has most often been conducted on shoaling fish and flocking birds, but very large colonies of bats – some comprising more than a million individuals – occur globally, and are subject to intense depredation wherever they occur [5]. Swarming bats form a conspicuous aerial display when departing their roost sites, making them an obvious target for predatory birds. In the temperate zones, owls (Strigiformes) are the most significant avian predators of bats [6], presumably owing to the fact that both they and the bats fly mainly at night. In the tropics and subtropics, however, daytime flying by bats is a more regular occurrence. Predation by diurnal birds is therefore more prevalent in these zones; particularly where dense swarms of bats emerge from their roosts in daylight [5]. In fact, predation of bats by diurnal birds has been identified in at least 107 species of hawks, buzzards, eagles, and kites (Accipitriformes), 36 species of falcons (Falconidae), and 94 species from 28 other families, notably Corvidae [5]. Predation by – or competition with – diurnal birds is often cited as an evolutionary explanation driving nocturnality in bats [5, 6], but little is known of the underlying selection pressures.

Most avian predation of bats is opportunistic, involving hunting of bats as part of a broader diet; usually at colonies where bats swarm at dawn or dusk, but sometimes of lone bats [5]. Only one species – the bat hawk (*Macheiramphus alcinus*) – is considered morphologically, behaviourally, and ecologically specialized for hunting bats [7]. This is the only diurnal raptor that preys mainly on bats, and its unusually large gape is supposed to have evolved as an adaptation for swallowing large prey intact on the wing [7]. As the archetypal bat-hunter, bat hawks have been observed chasing lone and swarming bats [8-12], with 54% of all recorded attacks ending in a kill (Table S1). Bat hawks pursue lone bats in a tail-chase involving powered flight; usually attacking from above, but sometimes from below [5-9]. Swarming bats may also be pursued in a tail-chase, but are more commonly intercepted in a cross-stream attack launched from a series of back-and-forth glides as the swarm emerges from its roost [5-9]. In contrast, the eponymous bat falcon (*Falco rufigularis*) has no known adaptations for bat-hunting, and has a much broader diet than its name might suggest [7]. Observations of its bat-hunting behaviour are scarce, owing to the difficulty of studying a species that usually inhabits tropical forests. Bat falcons have been observed diving at individual bats – sometimes from a high perch, but more usually from flight – with a recorded success rate of just 13% [13-15]. Hunting strategy and efficiency therefore vary greatly between those species of raptor that are named for their bat-hunting behaviours, and they vary to an even greater extent across the many other birds that have been observed hunting bats opportunistically (for review, see Table S1).

Many different factors influence hunting efficiency, including environmental factors such as seasonality, meteorological conditions, or prey abundance, and individual factors such as age, experience, or hunger [16]. Here we ask what specific aspects of flight behaviour influence observed variation in the catch success of Swainson's hawks (*Buteo swainsoni*) hunting swarming Brazilian free-tailed bats (*Tadarida brasiliensis*). Bats are often characterised as slow, inefficient fliers that could be easily outpaced by a raptor, but very high flight speeds

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have been reported from the Brazilian free-tailed bat, with one recent telemetric study reporting ground speeds at least comparable to those of the fastest birds [17]. In contrast, the Swainson's hawk is an opportunistic diurnal hunter that consumes a wide variety of mainly-terrestrial mammals, reptiles, birds, and insects [18]. Predator-prey interactions have been documented between these species in at least three localities [19-21], but there have been no detailed observations of the behaviour to date. Here, we investigate how one such population of Swainson's hawks has learned to exploit a massive seasonal population of Brazilian free-tailed bats as they emerge from their maternal roost in the Chihuahuan desert. We detail the hawks' behavioural strategies and hunting efficiency over 239 attacks, testing how variation in catch success is related to variation in hunting strategy. We also test whether the swarming bats benefit from lowered predation risk through either a dilution or a confusion effect. This work represents one of the most detailed ecological studies to date of the behavioural interaction between aerial predators and moving aggregations of their aerial prey; see also [3].

2. Methods

We observed Swainson's hawks hunting Brazilian free-tailed bats at the Jornada Caves, New Mexico, USA. This remote site is located on a lava field, where a collapsed lava tube forms a connected pair of caves (Fig. 1A). The caves are home to a maternal colony of 700,000 to 900,000 individuals [22], which migrate to the area during their natal season from May to September. The bats roost during the day, emerge before dusk to fly to their feeding grounds, and return individually or in small groups towards dawn. The emerging bats form a dense horizontal stream (Fig. 1C) which climbs away from the cave, giving the appearance first of a rising column of smoke, then of distant clouds as the swarm splits into smaller groups. A local population of Swainson's hawks (Fig. 1B) hunts the emerging bats daily. The bats are subject to regular predation by great horned owls (*Bubo virginianus*) within the cave mouth, but the only other aerial predation events that we witnessed over three field seasons involved a single peregrine falcon (*Falco peregrinus*) hunting on three consecutive evenings in 2018.

(a) Behavioural observations

We recorded the hawks' hunting behaviour on 15 evenings from 01/06/18 to 24/06/18, having watched them perform the same behaviours in the two preceding years. Emergence began between 18:19h and 19:52h, and hence well before sunset, which was between 20:13h and 20:21h. The timing of the bats' emergence was quite variable, but the hawks usually appeared within a few minutes of its start, suggesting that they must have been watching the cave at a distance. The number of hawks varied through the observation period, peaking at ~20. The largest and most reliable emergence was from the South cave, and occurred every evening without exception. During the first week of observation, there were some nights on which the North cave had no bats emerging at all, probably owing to there being few bats present, but bat numbers were topped up in the second week by the arrival of new migrants. Each emergence lasted 10 to 25 mins, depending on the number of bats, and we occasionally observed a second emergence from the same cave. We measured wind speed and direction using a Kestrel 4500 Pocket Weather Tracker (Nielsen-Kellerman, PA, USA). We used the NOAA Solar Calculator to determine the time of emergence relative to sunset, and the azimuth of the sun at emergence.

We conducted focal follows using a voice recorder to document real-time observations made through 8×4 binoculars, or using a Lumix DMC-FZ1000/2500 camera (Panasonic Inc., Osaka,

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Japan; 1920×1080 pixels; 50 fps) to record video for later analysis (see Movie S1). Each observer aimed to document the entire hunting bout of one focal hawk, from first appearance to final departure. We began observing the hawks from makeshift hides, but phased these out as the birds became habituated to our presence. The hawks usually made multiple attacks during a single hunting bout, which we categorised according to: 1) approach type (level flight, or stooping dive); 2) approach direction (downstream, cross-stream, or upstream relative to swarm); 3) grab direction (above, beside, or below bat); 4) targeting strategy (lone bat, or column of bats); and 5) capture outcome (success or failure); see Box 1, Figs. 2, S1 and Movie S1. Attacks on the column sometimes involved more than one attempted grab, in which case we only recorded the direction and outcome of the final grab.

(b) Statistical analysis

In total, we observed the outcomes of 239 attacks from 64 hunting bouts lasting 2h50m (Fig. 3B), and were able to categorise 202 of these attacks fully (Fig. 3A; Table S2; Data S1). We conducted the statistical analysis in *R* version 3.6.1 [23], using the "PropCIs", "plyr", and "boot" packages (see Code S1). We report the overall sample proportions ($\hat{P}$) of attacks within each behavioural category, together with 95% score confidence intervals (CIs) calculated using Wilson's method. Because consecutive attacks within a bout are non-independent, these CIs are expected to have an actual coverage probability <95%, but we report them in preference to stating only a point estimate of the proportion. In addition to reporting the overall catch success, $\hat{P}(\mathrm{S})$, we also report $\bar{P}(\mathrm{S})$, defined as the mean proportion of successful attacks per hunting bout, which we report together with a bias-corrected and accelerated bootstrap CI computed using stratified resampling over 10^6 resamples. This statistic eliminates repeated measures within a hunting bout, but does not eliminate pseudo-replication completely, because a given individual may have been sampled repeatedly across days. Unfortunately, there was no way of identifying individuals to control for this.

To test for autocorrelation within a hunting bout, we computed the 1st order autocorrelation coefficient of the outcomes of the 175 attacks immediately preceded by another in the same hunting bout. The result ($r_1 = 0.239$) fell well outside the 95% CI for white noise (-0.148, 0.148), indicating that there were significant runs of successful or unsuccessful attacks in the data. For statistical inference, we therefore used autoregressive logistic regressions to control for this autocorrelation, concatenating the different time series across bouts. This approach introduces white noise into the lagged variable at the start of each bout, but allows us to control for autocorrelation without discarding the first attack of every bout as above. Provisional model-order selection using the Akaike Information Criterion (AIC) for pure autoregressive models from AR(0) to AR(5) supported use of a model of order AR(1) for capture outcome, AR(2) for target type, and AR(0) for approach type (see Code S1). In practice, we report only AR(1) logistic regression models here, because AR(2) offered minimal improvement over AR(1) for target type ($\Delta\mathrm{AIC} = 0.45$), and AR(1) was better supported than AR(0) for approach type when other predictors were added ($\Delta\mathrm{AIC} = 1.16$); see Code S1. We use likelihood ratio tests to assess the significance of the model factors, Wald tests to assess the significance of their different levels, and report profile-likelihood CIs for the parameter estimates.

We estimated the proportion of bats meeting the criteria for classification as lone bats in 18 frames selected from across the videos (Fig. S2). These frames were chosen as meeting the following criteria: (i) each frame recorded in a separate attack; (ii) camera zoomed out and in focus; (iii) bats near enough to see their wings; and (iv) background composed entirely of sky.

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We counted the number of lone bats in each frame manually, and estimated the total number of bats automatically using the count function in Adobe Photoshop CC2019, having binarized each image using a threshold just sufficient to make the background entirely white. Because individuals with overlapping silhouettes are counted as a single object, this method results in a conservative estimate of the number of bats in each frame (Table S2).

(c) Variation in hunting efficiency and behaviour across species

Most previous observations of birds hunting bats are anecdotal (but see: [8, 11, 16, 24-26]. In order to compare hunting efficiency across a range of species, we therefore pooled data from all published studies (Table S1). We excluded any study that only reported the number of successful attacks without also stating the total number of attacks observed. For consistency with our own reporting (see Box 1), we defined a successful attack as any in which a bat was caught, regardless of whether it was subsequently dropped or eaten. For the nine diurnal raptors and one owl with ≥15 recorded attack outcomes, we report overall catch success as a percentage, together with an approximate 95% CI calculated using the Agresti-Coull method (Table S1).

3. Results

(a) Hawks use a flexible range of behaviours to hunt swarming bats

A typical attack involved an initial approach phase, during which the hawks closed in on the swarm using slow flap-gliding along a shallow path (Fig. 2A), or a fast stooping dive from altitude with the wings tucked (Fig. 2B). Less frequently, the hawks swooped at lone bats that had become separated from the column (Fig. S1C-F). Most attacks involved either a downstream or cross-stream approach (see Fig. 2C). Each attack ended with a manoeuvre aimed at grabbing an individual bat (Fig. 2D-F). This involved pulling the wings back, while either rolling about the body axis and extending the legs horizontally, or performing a rapid pitch-up or pitch-down manoeuvre and extending the legs vertically. The legs were extended in a sharp, deliberate thrusting action. If the hawk failed to capture a bat when attacking the column, then it would typically attempt one or two further grabs. Having caught a bat, the bird would then drift away from the swarm to consume its prey on outstretched wings, tearing pieces of food from its talons (Fig. 3C).

(b) Hawks hunting swarming bats achieve high efficiency at high intensity

The hawks made a total of 239 attacks over the 10,228s duration of our focal follows, giving a mean attack rate of $\lambda = 0.023\text{s}^{-1}$ (i.e. one attack per hawk every 43s). Of the 239 attacks, 74 were successful, giving an overall catch success of 31% ($\hat{P}(\text{S}) = 0.310$; CI: 0.254, 0.371). This statistic estimates the probability that an attack drawn at random from the population will result in the capture of a bat, and therefore summarises the hunting efficiency that the bats experienced at a population level. In contrast, the mean proportion of successful attacks by bout was higher at 43% ($\bar{P}(\text{S}) = 0.434$; CI: 0.395, 0.475). This statistic estimates the expected success rate of an attacker drawn at random from the population, and therefore summarises the hunting efficiency that the hawks experienced individually. The overall catch success is

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expected to be lower than the mean proportion of successful attacks by bout, because hawks with a higher success rate will satiate sooner than hawks with a lower success rate, and therefore contribute disproportionately fewer attacks to the mean. Because most hunting bouts comprised multiple attacks (median: 3, 1st, 3rd quartiles: 2, 5), only 16 of the 64 bouts that we recorded were outright unsuccessful: on average, a hawk could therefore expect to feed on 75% of hunting bouts (CI: 63.2%, 84.0%; Fig. 3C). Moreover, as the bats were invariably consumed on the wing, individual hawks were able to catch more than one bat per bout, and did so on 25% of hunting bouts (CI: 16.0%, 36.8%; Fig. 3C). One highly-motivated hawk captured 5 bats over 15 attacks in a single hunting bout, these being the maxima on both measures.

(c) Hawks preferentially target lone bats but do not catch them more readily

The great majority of attacks targeted the column ($\hat{P}(\mathrm{C}) = 0.899$; CI: 0.853, 0.932; Fig. 3B), but the proportion that targeted lone bats ($\hat{P}(\mathrm{L}) = 0.101$; CI: 0.068, 0.147; Fig. 3B) was >50 times higher than the proportion of bats classified as flying alone (0.2% of >34,000 bats visible in 18 frames; Fig. S2, Table S3). It follows that the hawks were preferentially targeting bats that had become separated from the swarm (Fig. S2C-F). Despite their targeting preference for lone bats, the hawks' overall catch success was higher for attacks on the column ($\hat{P}(\mathrm{S}|\mathrm{C}) = 0.307$; CI: 0.248, 0.374) than for attacks on lone bats ($\hat{P}(\mathrm{S}|\mathrm{L}) = 0.130$; CI: 0.045, 0.321; see Fig. 3B), albeit not significantly so (likelihood ratio test in AR(1) logistic regression: $\chi^2(1) = 2.094$, $p = 0.148$). This makes sense, because a hawk may have several opportunities to grab a bat in a single attack on the column if its first grab is unsuccessful. In fact, the expected catch success, $E(\mathrm{S})$, of an attack involving up to k independent grabs is $E(\mathrm{S})|_k = 1 - (1-q)^k$, where q is the probability that a given grab proves successful. Treating the observed catch success against lone bats, $\hat{P}(\mathrm{S}|\mathrm{L}) = 0.130$, as an estimate of q, the expected catch success of an attack involving up to k independent grabs is statistically indistinguishable from the overall catch success for attacks on the column when $k = 3$, because $E(\mathrm{S})|_{k=3} = 0.342$ as compared to $\hat{P}(\mathrm{S}|\mathrm{C}) = 0.307$ (CI: 0.248, 0.374). Interestingly, this value of $k = 3$ coincides with the maximum number of attempted grabs that we observed in a single attack. It is still possible that the success rate of each grab might be depressed by a confusion effect in the swarm, but the data provide no evidence that the bats' swarming caused any net reduction in the hawks' hunting efficiency. On the contrary, the observed odds of success were 3 times higher when targeting the column than when targeting lone bats, though not significantly so (odds ratio: $\widehat{OR} = 2.958$; CI: 0.898, 9.672).

(d) Swarming bats benefit from a dilution effect

If hawks achieve higher catch success when attacking the swarm, how does the bats' swarming affect their odds of survival? Only 5% of the bats that we observed being captured were classified lone individuals ($\hat{P}(\mathrm{L}|\mathrm{S}) = 0.045$; CI: 0.016, 0.125). This represents a small proportion of the bats that were caught, but is >20 times higher than the proportion of the total population that we classified as lone bats (0.2% of >34,000 bats visible in 18 frames; Fig. S2, Table S3). It follows that the relative risk must have been many times greater for lone bats than for bats flying in the column. The expected risk ratio ($\widehat{RR}$) is determined as the relative catch success for attacks on lone individuals versus attacks on the column, multiplied by the preference for targeting lone bats versus bats in the column:

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$$\widehat{RR} = \frac{\hat{P}(\mathrm{S}|\mathrm{L})}{\hat{P}(\mathrm{S}|\mathrm{C})}\frac{\hat{P}(\mathrm{L})N_{\mathrm{C}}}{\hat{P}(\mathrm{C})N_{\mathrm{L}}} \tag{1}$$

where N_{C} and N_{L} are the numbers of bats flying in the column or alone, the ratio of which we will call the swarm dilution factor, $D = N_{\mathrm{C}}/N_{\mathrm{L}}$. Using Bayes' theorem to rewrite Eq. 1:

$$\widehat{RR} = \frac{\hat{P}(\mathrm{L}|\mathrm{S})}{\hat{P}(\mathrm{C}|\mathrm{S})}D \tag{2}$$

we find that $\widehat{RR} = \hat{O}D$, where $\hat{O} = \hat{P}(\mathrm{L}|\mathrm{S})/\hat{P}(\mathrm{C}|\mathrm{S})$ is the odds that the victim of a successful attack was flying alone rather than in the column ($\hat{O} = 0.048$; CI: 0.016, 0.143). The expected risk ratio for bats flying alone versus in the column would therefore have been $\widehat{RR} = 0.048D$, from which we can conclude that $\widehat{RR} > 1$ if and only if $D \geq 21$ (CI: 7, 63). Hence, as we estimate that $D > 500$ (see Table 3), we deduce that dilution is both necessary and sufficient to explain the higher observed survival rates of bats flying in the swarm.

(e) Hawks favour specific combinations of hunting behaviours

The hawks used a flexible range of hunting behaviours to execute their attacks (Figs. 3,4). The majority of attacks that we observed were made in level flight (78.7%; CI: 72.6%, 83.8%). By far the commonest behaviour that we observed (Fig. 3A) combined level flight with a cross-stream approach and a grab from the side (30.7%; CI: 24.7%, 37.4%; Fig. 4A,B). Stooping was used in 21.3% of attacks (CI: 16.2%, 27.4%), usually in combination with a cross-stream approach and a grab from above (15.8%; CI: 11.5%, 21.5%; Fig. 4A,B). To determine whether the various components of the behavioural strategies that we observed were associated statistically, we used an additive AR(1) logistic regression model to test whether the odds that an attack involved stooping were related to approach direction, grab direction, wind speed, time of emergence before sunset, or absolute angle between the wind and sun. We found no evidence that the choice of stooping versus level flight depended on any of the environmental conditions (likelihood ratio tests at $\alpha = 0.05$), so dropped these terms from the model to give a reduced AR(1) model with better statistical support ($\Delta\mathrm{AIC} = 3.33$). This model confirmed that stooping was strongly associated with grabbing from above (Fig. 4B), rather than beside (Wald test: $z = 5.70$, $p < 0.0001$) or below (Wald test: $z = 2.31$, $p = 0.021$), and also showed that flights involving a downstream rather than cross-stream approach were more prevalent in level flight than in stooping (Wald test: $z = 3.44$, $p = 0.0006$; Fig. 4A). An upstream attack was only ever used in level flight (Fig. 4A), being the least frequent approach direction (10.6% of all attacks; CI: 7.1%, 15.3%). We found no evidence that the hawks modulated their attack behaviour according to whether they were targeting the column or a lone bat, as the odds of targeting a lone bat were not significantly related to approach type (Fig. 4C), approach direction, or grab direction in an AR(1) logistic regression (likelihood ratio tests at $\alpha = 0.05$).

(f) Catch success is higher when stooping and when grabbing side-on

The observed variation in attack behaviour might reasonably be expected to influence catch success. We used an AR(1) logistic regression to test whether the odds of capture were dependent on targeting strategy, approach type, approach direction, grab direction, wind speed,

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time of emergence before sunset, or absolute angle between the wind and sun. Of these predictors, only approach type and grab direction were statistically significant, and only when each factor was entered sequentially after the other (likelihood ratio tests at $\alpha = 0.05$). The reduced AR(1) model retaining only these significant factors had considerably better statistical support than the full AR(1) model ($\Delta\text{AIC} = 9.22$), and offered substantial improvement over the corresponding pure AR(1) model ($\Delta\text{AIC} = 6.04$). The expected odds of catch success in this reduced model were 3.46 (95% CI: 1.43, 8.82) times higher in a stoop than in level flight (Wald test: $z = 2.70$, $p = 0.007$), and 3.45 (95% CI: 1.54, 8.48) times higher if the bat was grabbed from the side rather than above (Wald test: $z = 2.87$, $p = 0.004$). There was no evidence of any interaction between approach type and grab direction as predictors of catch success (Fig. 4D), and the AIC value of the model increased if the interaction was added. In summary, catch success was higher in a stoop, and higher when grabbing a bat side-on in a rolling grab manoeuvre (Fig. 4D). One or both of these behaviours were observed in 73.3% of attacks (CI: 66.8%, 78.9%), such that the most successful categories of attack behaviour were also the most frequently used. Interestingly, they were only combined in 3.0% of attacks (CI: 1.4%, 6.3%; Fig. 3A), suggesting that they represent alternative attack strategies.

(g) Hunting success across species

The overall catch success of our Swainson's hawks (31%) was similar to that of the nine other species of diurnal raptor for which ≥15 capture outcomes have been recorded previously (median catch success by species: 31%; Fig. 5). Of these nine species, only the specialist bat hawk and opportunistic red-tailed hawk had significantly higher catch success (54% and 68%, respectively), as judged from the non-overlap of their respective 95% CIs (Fig. 5).

4. Discussion

(a) Opportunistic raptors achieve high catch success against swarming bats

The Swainson's hawks that we observed achieved 31% catch success without any morphological specializations for bat-hunting. Other raptors that hunt bats opportunistically do so using a broad range of behaviours, including stooping or swooping, level pursuit, and perch hunting (Table S1). We observed a similar variety of behaviours in Swainson's hawks, although we did not observe them perch hunting, which is unsurprising given the absence of elevated perches in the vicinity. Paralleling a well-known behavioural adaptation of the specialist bat hawk [8-12], the Swainson's hawks that we observed invariably consumed their prey on the wing. This behaviour is unusual among raptors, except those like the bat hawk or hobby (*Falco Subbuteo*) specialising on smaller aerial prey. Swainson's hawks [19-21] and peregrine falcons [27] have both been reported feeding on the wing when hunting swarming bats, which may represent a behavioural specialization used when the glut of prey makes it possible to catch many in a limited time window. Interestingly, this behaviour has not been observed for red-tailed hawks, which have previously been recorded returning to a perch at the end of every attack in hunts achieving 68% catch success [24]. This exceptionally high hunting efficiency may have been driven by the emergence of juvenile bats mid-way through the observation period [24], as the red-tailed hawks' catch success was significantly lower before any juvenile bats had begun to forage (47% versus 88%). Our own observations of opportunistic bat-hunting by Swainson's hawks were made prior to the emergence of any

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juvenile bats from the maternal colony, so it is possible that a higher catch success would have been observed later in the season.

(b) Why should catch success be higher in a stooping or rolling attack?

The great majority of attacks were made in level flight (Fig. 3A), usually in combination with a grab from the side (Fig. 4B) and a cross-stream approach (Fig. 4A). In contrast, stooping was most commonly associated with a grab from above (Fig. 4B) – usually in a cross-stream approach (Fig. 4A). Stooping has not previously been recorded in Swainson's hawks attacking bats, but was deployed in one-fifth of all attacks here. Stooping often occurred at some altitude and distance from the cave, so in selecting focal individuals that were flying close to the cave, we may have underestimated the overall frequency of stooping. Remarkably, for a given grab direction, we found that stooping roughly doubled the observed catch success relative to level flight (Fig. 5). This is interesting, as a recent physics-based simulation study has shown that the catch success of model falcons is maximised against agile model prey by initiating an attack in a high-speed, high-altitude dive [28]. This is because the attacker's manoeuvrability is enhanced by the higher aerodynamic forces and lower roll inertia that result as its airspeed increases and its wings are tucked in a stoop. Our observations provide the first empirical evidence that stooping actually enhances catch success against agile prey. Moreover, grabbing the target from the side in a roll manoeuvre also roughly doubled the observed catch success relative to the alternative of grabbing from above or below in a pitch manoeuvre (Fig. 6). This presumably reflects the fact that rolling is the most natural way for a bird to turn quickly [28], and that the alternative of pitching quickly in a grab from above or below causes strong aerodynamic braking.

(c) Role of predation in bat swarming

Our observations shed new light on the selective pressures at work in the aerial predation of aggregated prey. Remarkably, we find no evidence that the very high density of the swarm causes any confusion effect leading to a measurable reduction in catch success. On the contrary, catch success was several times higher for attacks on the column than for attacks on lone bats, albeit not significantly so. This may be explained by the fact that an attack on the swarm could sometimes involve up to three attempted grabs if the first grab was unsuccessful. Paradoxically, although their expected catch success may have been reduced as a result, the hawks still targeted lone bats in preference to those flying in the column. Overall, the proportion of attacks classified as involving lone bats (~10%) was >50 times higher than the proportion of individuals classified as lone bats (~0.2%). The actual rate of attacks on lone bats may in fact have exceeded 10%, because lone bats are liable to be reported as flying with the column if silhouetted against it, but this should not cause us to underestimate the dilution effect itself, because the population of lone bats is defined similarly in all of the proportions that we compare.

A tendency toward marginal predation is expected statistically, given the larger domain of danger that individuals experience when positioned further from the swarm [1-3]. Even so, given the very low proportion of bats flying alone (~0.2%), it is unlikely that this sampling bias provides a complete explanation of the hawks' tendency to target lone bats. An alternative explanation of their observed preference for marginal predation is that it reflects the risky and

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aversive nature of flying through a dense aggregation of sharp teeth and claws – particularly for a visually-guided predator that must keep its eyes open and hence unprotected. In any case, as a result of the hawks' preferential targeting of lone bats, and accounting for their marginally higher catch success against the column, those bats which did not remain in column formation were at higher risk of capture than those which did. This higher survival rate of bats in the column is therefore attributable to a dilution effect, which we estimate should have been sufficient to enhance their overall survival rate, provided that there were at least ~20 bats flying in the column for every one individual flying alone. In practice, since there were >500 bats flying in the column for every lone bat, it follows that a dilution effect is both necessary and sufficient to explain the higher observed survival rates of bats in the column.

(d) Predator avoidance in bats

The mass emergence of the bats during daylight hours is presumably driven by their need to fly long distances to obtain food or water in this harsh desert environment. As a result, the bats experience intense predation by diurnal raptors, which we have found can expect to feed on three-quarters of their hunting bouts. Although the 74 bats whose demise we have documented here constitute a mere ~0.01% of the total population, they represent only a small fraction of the total catch. Noting that we recorded data from 64 focal follows, made over 15 evenings with up to 20 hawks present, and considering that the hawks sustain their hunting activity throughout the bats' 4 to 5-month natal season, it is likely that at least ~0.1% and perhaps up to ~1% of the bat population falls victim to the hawks every year. It is little wonder, therefore, that bats choose to fly nocturnally when they can [5, 6].

Given the benefits of dilution that we have measured, there is clearly selection pressure for individual bats to remain part of a cohesive swarm – at least in the vicinity of the cave. Away from this central place, the expected encounter rate of lone predator and prey may be so low as to make the benefits of maintaining column formation negligible, and perhaps even negative given the long detection range [29] at which their swarms are visible in the clear desert air. This may explain why the swarm retains a tight column formation on emergence, but quickly loses its coherence away from the cave. Interestingly, although the majority of bats return to the roost in darkness, a substantial number return as it is becoming light. These returning bats arrive individually or in small groups, diving vertically into the cave entrance at very high speed, and flying so fast that their wings make an audible zipping sound due to aeroelastic flutter. Although we did not observe any morning predation events, this has been witnessed at other roosts of this species [24]. We hypothesise that the bats' very high flight speed when re-entering the cave singly may reflect their perceived vulnerability to aerial predation when not in a swarm.

Evasive behaviour was observed informally during some of the attacks, with the swarm becoming visibly scattered by the attack on some occasions. Bats sense their environment using echolocation and vision, which owing to their directional biosonar [30] and forward-facing vision can result in blind zones above and behind the bat [31]. This offers a possible functional explanation for the infrequency of upstream approaches that we observed, since a downstream or cross-stream approach avoids placing the attacker within the primary visual and acoustic gaze of its target, whilst also reducing the demands on the attacker's guidance and control system [28]. Nevertheless, if evasive manoeuvres had strongly influenced catch success, then grabs from within the blind zones above and/or behind the bat ought to have had the highest success rate. Our finding that grabs were most successful when made from the side may suggest

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a trade-off between the sensory abilities of the bat on the one hand, and the manoeuvrability of the hawk on the other.

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Ethics This work has received approval from the Animal Welfare and Ethical Review Board of the Department of Zoology, University of Oxford. As an observational study, this work was not subject to approval by the Institutional Animal Care and Use Committee at Saint Mary's College.

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Data and Code Data and code implementing the statistical analysis are available through figshare: https://doi.org/10.6084/m9.figshare.11823393. The original video data are archived institutionally, and will be made available by the corresponding author upon reasonable request. Example videos are provided as Movie S1, and are available through figshare.

Competing interests We declare that we have no competing interests.

Authors' contributions CB, LK, and GT conceived the study. All authors contributed field observations. LZ and CB analysed video data. CB, LZ and GT performed statistical analysis. CB and GT wrote the paper, with input from LZ and LK. All authors commented on and approved the final version of the manuscript.

Figure 1. Study overview. (A) Aerial view of the Jornada caves. (B-C) Swainson's hawk hunting Brazilian free-tailed bats at the caves. Note the column formation of the swarm, with only a small proportion of bats flying alone.

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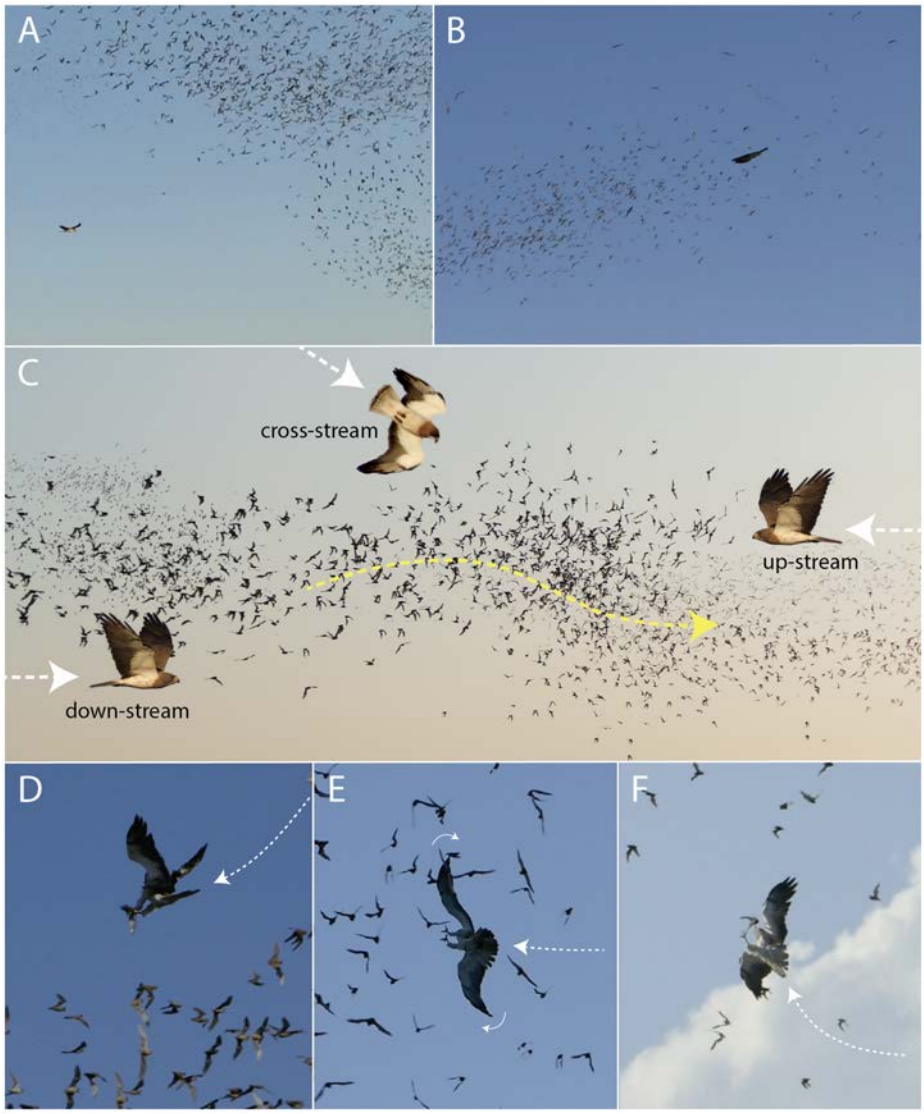

Figure 2. Examples of categorised attack behaviours. (A,B) Approach type, showing: (A) level flapping flight toward the column; (B) stooping dive into column, with tucked wings. (C) Approach direction, with composite image comprising video frame of swarm moving from left to right, superimposed with separate images of Swainson's hawks to illustrate upstream, downstream, and cross-stream approach. (D-F) Grab direction, with video frames showing: (D) grab from above: bird extending feet downwards in an overhead pitch manoeuvre; (E) grab from side: bird extending feet horizontally in a roll manoeuvre; (F) grab from below: bird extending feet upwards in a pitch-up manoeuvre from beneath. See Movie S1 for video examples.

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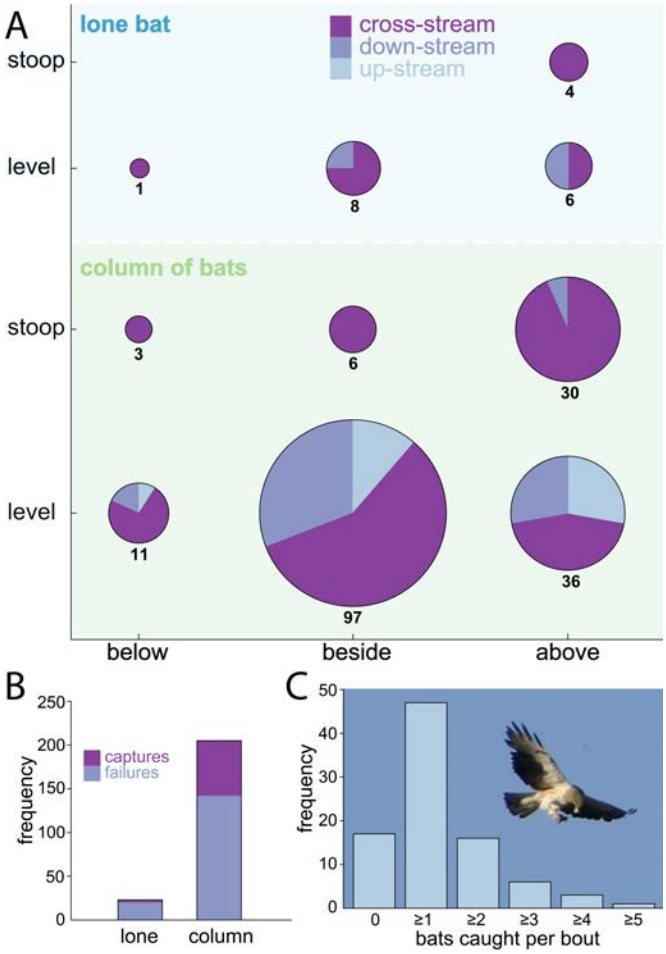

Figure 3. Behavioural strategies of bat-hunting Swainson's hawks. (A) Pie charts showing frequency of each combination of behaviours for all 202 fully classified attacks; area proportional to number of observations shown below each chart. (B) Bar chart showing number of successes and failures for all 239 attacks, grouped by targeting strategy. (C) Frequency distribution of number of bats caught per hunting bout; inset shows typical feeding posture.

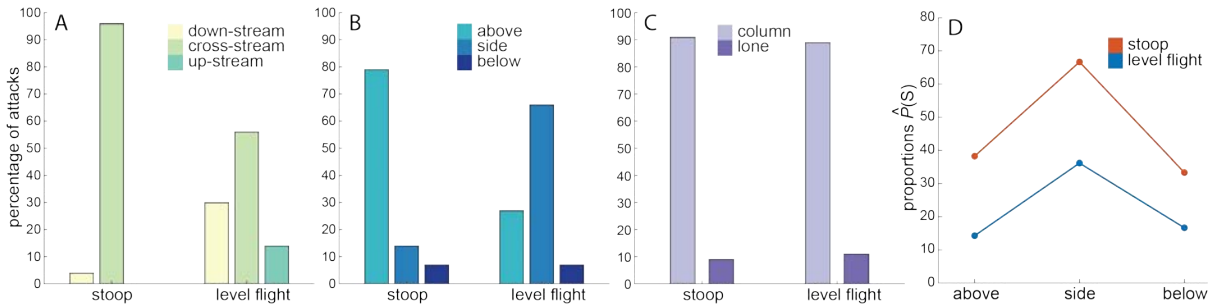

Figure 4. Behavioural interactions in bat-hunting Swainson's hawks. (A-C) Proportions of attacks involving different categories of behaviour in stooping versus level flight for (A) approach direction; (B) grab direction; (C) targeting strategy. (D) Interaction plot showing that stooping or grabbing the bat from the side both increase catch success $\hat{P}(S)$ independently.

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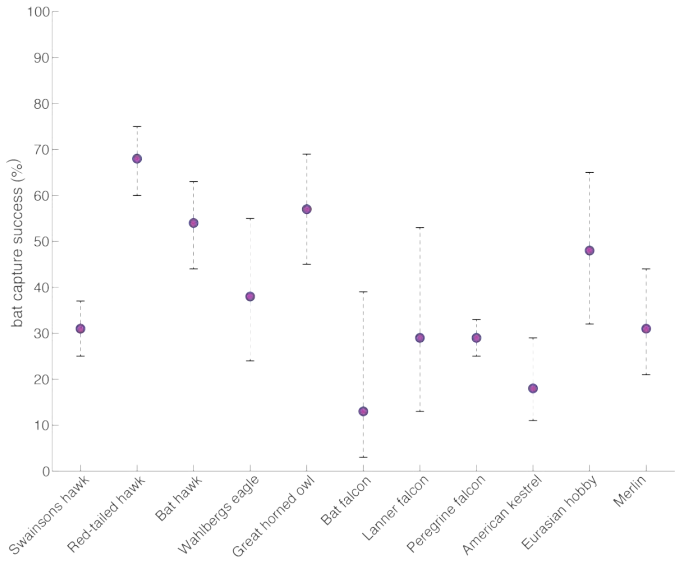

Figure 5. Recorded catch success against bats for 10 species of predatory bird with ≥15 attacks recorded in the literature (Table S1), compared with the results of this study for Swainson's hawks. Error bars display approximate 95% CIs calculated using the Agresti-Coull method.

1. approach type	**level flight:** flapping or gliding along a straight shallow flight path (Fig. 2A). **stooping dive:** fast descending flight with tucked wings, usually initiated from soaring, beginning with a sudden acceleration and steepening of the dive path (Fig. 2B).
2. approach direction	**downstream:** hawk flying in same direction as swarm (Fig. 2C). **upstream:** hawk flying in opposite direction to swarm. **cross-stream:** hawk flying in any other direction to swarm.
3. grab direction	**above:** grab initiated from an overhead position, with hawk extending feet downwards (Fig. 2D). **beside:** grab initiated side-on, with hawk extending feet horizontally (Fig. 2E). **below:** grab from beneath bat, with hawk extending feet upwards (Fig. 2F).
4. targeting strategy	**column of bats:** attack on one or more bats within a cohesive group of individuals all flying in same general direction (Fig. S2 A,B). **lone bat:** attack on bat flying >1m from edge of column, typically in a different direction to swarm (Fig. S2 C-F).
5. capture outcome	**success:** bat caught; may be dropped or eaten. **failure:** bat not caught.

Box 1. System used to classify the attack behaviours of each hawk.