

Supplementary information

Supplementary Tables

Supplementary Table 1. Comparisons between the flush-pursue hypothesis and the previously proposed hypotheses that may explain the function and evolutionary origin of the proto-wings and caudal plumage in the basal pennaraptoran theropod dinosaurs. Predictions are derived either directly from the studies in avian flush-pursuers and their prey, and from the effects/mechanisms discussed in the hypotheses proposed earlier in the literature.

HYPOTHESES' DESCRIPTIONS: Brief descriptions of the hypotheses to explain the function of proto-wings and caudal plumage in feathered dinosaurs, especially at the initial stages of the evolution of these structures in the basal taxa of pennaraptoran theropods.	PREDICTIONS: predictions of the hypotheses in terms of location and color of plumage, and in terms of specific hypothetical adaptive functions/benefits from the pennaceous surfaces on forelimbs and tail in a diversity of feathered dinosaurs from the most basal taxa of pennaraptoran theropods with relatively small proto-wings and caudal plumage to more derived cursorial taxa with more developed proto-wings and caudal plumage (the benefits may depend on the size/the surface area of the pennaceous feathers on forelimbs and tail).				Main literature (reference numbers in the reference list)	CONSISTENCY BETWEEN BASAL PENNARAPTORS AND PREDICTIONS. Here we evaluate the question: <i>do the observed characteristics of the basal pennaraptoran theropods match the predictions from the hypothesis?</i> [Y/N/x; stand for Yes/No/Irrelevant]. We narrow down the scope to only the most basal taxa of pennaraptoran theropods to focus on the very initial evolution of proto-wings and caudal plumage.						
	P1: Location of the proto-wings and sex dimorphism (SD)	P2: Presence of the caudal plumage and sex dimorphism (SD)	P3: Bright patches on the forelimb and caudal plumage and sex dimorphism (SD)	P4: Predicted functions/traits/evolutionary trends of forelimbs (F:), neck/head (N:), hindlimbs (H:), and tail (T:) that benefit the hypothetical mechanism.		P1	P2	P3	P4(F)	P4(N)	P4(H)	P4(T)
MECHANISMS RELEVANT TO FORAGING: Flush-pursue (FP) hypothesis: It involves three elements, two of which are shared with other hypotheses: (1) visual flush-displays with feathered forelimbs/tails combined with (2) the use of feathered forelimbs/tails in drag and/or lift generation for pursuing prey (as in the less explored function of turning in the “flapping proto-wing hypothesis” and as in “leaping” hypothesis) or for attacks on flushed prey immediately after it lands on a substrate (similar to “pouncing” hypothesis), followed by (3) the use of quick forward moves of head on a long neck as extant birds do, or possibly the use of hindlimbs or even forelimbs to capture the prey, possibly aided by the use of proto-wings as insect nets or to immobilize the prey in the final stages of pursuing.	Distal; no SD	Yes; no SD	Yes; no SD	F: Increase the surface area for more substantial display and for better assistance in motor control during pursuing and capturing the prey during prey’s escape flights/jumps or immediately after prey landing; forelimb movements within anatomical constraints of early pennaraptorans sufficient for the efficient looming display function. Developing more conspicuous folding and more extreme expansion of forelimbs is beneficial for the flush-element of FP strategy by the increasing size contrast between display/no display. The development of stronger forelimb musculature for lifting/spreading and folding/closing forelimbs is beneficial, especially for drag-based motor control during Pursue element of FP.	This paper	Y	Y	Y	Y	Y	Y	Y
				N: Long-neck with skeleton/musculature that permits quick forward movement during a strike on prey increases the efficiency of the last stages of pursuits after prey (attacks), visual system and inner ear promote visuomotor coordination and morphology of jaws/beaks helps in precise striking at and grasping the prey.								
				H: Hindlimb that aids in fast-running locomotion during pursuits after flushed prey will increase the efficiency of FP foraging.								
				T: Long-tail with distal surface benefits FP foraging; increase in surface area at the distal end of a long-tail that is moved forward above the body or sidewise with fan-like opened feathered surface for more vigorous display and for better assistance in motor control during pursuing and capturing the prey during prey’s escape flights/jumps or immediately after prey landing.								

<p>Flapping proto-wing hypothesis (running while flapping): Use distal proto-wings to create weak lift that may help in running, as shown in a study of robotic <i>Caudipteryx</i>, and possibly also while pursuing prey. However, as the real <i>Caudipteryx</i> might have possessed a narrower range of forelimb movement than tested in the robot, the hypothesized beneficial effect during running might have been small in the basal pennaraptoran theropods</p>	Distal; no SD	Irrelevant; no SD	Irrelevant	<p>F: Increase the surface area for better assistance in motor control during flapping; the powerful muscle, connected to the humerus, for sufficient stability in flapping. Efficient flapping requires the distal proto-wings to generate a strong power stroke ¹⁰, and an increase in the range of forelimb movements would benefit the “flapping proto-wing” mechanism; those benefits may be relatively small for small proto-wings on forelimbs with a restricted range of movements.</p> <p>N: Irrelevant.</p> <p>H: Hindlimb that aids in cursorial locomotion.</p> <p>T: long and stiff tail assists in motor control (balance and quick turns) during running.</p>	13,14	Y ^a	x	x	Y	x	Y	Y
<p>Leaping hypothesis (leaping for prey): The core of the hypothesis is the use of distal proto-wings to create lift that may help in jumping/leaping after flying prey and in landing, and the use of the tail to control the body balance during a jump. If those pennaceous surfaces are relatively small, then the direct effect on leap trajectory is expected to be small but the effect on body orientation (pitch and roll) during leaps still remains noticeable and may increase the efficiency of foraging as evaluated in theoretical calculations (9).</p>	Distal; no SD	Yes; no SD	No; higher crypticity is expected for effective foraging.	<p>F: Extended forelimbs; increase surface area at the distal location for better assistance in orientational control during leaping and landing.</p> <p>N: Irrelevant.</p> <p>H: Hindlimb morphology and musculature that aids in running/jumping/landing.</p> <p>T: Increase surface area at the distal location on the long tail moved forward above the body or sideways with a fan-like opened feathered surface for better assistance in motor control body axes during running.</p>	11	Y	Y	N	Y ^b	x	Y	Y
<p>Pouncing Proavis model (pouncing on prey): It assumes that dinosaurs specialize in ambush from elevated sites (e.g., trees; this element is shared with the “gliding” hypothesis) and in pouncing prey; the use of proto-wings and caudal plumage for drag-based control of body orientation and trajectory during descent. Drag-based control is available to any animal with an aerodynamic surface, irrespective of whether that surface creates useful lift. Hence, even small proto-wings might be used to control the body orientation.</p>	Distal; no SD	Yes; no SD	No; higher crypticity is expected for effective foraging.	<p>F: Increase surface area at the distal location for better assistance in orientational control and a strong power stroke; use of proto-wings for assistance in balance during descending up its prey.</p> <p>N: Irrelevant.</p> <p>H: Hindlimb morphology and musculature for climbing and balancing at elevated sites.</p> <p>T: Tail with distal surface additional assistance in maintaining the body balance at elevated places during ambushing ⁹⁴ and descending.</p>	10	Y	Y	N/x ^c	Y	x	N ^d	Y
<p>Insect net hypothesis: Use distal proto-wings in catching the escaping prey in a manner reminiscent of the use of insect nets to catch prey by sweeping it against the prey.</p>	Distal; no SD	Irrelevant; no SD	No; higher crypticity is expected for effective foraging.	<p>F: Large and continuous trapping surfaces (feathered area) will increase the efficiency of insect net foraging; the powerful ventral adductor muscles are needed to activate the large insect nets (feathered forelimbs). Long forelimbs with long forward reach are needed for the function.</p> <p>N: Long neck will increase visual range by elevation of the head; for the efficiency of chasing prey, especially visuomotor coordination helps in precise strikes to snare the prey.</p> <p>H: Hindlimb that aids in fast-running locomotion while pursuing prey will increase the efficiency of insect net foraging.</p> <p>T: long and stiff tail assists in motor control (balance and quick turns) during running.</p>	8,9	Y/N ^e	x	N	Y/N ^e	Y	Y	Y

<p>Immobilizing large prey: Use of proto-wings to maintain the body balance while grasping prey using the feet, and use of forelimbs with proto-wings to restrict the prey's escape route ("mantling" the prey) while tearing the prey with jaws or a beak. The presence of sharp hook-shaped claws on hindlimbs has been proposed as an indicator of this type of prey handling in large predatory dinosaurs that hunt large prey, and it is less likely in smaller theropods without this type of claws.</p>	Distal; no SD	Yes; no SD	Irrelevant	<p>F: Increase surface area for better assistance in motor control (e.g., capable of generating relatively strong power stroke) during flapping; the powerful muscle, connected to the humerus, for sufficient stability in flapping.</p> <p>N: Long neck enabling a dinosaur to reach with its head down between the feet to handle the prey that is held by the hindlimbs and additionally immobilized by the forelimbs.</p> <p>H: Hindlimb anatomy for hooking and grasping prey. Hook-shaped claws for maintaining a grip on large prey.</p> <p>T: Long tail with feathers for better assistance in balance during stability flapping and also predation (immobilizing prey).</p>	12	Y	Y	x	Y	Y ^f	N ^g	Y
<p>MECHANISMS NOT RELEVANT TO FORAGING:</p> <p>Wing-assisted incline running: Flapping proto-wings to create aerodynamic forces while running on inclined substrates.</p>	Distal; no SD	Yes; no SD	Irrelevant	<p>F: Increase surface area for generating more vital aerodynamic forces during flapping; wide range in the pitch of shoulders to create more vital aerodynamic forces. The expected traits (e.g., supracoracoideus muscle) are inconsistent with the traits in the basal pennaraptorans^{7,95}.</p> <p>N: Irrelevant.</p> <p>H: Hindlimbs for upward running, climbing, and balancing at elevated sites. However, even without special anatomical adaptations, the upward running would still be possible, and the hypothesis is feasible even in the absence of special hindlimb adaptations.</p> <p>T: Tail with distal surface additional assistance in balance during climbing and aerial descending⁹⁶.</p>	16,96,97	Y	Y	x	N	x	Y	Y
<p>Gliding: It assumes that dinosaurs specialized in jumping from elevated sites (e.g., trees; this element is shared with the "pouncing <i>Proavis</i>" hypothesis) and in gliding. Use of surface area of proto-wings for gliding to reach a particular destination.</p>	Proximal; no SD	Yes; no SD	Irrelevant	<p>F: Increase surface area at a proximal location for better performance in gliding¹⁰, and control and stability during gliding.</p> <p>N: Irrelevant.</p> <p>H: Hindlimb morphology and musculature for climbing and balancing at elevated sites, with feathers for assistance in gliding.</p> <p>T: Caudal plumage surface helps lift or stability during gliding^{13,14,98}.</p>	9,17	N	Y	x	N	x	N	Y

Brooding: Use forelimb and tail feathers in nestling and chick-rearing, especially heating or shading the eggs and/or chicks.	Distal; no SD	Yes; no SD	Irrelevant	<p>F: An optimal posture [the extended forelimbs as in a brooding <i>Citipati</i> specimen ⁹⁹] to cover their nest</p> <p>N: Irrelevant.</p> <p>H: An optimal posture [crouching like in a brooding <i>Citipati</i> specimen ⁹⁹] to incubate their eggs and/or to protect their chicks.</p> <p>T: Tail with feathers may help additionally assistance in brooding and/or shading their eggs and/or chicks.</p>	15	Y	Y	x	Y	x	Y	Y? ^h
Intraspecific displays: Use of forelimb and tail feathers in visual displays; distinct color patch and/or ornament feather (e.g., elongated feather) benefits display function; high within-species differences (e.g., sexual dimorphism, ontogenetic variation) are expected.	Distal; yes SD	Yes; yes SD	Present; yes SD	<p>F: Increase surface area at distal and conspicuousness for a more vivid display; movements for assistance in displays.</p> <p>N: Cranial ornamentations for a more vivid display.</p> <p>H: Irrelevant.</p> <p>T: Increase surface area and conspicuousness for a more vivid display; movements for assistance in displays.</p>	18,19,80,81	Y	Y	Y ⁱ	Y	x	x	Y

^a – although experiments with a robotic dinosaur based on *Caudipteryx* suggested a weak beneficial effect of proto-wings in running as described in the “flapping proto-wings” hypothesis, it is not certain if such an effect was sufficiently strong in the real *Caudipteryx*, whose anatomy suggests to us that the range of flapping movements might have been narrower than that one used in the robot.

^b – The basalmost pennaraptoran theropods possessed relatively small pennaceous surfaces on forelimbs and tails. Therefore, the direct effect on leap trajectory is expected to be small but the effect on body orientation (pitch and roll) during leaps is predicted to be sufficient to increase the efficiency of foraging as evaluated in the theoretical calculations (9).

^c – Color patterns are only known for a few species of the basalmost pennaraptoran

^d – Arboreal lizards have distinct curved claws for climbing; those types of claws are not seen in the basalmost pennaraptorans. Therefore, we decided to put “N” for the prediction P4(H)

^e – distal location of proto-wings is consistent with the “insect net” hypothesis, but short forelimbs are not consistent with it: many pennaraptoran theropods and earlier dinosaurs seem to have relatively short forelimbs, especially relative to their long necks that can reach forward extensively during prey capturing; this effectively precludes the use of short forelimbs as efficient insect net. Additionally, the relatively narrow range of forelimb movements permitted by the anatomy, as reviewed in Supplementary Materials: Methods Part 1-3, will decrease the functionality of proto-wings as “insect nets”.

^f – The relatively long necks would have allowed the basal pennaraptoran theropods to reach down to the prey kept by feet, and strong hard beaks might have been easily used to handle/tear the prey

^g – The presence of special hook-shaped claws only applicable for large predatory dromaeosaurids, but not for the basalmost pennaraptorans that are the focus of our study. Hence, “N” for prediction P4(H).

^h – As the tails are feathered, and multiple brooding specimens have been found only in pennaraptorans and not in non-pennaraptoran dinosaurs we suggested the Y? category for the prediction P4(T).

ⁱ – no sexual dimorphism is currently definitively accepted for any dinosaurs - mostly due to the small sample size and lack of adult specimens. However, the intraspecific signaling function can also be performed by bright patches in monomorphic species

Supplementary Table 2. The number of grasshoppers that showed escape behavior at each test distance and the number of grasshoppers that did not respond to experimental conditions even at 20 cm in experiment 1. We treated grasshoppers with three experimental conditions: (1-1) play motor sound without forelimbs' movement; (1-2) without proto-wings; (1-3) with proto-wings. *P* values for each pair of experimental conditions were (1-1) vs. (1-2) < 0.001, (1-1) vs. (1-3) < 0.0001, (1-2) vs. (1-3) < 0.0001 (Dunn's test with Bonferroni correction). The number in parentheses indicates the number of grasshoppers tested with the displaying robot placed directly in front or behind them. Additional analysis of the data set excluding these points showed similar results [Dunn's test with Bonferroni correction, *P* for (1-1) vs. (1-2) < 0.001, (1-1) vs. (1-3) < 0.0001, (1-2) vs. (1-3) < 0.0001]. This table concerns Fig. 2b and Extended Data Fig. 9.

Test distance	Experimental condition		
	Motor sound play without movement (1-1)	Flushing movement without the proto-wings (1-2)	Flushing movement with the proto-wing (1-3)
100	0	0	1
80	0	1 (1)	0
60	0	0	9 (2)
40	0	9 (2)	15 (2)
20	2 (1)	10	17 (8)
No response	44 (6)	23 (7)	3 (1)
Total	46 (7)	43 (10)	45 (13)

Supplementary Table 3. The number of grasshoppers that showed escape behavior at each test distance and the number of grasshoppers that did not respond to experimental conditions even at 35 cm in experiment 2. We treated grasshoppers with three experimental conditions: (2-1) without proto-wings; (2-2) with proto-wings presented in proximal; (2-3) with proto-wings presented in distal. *P* values for each pair of experimental conditions are (2-1) vs. (2-2) = 0.02, (2-1) vs. (2-3) < 0.0001, (2-2) vs. (2-3) < 0.0001 [Chi-square test with Bonferroni correction]. The number in parentheses indicates the number of grasshoppers tested with the displaying robot placed directly in front or behind them. Additional analysis of the data set excluding these points showed similar results [Chi-square test with Bonferroni correction, *P* for (2-1) vs. (2-2) = 0.02, (2-1) vs. (2-3) < 0.0001, (2-2) vs. (2-3) < 0.001]. This table concerns Fig. 2c.

Test distance	Experimental condition		
	Without proto-wings (2-1)	Proto-wings located in proximal (2-2)	Proto-wings located in distal (2-3)
70	0	0	0
35	1	10	27 (1)
No response	29 (2)	20 (1)	3
Total	30 (2)	30 (1)	30 (1)

Supplementary Table 4. The number of grasshoppers that showed escape behavior at each test distance and the number of grasshoppers that did not respond to experimental conditions even at 40 cm in experiment 3. We treated grasshoppers with two experimental conditions: (3-1) plain black proto-wings; (3-2) white-patched proto-wings. P value for (3-1) vs. (3-2) < 0.01 (Chi-square test with Yates' continuity correction). The number in parentheses indicates the number of grasshoppers tested with the displaying robot placed directly in the front or behind them. Additional analysis of the data set excluding these points showed similar results. (Chi-square test with Yates' continuity correction, $P < 0.001$). This table concerns Fig. 2d.

Test distance	Experimental condition	
	Plain black proto-wings (3-1)	White-patched proto-wings (3-2)
60	0	0
40	3 (1)	15 (1)
No response	27	15 (4)
Total	30 (1)	30 (5)

Supplementary Table 5. The number of grasshoppers that showed escape behavior at each test distance and the number of grasshoppers that did not respond to experimental conditions even at 60 cm in experiment 4. We treated grasshoppers with three experimental conditions: (4-1) without caudal plumage; (4-2) caudal plumage was present as the same size in the fossil; (4-3) caudal plumage twice the area of (4-1) was present. *P* values for each pair of experimental conditions were (1-1) vs. (1-2) = 0.02, (1-1) vs. (1-3) < 0.0001, (1-2) vs. (1-3) < 0.01 (Dunn's test with Bonferroni correction). The number in parentheses indicates the number of grasshoppers tested with the displaying robot placed directly in the front or behind them. Additional analysis of the data set excluding these points showed similar results [Dunn's test with Bonferroni correction, *P* for (4-1) vs. (4-2) = 0.03, (4-1) vs. (4-3) < 0.0001, (4-2) vs. (4-3) < 0.01]. This table concerns Fig. 2e.

Test distance	Experimental condition		
	Without caudal plumage (4-1)	Normal-sized caudal plumage (4-2)	Twice-sized caudal plumage (4-3)
80	0	3	11
60	0	10	16
No response	30 (2)	35 (1)	21
Total	30 (2)	48 (1)	48

Supplementary Table 6. The number of recorded DCMD spikes in response to the “without proto-wings” animation for three individuals. The spike numbers are summed up in every bin (25 ms). We recorded the neural response six times for each individual. This table concerns Fig. 2g; Extended Data Fig. 8a2–a4.

Bin order (25 ms)	Individual 1						Individual 2						Individual 3					
	Record number						Record number						Record number					
	R1	R2	R3	R4	R5	R6	R1	R2	R3	R4	R5	R6	R1	R2	R3	R4	R5	R6
1	4	3	4	3	3	3	5	9	5	4	7	6	4	5	4	4	4	3
2	2	4	1	2	2	2	2	1	2	2	0	2	4	3	4	2	3	3
3	0	0	0	0	0	0	3	2	3	1	2	2	5	3	4	3	3	2
4	2	2	2	0	1	2	3	2	1	2	1	0	2	3	2	2	3	2
5	2	0	0	1	1	1	2	2	2	0	0	1	0	0	1	1	0	0
6	0	0	0	1	2	0	1	0	0	0	0	0	0	2	0	1	1	0
7	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	2	1	2	1	1	0	2	2	1	3	1	1	0	1	0	0	0	0
16	1	1	1	0	3	0	1	1	1	1	1	0	1	0	0	0	1	0
17	1	2	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
18	0	1	0	1	1	1	3	1	0	0	1	0	0	0	0	0	0	0
19	0	0	1	0	2	0	0	0	1	0	2	0	0	0	0	0	0	0
20	1	1	1	0	0	1	0	2	0	0	0	2	1	0	0	0	0	0
21	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Supplementary Table 7. The number of recorded DCMD spikes in response to the “with distal proto-wing” animation for three individuals. The spike numbers are summed up in every bin (25 ms). We recorded the neural response six times for each individual. This table concerns Fig. 2g; Extended Data Fig. 8a2–a4.

Bin order (25 ms)	Individual 1						Individual 2						Individual 3					
	Record number						Record number						Record number					
	R1	R2	R3	R4	R5	R6	R1	R2	R3	R4	R5	R6	R1	R2	R3	R4	R5	R6
1	7	6	5	6	6	6	8	5	7	5	6	6	8	8	8	7	7	7
2	6	7	8	6	6	7	2	1	3	1	1	0	5	4	2	3	2	2
3	3	0	0	0	0	0	1	0	2	1	2	1	4	5	3	3	2	1
4	0	0	0	0	0	0	2	1	1	1	0	1	3	2	3	1	1	1
5	0	0	0	0	0	0	0	0	0	2	0	0	1	0	1	1	0	0
6	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
12	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
13	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1
14	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
15	1	0	1	2	2	0	1	2	2	0	2	1	1	1	1	0	1	1
16	4	3	4	4	4	5	1	1	1	1	1	1	2	1	0	1	1	1
17	3	3	3	2	5	2	2	2	1	0	2	2	2	1	1	1	1	1
18	2	3	3	3	2	4	2	1	1	0	2	2	3	2	0	1	2	0
19	2	2	2	2	2	2	4	1	1	0	1	0	1	1	1	1	1	0
20	0	0	0	1	0	1	1	0	0	0	0	0	3	0	1	0	1	0
21	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary Table 8. Estimated possible angular ranges (min value – max value) in *Caudipteryx*'s forelimb. The ranges were inferred from the nearest group [more primitive (*Acrocanthosaurus*) and advanced species (*Bambiraptor*)]. Details are described in Methods part 3. This table concerns Extended Data Fig. 4.

Angle	Theropod species		
	Primitive species: <i>Acrocanthosaurus</i> ⁶⁸	Advanced species: <i>Bambiraptor</i> ⁶⁷	Model (intermediate) species: <i>Caudipteryx</i>
Shoulder (S)	-19° – 144°	2° – 123°	-19°~2° – 114°~123° = <i>Acrocanthosaurus</i> ~ <i>Bambiraptor</i> – <i>Acrocanthosaurus</i> ~ <i>Bambiraptor</i>
Elbow (E)	104° – 159°	55~59° – 127~136°	55° – 136° = <i>Bambiraptor</i> Maybe it could fold up to 30° ¹⁰⁰
Wrist (W)	?	104° – 167°	0° – ~180° = can fold like current birds – cannot be fully unfolded due to its joint structure, < 180°
Lifting (L)	?	~88°	? – 88° = maximum value in <i>Bambiraptor</i> <i>Caudipteryx</i> group could not raise the arm horizontally due to its joint structure

Supplementary Table 9. The number of recorded DCMD spikes in response to the “looming circle” animation for three individuals. The spike numbers are summed up in every bin (25 ms). We recorded the neural response two times for each individual at the beginning and at the end of recording neurophysiological responses. This table concerns Extended Data Fig. 8c.

Bin order (25 ms)	Individual 1		Individual 2		Individual 3	
	Record number		Record number		Record number	
	R1	R2	R1	R2	R1	R2
1	0	0	0	0	0	0
2	1	1	0	0	0	0
3	0	0	0	0	1	0
4	0	0	0	0	0	0
5	0	0	0	0	0	0
6	0	0	0	0	0	0
7	0	0	0	0	0	0
8	0	0	1	0	0	0
9	0	0	2	0	1	1
10	0	0	0	0	0	0
11	0	0	0	2	0	1
12	0	0	0	0	0	1
13	0	0	0	0	0	0
14	0	0	0	0	0	1
15	0	0	0	0	0	0
16	0	0	0	0	0	0
17	0	0	0	1	0	0
18	0	0	0	0	0	0
19	0	0	0	0	0	0
20	0	0	0	0	0	0
21	0	0	0	0	0	0
22	0	0	1	0	0	0
23	0	0	0	0	0	1
24	0	0	0	0	0	0
25	0	0	0	0	0	0
26	0	0	0	0	0	0
27	0	0	1	0	1	0
28	0	0	0	0	0	0
29	0	0	0	0	1	1
30	0	0	1	0	0	0
31	1	2	1	0	1	1
32	2	0	0	1	3	1
33	0	1	2	0	1	1
34	1	1	3	1	5	4
35	3	2	4	1	4	4
36	3	5	3	3	5	6
37	5	5	3	4	7	7
38	7	6	3	5	3	7
39	6	3	0	3	5	6
40	5	1	1	2	4	6

Supplementary Notes

Note 1

List of all the families marked in Extended Data Fig. 1 as “confirmed” (pink dots) and “suspected” (blue dots) visual flush-pursuers

Here we briefly describe the type of evidence available regarding flush-pursue foraging of these species, and we provide links to movie clips with examples of displays.

Visual flush-display foraging (using visual stimuli to make prey move/escape) is the most common, and we focus here only on this type. However, it has to be noted that some birds in several families use non-visual flush strategies that work through tactile stimuli on the prey and cause prey to become visible and available for attacks. Examples are the Scaly Thrush [*Zoothera dauma*¹⁰¹] and the Herring gull [*Larus argentatus*¹⁰² cited in¹⁰³].

About the visual flush-pursue foraging, it must be noted that the same or similar visual displays used in flush-display foraging may also be used as an element of antipredator reactions (e.g., as signals of vigilance) or in social interactions. We tried to minimize the possibility of an error involving the classification of social signals as flush-pursue displays by critically evaluating the literature to focus only on displays during solitary foraging activity without other individuals present nearby (as much as it can be confirmed). Additionally, we excluded situations in which the bird might have felt threatened (by a predator, observer, or birdwatcher using predator calls or “pishing” sounds to attract the birds). The numbers identifying the links refer to the numbers put on the schematic phylogeny in Extended Data Fig. 1. It is not a complete list. We list below all the families marked in Extended Data Fig. 1. For some families, we do not have a clip with bird behavior, but we present the professional literature statements/results on which the classification is based. The list below serves only as an overview of visual display behaviors during foraging. A complete phylogenetic analysis of displays’ evolutionary history for flush-pursue foraging will be addressed in a separate paper⁹³.

Also note that flush-pursuers use various foraging methods, including the flush-pursue strategy; no species uses the flush-pursue strategy solely.

Classification:

Confirmed flush-pursuers (marked with *) are species with evidence that illustrates the link between visual displays and pursuing prey during foraging (“solid evidence of F-P”). If a family includes at least one confirmed flush-pursuer, it is also marked with the asterisk (*; marked with pink dots in Extended Data Fig. 1). If a family contains multiple flush-pursuer species, then some examples have been listed here.

Suspected flush pursuers (marked with ^) are actively foraging species (i.e., not sit-and-wait predators) with clear evidence for the use of displays during solitary foraging (i.e., excluding cases of possible communication among members of a foraging group), but with weaker professional-literature-based evidence for direct links between the display and pursuing prey albeit video evidence suggesting the link may exist in Macaulay library or on YouTube, and so on. All these species perform wing and/or tail displays of various characteristics in the absence of other individuals and in the context of foraging, which suggests the suspected function of flushing/disturbing prey. However, in some cases, other functions have also been suggested (e.g.,

signaling vigilance to predators), while flush-pursue was not clearly rejected (e.g., in Motacillidae).

The list below includes only one to several species per family, and a comprehensive review of all avian species that include the flush-pursue foraging strategy among all the foraging strategies of a species will be a subject of a separate review paper. Nevertheless, this brief list below clearly illustrates that many bird families include species that use flush-pursue foraging. The species are grouped by family, and families are ordered counterclockwise on the circular representation of the phylogenetic tree in Extended Data Fig. 1. Fifteen families are classified as containing “confirmed” flush pursuer(s), and 16 families are classified as containing “suspected” flush-pursuer(s). While some of the suspected flush-pursuers may use wing-flicking or other continuously repeated displays as signals of vigilance (interspecific communication is less likely because we attempted to include information about the behavior of solitary birds only) rather than in foraging or in addition to foraging context, the evidence for some species in the “suspected” category clearly points to the flush-pursue foraging. However, even if we discard all information about “suspected” flush-pursuers, we still end up with 15 families with confirmed flush-pursuers. Those families are distributed in different parts of the phylogenetic tree, indicating multiple independent origins of flush-pursue foraging in birds (Extended Data Fig. 1).

The detailed reconstruction of the ancestral states and evolutionary transitions between non-flush-pursue foraging styles and flush-pursue foraging will be the subject of quantitative phylogenetic analyses in the future⁹³.

List of families with confirmed (*) and suspected (^) flush-pursuers:

*Pluvianidae

*Egyptian plover (*Pluvianus aegyptius*)

From the Birds of the World species account¹⁰⁴: “*catching flying insects on the run (these sometimes flushed by bird running with wings slightly spread).*”

Turnicidae

^Black-breasted Buttonquail (*Turnix melanogaster*)

From the Birds of the World species account: “*Sometimes shades litter with outstretched wings while scratching.*” Scratching refers to activity performed during solitary foraging. It potentially may indicate that visual stimulus from outstretched wings affects the prey, although it may also serve to increase the visibility of the prey in the shadow of the wings.

*Cuculidae

*Greater roadrunner (*Geococcyx californianus*)

From the Birds of the World species account⁵⁰: “*Frequently flashes white spots visible on open wings to startle or flush prey.*”

Link 1) <https://www.youtube.com/watch?v=qmXGDWkZSek>, © Kat Avila, uploaded on 4th October 2017; in this clip, the species uses relatively simple wing opening and closing movements during foraging.

*Striped Cuckoo (*Tapera naevia*) uses its alulae in flush-pursue foraging¹⁰⁵.

Link 2) <https://macaulaylibrary.org/asset/300506951>

Link 3) <https://macaulaylibrary.org/asset/201222491>; the species uses alulae spreading and folding movements during foraging in these clips.

Eurypygidae

^Sunbittern (*Eurypyga helias*)

Link 4) <https://birdsoftheworld.org/bow/species/sunbit1/cur/multimedia?media=video;ML201989021IBC1149920>; this clip shows the species using one wing as if to affect the behavior of prey, maybe by affecting the direction of the prey escape/move, which is followed by an attack. However, we cannot exclude the possibility that this asymmetric display's function was to simply provide shadow to the area where the prey may be located.

***Trogonidae**

***Malabar Trogon (*Harpactes fasciatus*)**

It has been described that this species uses a flush-pursue strategy to flush prey out from hiding places and then pursue the prey¹⁰⁶.

Acanthisittidae

^Rifleman (*Acanthisitta chloris*)

From the Birds of the World species account¹⁰⁷: “*Restless forager along trunks and branches; wings constantly flicked.*”

Pittidae

^Ornate Pitta (*Pitta concinna*)

Link 5) <https://macaulaylibrary.org/asset/201662871>; in this clip, the species spreads its wings during foraging and then apparently pounces on prey. As pittas are challenging to observe among the thick undergrowth of their natural habitats, no more evidence corroborating or rejecting the use of flush-pursue foraging in this taxon is available at the moment.

***Oxyruncidae**

***Tawny-breasted Flycatcher (*Myiobius villosus*)**

From the Birds of the World species account¹⁰⁸: “*droops wings, often pivots, uses flush-and-chase strategy.*”

***Tyrannidae**

***Golden-faced Tyrannulet (*Zimmerius chrysops*)**

This species has been mentioned using the flush-pursue strategy¹⁰⁹.

From the Birds of the World species account¹¹⁰: “*Actively hops, tail often cocked slightly above horizontal.*”

***Thamnophilidae**

***Dot-winged Antwren (*Microrhophias quixensis*)**

This species has been confirmed to use flush-pursue foraging¹¹¹.

Link 6) <https://macaulaylibrary.org/asset/200781261>; in this clip, the species flicks its wings during foraging through the foliage.

***Rufous-backed Stipplethroat (*Epinecrophylla haematonota*)**

This species has been confirmed using flush-pursue foraging¹¹¹.

216 ***Furnariidae**

217 ***Plain-brown Woodcreeper (*Dendrocichla fuliginosa*)**

218 The flush-pursuing with wing-flashing displays behavior has been noted by observers¹¹²: “*Plain-*
219 *brown Woodcreepers frequently use wing-flashing when prey stops and is concealed. The bird*
220 *moves to the trunk where prey disappeared and briefly flashes one wing widely along the surface*
221 *of the trunk. On slender trunks the bird may simultaneously sidle and peer around the trunk from*
222 *the opposite direction, so that it will run into prey fleeing the wing.*”

223 ***White-chinned Woodcreeper (*Dendrocincla merula*)**

224 The flush-pursuing with wing-flashing displays behavior has been observed¹¹²: “*I recorded*
225 *successful wing-flashing to flush prey by a White-chinned Wood-creeper at Cashibococha,*
226 *Peru.*”

227 ***Tawny-winged Woodcreeper (*Dendrocincla anabatina*)**

228 As in the White-chinned woodcreeper, the flush-pursuing with wing-flashing displays behavior
229 has been noted¹¹²: “*Tawny-winged Woodcreepers flash the wings even more frequently than do*
230 *Plain-brown Woodcreepers. Perhaps the conspicuous tawny wing patches of the Tawnywing and*
231 *the yellow undersides of the wings of all three species are adaptations for flushing prey.*”

232 ***Rhipiduridae**

233 ***White-browed Fantail (*Rhipidura aureola*)**

234 From the Birds of the World species account¹¹³: “*Flushes prey by restlessly twisting and turning*
235 *along branches and tree trunks, flicking wings open and fanning tail.*”

236 Link 7) <https://www.youtube.com/watch?v=ifxkGriCaXM> © Shirishkumar Patil, uploaded on
237 22nd April 2014; the species spreads its tail and flicks wings in this clip.

238 ***Willie-wagtail (*Rhipidura leucophrys*)**

239 From the Birds of the World species account¹¹⁴: “*Forages mostly by flycatching, flush-pursuit*
240 *and gleaning.*”

241 Link 8) <https://www.youtube.com/watch?v=6B0YdC1FxBE> © oceanbirds1, uploaded on 24th
242 July 2015; the species flush prey by fanning/wagging tail and flicking wings in this clip.

243 ***White-throated Fantail (*Rhipidura albicollis*)**

244 Link 9) <https://macaulaylibrary.org/asset/201032211>; the species shows tail fanning and wing
245 dropping during foraging in this clip.

246 ***Monarchidae**

247 ***Blue-headed Crested-Flycatcher (*Trochocercus nitens*)**

248 From the Birds of the World species account¹¹⁵: “*Moves actively, with tail held fully fanned and*
249 *wings spread and drooped. Rapidly beats wings, or stretches wings wide and twists tail, to*
250 *disturb prey; snaps up insects in air in short sally or circular descending flight.*”

251 ***African Paradise-flycatcher (*Terpsiphone viridis*)**

252 The flush-pursuing with fan-fail displays behavior has been observed¹¹⁶.

253 ***Stenostiridae**

254 ***Yellow-bellied Fairy-fantail (*Chelidorhynch hypoxanthus*)**

255 From the Birds of the World species account¹¹⁷: “*Prey flushed by fluttering, and captured in*
256 *aerobatic sallies.*”

257 ***African Blue Flycatcher (*Elminia longicauda*)**

258 From the Birds of the World species account¹¹⁸: “*Actively forages in canopy, with wings held*
259 *half-drooped and tail continually spread.*”

Link 10) <https://macaulaylibrary.org/asset/201957981>; in this clip, the species droops wings and spreads tail.

Paridae

^Yellow-browed Tit (*Sylviparus modestus*)

From the Birds of the World species account¹¹⁹: “*Restless, including nervous wing-flicking.*”

Link 11) <https://macaulaylibrary.org/asset/201403521>; the species constantly flicks wings. in this clip.

***Scotocercidae**

***Chestnut-capped Flycatcher (*Erythrocercus mccallii*)**

From the Birds of the World species account¹²⁰: “*dislodges insects by flicking wings and making wide sweeps with tail spread; also makes short dashing flights in pursuit of insects.*”

Link 12) <https://macaulaylibrary.org/asset/201274401>; the species flicks wings, spreads tail, and pivots its body in this clip.

Phylloscopidae

Some species in this family flick wings during foraging nearly constantly, and it has been suggested¹²¹, however not fully proven, that this may flush prey that is subsequently pursued. While flush-pursuing is possible and has not been entirely rejected, the behavior and bright colors in Phylloscopidae may be under strong selection for communication¹²². Examples of wing-flicking:

^Common Chiffchaff (*Phylloscopus collybita*)

From the Birds of the World species account¹²³: “*Frequently dips tail when foraging.*”

Link 13) <https://macaulaylibrary.org/asset/201574941>; the species flicks its wings fast and moves its tail on the vertical axis in this clip.

^Willow Warbler (*Phylloscopus trochilus*).

Link 14) <https://macaulaylibrary.org/asset/201189341>; the species flicks its wings fast on the ground in this clip.

^Yellow-browed warbler (*Phylloscopus inornatus*)

Link 15)

https://macaulaylibrary.org/asset/201155071#_ga=2.79597201.406411207.1661192359-1542159533.1661192358; the species flicks its wings while foraging, but observer seems to imitate the sound of an owl in this clip.

Pycnonotidae

^Fischer's Greenbul (*Phyllastrephus fischeri*)

From the Birds of the World species account¹²⁴: “*Flicks tail and wings.*”

^Northern Brownbul (*Phyllastrephus strepitans*)

From the Birds of the World species account¹²⁵: “*Flicks wings tail constantly, both when foraging and when perched.*”

Acrocephalidae

^Upcher's Warbler (*Hippolais languida*)

From the Birds of the World species account¹²⁶: “*Waving tail to the sides, flicks wings rapidly while foraging, and sometimes stretches one wing straight out.*”

Cisticolidae

^Chestnut-throated Apalis (*Apalis porphyrolaema*)

From the Birds of the World species account¹²⁷: “While foraging, often sways body from side to side, with wings held drooped, and tail erect and fanned, and flicked sideways, in manner of a monarch-flycatcher (*Monarchidae*), which family contains confirmed flush-pursuers.”

^Black-collared Apalis (*Oreolais pulcher*)

From the Birds of the World species account¹²⁸: “Wagging its raised tail from side to side.”

^Cricket Warbler (*Spiloptila clamans*)

From the Birds of the World species account¹²⁹: “Tail continuously rotated and flirted.”

^Common Tailorbird (*Orthotomus sutorius*)

From the Birds of the World species account¹³⁰: “Hopping with tail held cocked and flicked from side to side.”

Link 16) <https://macaulaylibrary.org/asset/201469261>; the species flicks its wings and hops with cocked tail in this clip.

Pnoepyidae

^Scaly-breasted Cupwing (*Pnoepyga albiventer*)

From the Birds of the World species account¹³¹: “Frequently flicks its wings while foraging.”

Link 17) <https://macaulaylibrary.org/asset/339321481>; the species flicks its wings in this clip.

Timaliidae

^Golden Babbler (*Cyanoderma chrysaeum*)

Link 18) <https://macaulaylibrary.org/asset/201405711>

Link 19) <https://macaulaylibrary.org/asset/201976161>; the species actively move and flicks its wings in these clips.

Leiothrichidae

^Streaked Laughingthrush (*Trochalopteron lineatum*)

Link 20) https://www.youtube.com/watch?v=z_jAwj2ZFhc, © Shrikant Kelkar, uploaded on 10th August 2016; in this clip, the species flaps its wings lightly on the ground.

*Sittidae

*Velvet-fronted Nuthatch (*Sitta frontalis*)

From the Birds of the World species account¹³²: “Vigorous wing-flapping observed, apparently an attempt to flush insects from face of tree trunks.”

Link 21) <https://macaulaylibrary.org/asset/426344141>, the species spreads its wings and rapidly folds it in this clip.

Poliophtilidae

^Blue-grey Gnatcatcher (*Poliophtila caerulea*)

From the Birds of the World species account¹³³: “Moves tail constantly, which may flush unseen prey.”

Link 22) <https://macaulaylibrary.org/asset/330549521>; the species swings and rapidly moves its tail in the vertical axis in this clip.

Tichodromidae

^Wallcreeper (*Tichodroma muraria*)

Link 23) <https://macaulaylibrary.org/asset/723326>; the species spreads and folds its wings fast on the rock during foraging for prey that seems to be pecked from the substrate suggesting a possible role of flicking in revealing prey's presence to the bird, however, the suggested function of flicking in professional literature, based on observations only, is "signaling" in this clip.

*Mimidae

*Northern mockingbird (*Mimus polyglottos*)

Its flush-display consists of stereotypically performed hitches and pauses¹³⁴. See also Supplementary Note 2.

Link 24) <https://www.youtube.com/watch?v=boZz0ECyYEQ> © Linzy's Vids, uploaded on 17th October 2016.

Muscicapidae

^Rufous-tailed scrub robin (*Cercotrichas galactotes*)

Link 25) <https://macaulaylibrary.org/asset/201189121>

Link 26) <https://macaulaylibrary.org/asset/201956191>

Link 27) <https://macaulaylibrary.org/asset/200888551>

Link 28) <https://macaulaylibrary.org/asset/201291911>; the species uses its wings and tail movements simultaneously during foraging in these clips.

^Black Scrub-Robin (*Cercotrichas podobe*)

Link 29) <https://macaulaylibrary.org/asset/215171291>; the species moves on the ground while spreading its tail and wings. It uses wings and tail separately and sometimes uses both in this clip.

Motacillidae

^Gray Wagtail (*Motacilla cinerea*)

Link 30) <https://macaulaylibrary.org/asset/201514801>; the species wags its tail while foraging in this clip. Flushing prey was not rejected as a possible function of wagging, but it may be a signal of vigilance against predators¹³⁵.

*Thraupidae

*Guira Tanager (*Hemithraupis guira*)

This species uses the flush-pursue strategy¹⁰⁹. But there is no detailed description of the display characteristics.

*Parulidae

*Slate-throated Redstart (*Myioborus miniatus*) hops and pivots its body through foliage while spreading its tail and wings²⁰.

Link 31) <https://macaulaylibrary.org/asset/201955691>; the species spreads its wings and tail, combined with body pivoting and hopping in this clip.

*Painted Redstart (*Myioborus pictus*) uses tail and wing spreading and also body movements (e.g., pivoting) during foraging^{2,82,136}.

Link 32) <https://macaulaylibrary.org/asset/464937>; the species spreads its wings and tail, combined with body pivoting and hopping in this clip.

*Collared Redstart (*Myioborus torquatus*)

402 From the Birds of the World species account¹³⁷: “*sometimes advancing through foliage or along*
403 *branches with the wings drooped and the tail fanned, exposing the white outer rectrices; it*
404 *pursues small insects that are flushed by its approach.*”

405 Link 33) <https://macaulaylibrary.org/asset/201828251>; the species spreads its wings and tail in
406 this clip.

Note 2

Is the Northern Mockingbird a flush-pursuer? – the illustration of issues with research approaches to determine if a display is used for flush-pursue foraging.

This species exhibits wing-flashing behavior during walking or running on the ground. The behavior consists of stereotypically performed hitches and pauses. A long time ago observers proposed that it may be used for flushing or disturbing the prey. Among those, Hailman¹³⁴ provided quantitative data clearly suggesting that the function of this behavior is startling insects. However, some papers [for example¹³⁸] argued that the behavior has a different function (e.g., territorial display, startling predators). None of the authors have considered the natural possibility that display may serve multiple functions as recently documented for wing-flicking¹³⁹. Only the paper by Hailman¹³⁴ contained variables that can indeed be used to correctly evaluate the hypothesis that the probability of a pursue-attack after a wing display is more significant than without a wing display, and the data are consistent with the flush-pursue hypothesis.

Correct variables must be used in quantitative analyses. The variables should be constructed such that it is possible to differentiate attacks after the display from attacks that were not preceded by the display [e.g., in the manner used by Jablonski et al.² or Mumme et al.²⁰]. However, except data by Hailman¹³⁴, none of the papers about wing-flash displays by the Mockingbird have contained those variables. The best example is the relatively recent quantitative analyses by Hayslette¹⁴⁰ that were based on variables describing bouts of foraging rather than focusing on the consequences of movements with and without display. However, these variables extracted from the videos of foraging birds did not allow us to evaluate the flush-pursue hypothesis precisely. For example, the variables might have been affected by a hypothetical situation when the birds increase the use of wing-flashing to increase foraging efficiency in conditions of a relatively poor foraging rate leading to a negative relationship between total foraging rate in a bout of foraging and wing-flash display frequency in a bout even though a wing-flash display might have still increased the chance of pursuit after disturbed prey. This outcome is possible in a situation when birds modify the use of wing-flashing according to food availability. In this situation a negative relationship between rate of displays and rate of prey pursuits does not mean that the display does not help in foraging.

Nevertheless, despite the incorrect variables, Hayslette¹⁴⁰ concluded that wing displays might be beneficial for foraging because “*wing-flashing may improve foraging efficiency by allowing northern mockingbirds to assess prey mobility or defensive ability.*” Finally, our own unpublished personal observations show that not only the wing displays are used in flush-pursuit foraging, but that occasionally a bird can use one wing only to apparently direct the prey escape in the desired direction [a phenomenon documented in prey of the Painted redstarts^{136,141}] for an efficient pursuit and capture, similar to the use of one wing by the Sunbittern (*Eurypyga helias*) in the clip “ML201989021” at

https://macaulaylibrary.org/asset/201989021#_ga=2.78496017.406411207.1661192359-1542159533.1661192358

Note 3

Additional description of the Flush-pursue hypothesis

Multiple lineages of feathered dinosaurs reached powered flight before the true Aves^{6,142}, but the early proto-wings were proportionately too small to be used for powered flight⁷. Multiple interrelated functions might have led in a concerted manner, for example, in the context of predatory behavior, to the situation that initiated the origin of the true powered flight. Here we explore a previously overlooked function of dinosaurian proto-wings and tails by focusing on the flush-pursue foraging of extant birds. The function of flushing the prey in the flush-pursue foraging might have played an essential role in these evolutionary processes leading to the evolution of flight (the *Flush-Pursue* hypothesis).

According to this hypothesis, the self-reinforcing cycle of natural selection for traits (here: proto-wings and caudal plumage, and the associated anatomical adaptations to quick runs, leaps, and fast maneuvers) that increase adaptation to both functions, (1) flushing and (2) pursuing/capturing, can start with the flush-enhancing colors and movements of tail and/or forelimbs, and with an increase of forelimb surface area through the growth of non-pennaceous feathers, pro- and post-patagia, or membranes (as in Scansoriopterygidae and Pterosauromorpha). Also, the process of self-reinforcing evolution may later lead to an increase in the area and stiffness of those surfaces (for example, by replacing the non-pennaceous with the pennaceous feathers) needed for the efficient drag-based and/or lift-based control of the pursuits and leaps after prey, as well as using forelimbs to handle the prey after capture, as already suggested in several existing hypotheses (Supplementary Table 1). We also consider a possibility that the colors and feathery surfaces might have initially developed for non-foraging purposes according to some of the already existing hypotheses (Supplementary Table 1) and that, subsequently, they started being used in flush-pursue foraging, which exposed them to the natural selection pressure that causes co-evolutionary reinforcement of adaptations that serve the two aforementioned main functions associated with this type of foraging (flushing and pursuing/handling prey) and create pre-adaptations to the subsequent evolution of wings and avian flight. Hence, we propose that the comprehensive “flush-pursue” hypothesis does not contradict many already existing hypotheses but may provide the grounds to propose a network of hypothetical mechanisms that enhance each other.

The pennaceous proto-wings appeared in relatively small theropods³¹ that might have included small arthropod prey in their diet²⁸ even though feathery body cover was common across a wide range of body sizes, including large carnivores⁵⁸. It is generally consistent with the previously proposed foraging-related hypotheses (Supplementary Table 1) but not so much with the other hypotheses. For example, socio-sexual displays were likely present in dinosaurs across a wide range of body sizes. However, the drag-based and lift-based control of pursuing, maneuvers, and leaps after prey was invoked in several foraging-related hypotheses (Supplementary Table 1), and the *Flush-pursue Hypothesis* appears aerodynamically more feasible in small theropods (e.g., for quick switching direction during pursuing; Supplementary Table 1). Flush-pursue provides an additional hypothetical explanation for the occurrence of proto-wings in the smaller theropods that might have included arthropods in their diet. Flush displays are an exceptionally efficient predatory strategy toward prey such as arthropods whose visual and neural system precludes them from precisely evaluating of the distance to predator, predator speed, size, or type²¹. It leads to the critical role of simple looming-sensitive circuits in triggering the escapes in those prey animals, and this simplicity is exploited by flush-pursue

predators^{21,44}. The occurrence of the flush-pursue strategy primarily insectivorous or omnivorous birds, but not among purely carnivorous ones, is entirely consistent with this view, and it explains why within the framework of the flush-pursue hypothesis, the proto-wings are expected to have evolved in the smaller rather than larger carnivorous theropods. Similar miniaturization in the pterosaur ancestry¹⁴³ suggests that flush-pursue foraging might have played a role there too.

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