RESEARCH ARTICLE

Jumping mechanisms and strategies in moths (Lepidoptera)

Malcolm Burrows* and Marina Dorosenko

ABSTRACT

To test whether jumping launches moths into the air, take-off by 58 species, ranging in mass from 0.1 to 220 mg, was captured in videos at 1000 frames s^{-1}. Three strategies for jumping were identified. First, rapid movements of both middle and hind legs provided propulsion while the wings remained closed. Second, middle and hind legs again provided propulsion but the wings now opened and flapped after take-off. Third, wing and leg movements both began before take-off and led to an earlier transition to powered flight. The middle and hind legs were of similar lengths and were between 10 and 130% longer than the front legs. The rapid depression of the trochantera and extension of the middle tibiae began some 3 ms before similar movements of the hind legs, but their tarsi lost contact with the ground before take-off. Acceleration times ranged from 10 ms in the lightest moths to 25 ms in the heaviest ones. Peak take-off velocities varied from 0.6 to 0.9 m s^{-1} in all moths, with the fastest jump achieving a velocity of 1.2 m s^{-1}. The energy required to generate the fastest jumps was 1.1 µJ in lighter moths but rose to 62.1 µJ in heavier ones. Mean accelerations ranged from 26 to 90 m s^{-2} and a maximum force of 9 *g* was experienced. The highest power output was within the capability of normal muscle so that jumps were powered by direct contractions of muscles without catapult mechanisms or energy storage.

INTRODUCTION

Many insects from a wide range of orders have evolved diverse structural specialisations of their body that enable rapid and powerful jumping movements. These range from the very long hind legs of bush crickets (Burrows and Morris, 2003), through complex catapult mechanisms in fleas (Bennet-Clark and Lucey, 1967), froghoppers (Burrows, 2006) and locusts (Bennet-Clark, 1975), to unique arrangements of gears in planthoppers that ensure synchrony of leg movements (Burrows and Sutton, 2013). A number of underlying reasons for jumping can be proposed because the environments in which insects live are complex, diverse and often dangerous. First, jumping increases the speed with which an insect can escape from predators of all sizes and thus improves its chances of survival. Jumping propels an insect quickly away from the approach of a grazing herbivore, or a tiny parasitic wasp and to a distance outside the gaze of a hungry bird. Second, for an insect that is itself a predator, jumping enables pouncing movements on prey. Third, jumping provides the most efficient way of navigating through a complex environment of branches and leaves; a gap of a certain distance can most quickly and efficiently be crossed by a targeted jump. Finally, jumping enables take-off into flight by providing the initial impetus before the wing movements start to generate lift and forward momentum. Jumping also ensures that large wings are not damaged during their first depression movements by contact with the ground or plant upon which the insect was standing.

Lepidoptera are amongst those insects that can have large wings. Analyses of the complex movements of the wings at take-off into flight by butterflies (Sunada et al., 1993) indicate that the forces produced by the wings alone are insufficient to achieve take-off (Bimbard et al., 2013). The implication is that the propulsive movements of the legs in jumping contribute the necessary additional force.

Most moths are also adept at launching into flight, but a few species that live in exposed windy places such as Californian sand dunes (Powell, 1976) or at high elevations on the Hawaiian islands (Medeiros, 2008) have reduced wings or no wings at all (they are brachypterous). As a means of dispersal or as escape from predators they launch themselves into the air by jumping. The movements of the legs, which are not described, propel these moths for distances of about 10 cm or ten body lengths (Medeiros and Dudley, 2012). Jumping is also reported, but not analysed, in some winged moths and is suggested to have evolved approximately 20 times in Lepidoptera (Sattler, 1991). Could this indicate that jumping is widespread in this order, perhaps even providing a common mechanism for both winged and brachypterous species to launch themselves into the air or move rapidly?

This paper analyses the take-off mechanisms of winged moths to determine how the necessary propulsive forces are produced by asking the following questions. Do propulsive movements of the legs generate jumps and are these movements also used when launching into flight? Are there different strategies in which the legs and wings are used either separately or in combination with one another? Which of the legs might propel jumping and what is the sequence of action of their joints?

RESULTS
Body shape

Body mass and length varied greatly across the 58 species of moth from 13 lepidoteran families that were analysed; the smallest moth studied was a laburnum leaf miner, *Leucoptera laburnella*, which had a mass of 0.1 mg and a body length of 2.7 mm and the largest was a light arches, *Apamea lithoxylaea*, with a mass of 220 mg (2200 times heavier) and a body length of 22 mm (8 times longer). Selection of the moths for study reflected the method of capture – attraction to lights – and excluded the collection of heavier British moths. The basic features of the body plan and leg structure relevant to jumping and launching into flight were nevertheless similar in all moths analysed. These general features are described in the following paragraphs of this section and are presented in Table 1 for nine species belonging to five families.

The middle and hind legs were of similar length to each other but were, depending on the species, between 10 and 130% longer than the front legs. The ratio of leg lengths expressed relative to the front

Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK.

*Author for correspondence (mb135@hermes.cam.ac.uk)

Table 1. Body form of moths

	Body mass (mg)	Body length (mm)	Hind leg, femur (mm)	Hind leg, tibia (mm)	Ratio of leg lengths			Hind leg length	
					Front	Middle	Hind	% of body length	Length (mm)/body mass$^{1/3}$ (mg)
Oecophoidae									
Hofmannophila pseudospretella (N=7) brown house-moth	5.4±0.9	9.1±0.6	2.7±0.2	4.9±0.3	1	1.4	2.1	132	6.9
Tortricidae									
Acleris sparsana (N=3) ashy button	6.3±1.4	7	2.3±0.2	3.6±0.4	1	1.9	2.3	131	4.9
Epiphyas postvittana (N=3) light brown apple	7.7±0.3	7	2.9±0.2	4.5±0.2	1	1.7	2.2	152	5.4
Crambidae									
Crambus pascuella (N=3) grass veneer	11.9±3.4	9.2±0.6	3±0.1	4.7±0.2	1	1.6	1.6	134	5.3
Udea olivalis (N=2) olive pearl	19.1±5.5	10.8±0.3	3.1±0.3	5.7±0.4	1	1.7	1.6	137	5.5
Geometridae									
Idaea seriata (N=3) small dusty wave	4.6±1.4	6.8±0.2	3±0.3	2.2±0.4	1	1.2	1.1	141	5.8
Camptogramma bilineata (N=3) yellow shell	14.6±2.7	10.3±0.3	4.4±0.5	4.6±0.4	1	1.7	1.7	134	5.7
Xanthorhoe fluctuata (N=3) garden carpet	17.4±0.3	10	3.8	4.9±0.2	1	1.8	1.7	129	5
Noctuidae									
Apamea lithoxylaea (N=2) light arches	220.9±13.7	18.3±0.3	6±0.9	8.6±0.1	1	1.8	1.8	130	3.9

Body mass and length, and lengths of the hind femora and tibiae in 9 species belonging to 5 families of moths are means±s.e.m. The ratio of leg lengths is given relative to the front legs. *N* indicates the number of individuals from which the measurements were taken. The moths are arranged according to family and then mass.

legs thus ranged from 1:1.2:1.1 (front:middle:hind) to 1:1.9:2.3 in the different species. The hind legs were between 30 and 50% longer than the body length (excluding the wings).

In all moths the coxae of the three pairs of legs were closely apposed to each other at the longitudinal midline of the body, as illustrated by the example of *Acleris schalleriana* (Fig. 1A). Along the antero–posterior axis of the body the middle and hind pairs of legs were close to each other, whereas the front pair of legs was located more anteriorly. This implies that thrust of the middle and hind legs will be delivered through the same restricted region of the thorax, while the thrust of the front legs will be applied more anteriorly. The coxae of the front legs pointed more laterally while those of the middle and hind legs pointed more posteriorly. The small trochantera allowed the middle and hind legs in particular to be rotated (levated) forwards and dorsally about the coxae. Little rotation was possible between the trochanter and femur of the middle and hind legs, so that depression and levation of a trochanter about a coxa swung a whole leg upwards and forwards, or downwards and backwards. The middle and hind tibiae had regions with dense, long hairs and in the example of *Acleris schalleriana* there was a pair of prominent spines on the hind femur close to the articulation with the tarsus and a second more proximal pair (Fig. 1B). The increased length of the middle and hind legs was due largely to longer tibiae and femora compared with the front legs (Fig. 1B). The joint between the tibia and tarsus and between each joint of the tarsus had rows of long hairs which would be displaced when the tarsus was in contact with the ground.

Kinematics of the jump

All jumps by the 58 species of the moths analysed were propelled by rapid movements of the middle and hind pairs of legs acting together. Three strategies of jumps were recognised in these species. First were those jumps in which movements of the middle and hind legs provided all the propulsive forces for take-off whilst the wings remained folded over the body and did not move. In

some of the smaller species the wings remained folded even when the moth became airborne, so that the whole jump from the start of the propulsive movements through to landing was entirely
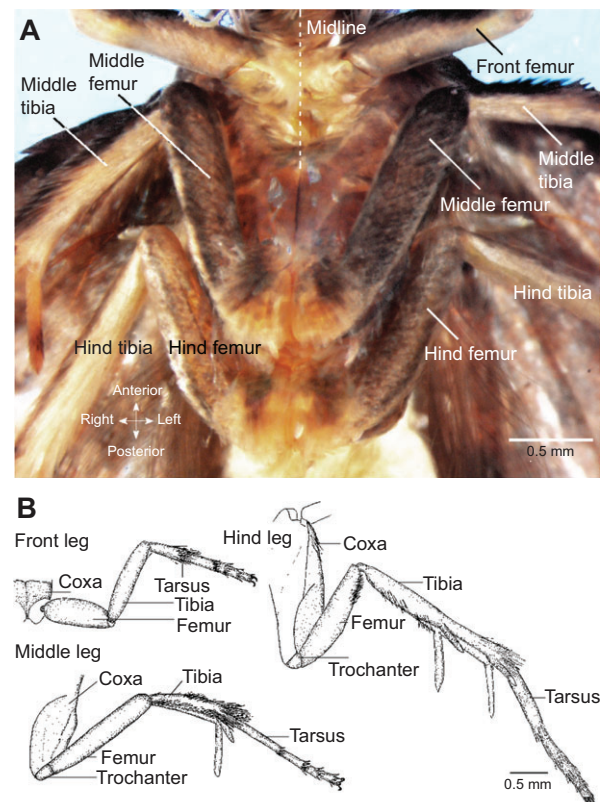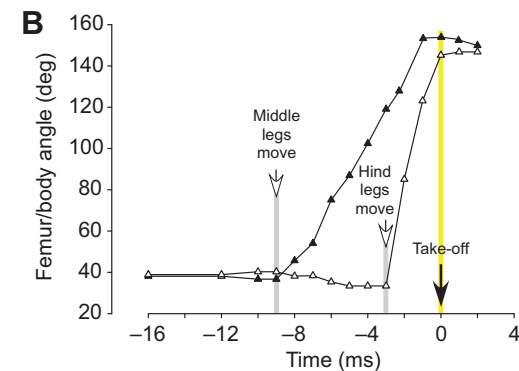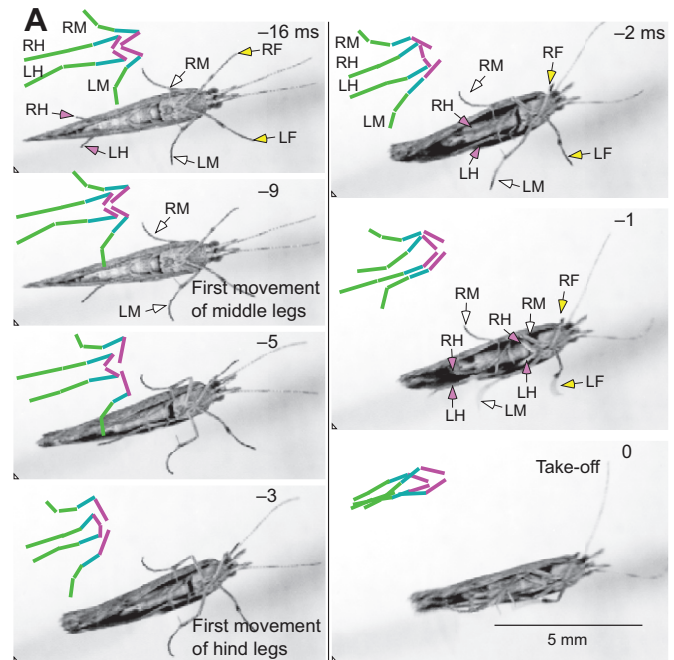

Fig. 1. Structure of the legs in the viburnum button moth *Acleris schalleriana*. (A) Ventral view of the thorax to show the proximal segments of the three pairs of legs and their articulations with the thorax. (B) Drawings of the left front, middle and hind legs to show the relative lengths and structures of their parts.
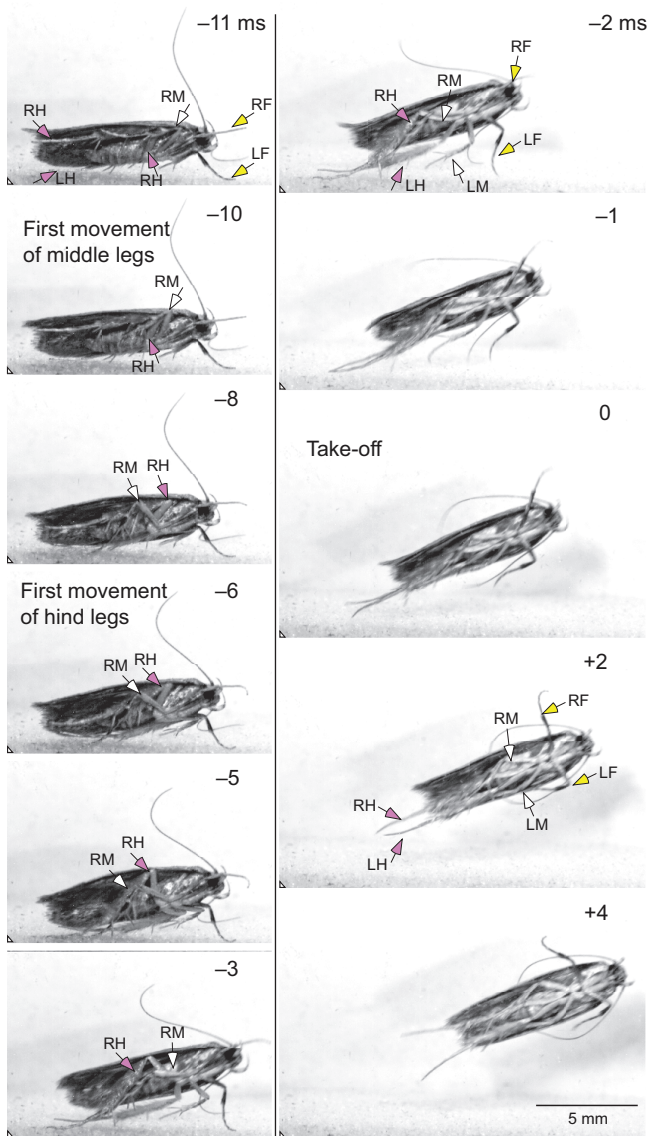
Fig. 2. Jump by the brown house-moth *Hofmannophila pseudospretella* propelled entirely by movements of the legs. The jump was from the horizontal floor of the chamber and is viewed from the side. The wings remain folded both before and after take-off. The following conventions are used here and in Figs 3–10. Selected images, at the times indicated, were captured at 1000 images s^{-1} and with an exposure time of 0.2 ms. The images are arranged in columns. The front legs (LF, left front; RF, right front) are indicated by arrows with yellow heads, the middle legs (LM, RM) by arrows with white heads and the hind legs (LH, RH) by arrows with pink heads. The triangles in the bottom left hand corner of each image indicate a constant spatial reference point.

Fig. 3. Jump by the diamond back moth *Plutella xylostella* in which the wings did not open. (A) Selected frames of a jump from the vertical front surface of the chamber allowing the legs of the moth to be viewed ventrally. The stick diagrams show the positions of the femur (pink) tibia (turquoise) and tarsus (green) of the middle and hind legs. The propulsive movements of the middle legs began before those of the hind legs and the wings remained folded throughout the jump. (B) Plot of the movements of the femur relative to the body against time, reflecting the movements of the trochanter about the coxa, of the right middle (filled triangles) and right hind leg (open triangles).

dependent on just the movements of the legs (Figs 2 and 3, supplementary material Movie 1). A series of these jumps could be strung together in a sequence to enable the moth to move forward by hopping.

Second were those jumps in which leg movements again were responsible for propelling take-off, but in which the wings now opened a few milliseconds after take-off and then began to move rhythmically in their flight pattern (Fig. 4 and Fig. 5A, supplementary material Movie 2). These jumps therefore provided a smooth launch into powered flight. Third were those jumps in which the wings started to move at the same time as the propulsive

movements of the legs so that they produced additional forces during take-off, often executing a depression phase of the wing beat cycle as the legs lost contact with the ground (Fig. 5B, Figs 6 and 7, supplementary material Movie 3). Take-off in these jumps was thus propelled by a combination of forces generated by both leg and wing movements. The propulsive movements of the middle and hind pairs of legs were the same as in the first two strategies. An individual moth of a particular species could change strategies in successive jumps (Fig. 5A,B).

Leg movements

The same sequence of propulsive leg movements could be recognised in the example jumps by *Hofmannophila pseudospretella* (Fig. 2) and *Plutella xylostella* (Fig. 3) in which the wings did not move at all (strategy 1), in the jumps by *Crassa unitella* (Fig. 4) and *Eudonia mercurella* (Fig. 5A) in which they moved only after the moth was airborne (strategy 2),

**Table 2. Jumping performance of moths**

	Body mass (m)	Acc. time (t)	Take-off velocity (v)	Trajectory angle (Θ)	Body angle at take-off (α)	Acc. (f)	g force	Energy (E)	Power (p)	Force (F)	Power/muscle mass
Formula						$f=v/t$	$g=f/9.81$	$E=0.5mv^2$	$p=E/t$	$F=mf$	$p/0.1m$
Units	mg	ms	m s^{-1}	deg	deg	m s^{-2}	g	μJ	mW	mN	W kg^{-1}
Idaea seriata small dusty wave											
Mean (N=3)	4.6	14.3	0.5	63.1	25.2	36	4	0.6	0.04	0.2	91
Best		8	0.7	63.4	18.5	88	9	1.1	0.1	0.4	306
Hofmannophila pseudospretella brown house-moth											
Mean (N=10)	5.4±0.9	11.8±1.1	0.8±0.1	44.4±5.1	34.4±4.5	71	7	1.9	0.2	0.4	299
Best		22	1.2	42.3	25.9	53	5	3.6	0.2	0.3	306
Acleris sparsana ashy button											
Mean (N=3)	6.3	19.9	0.7	53.7	30.2	37	4	1.7	0.1	0.2	137
Best		21	0.8	65.8	32.2	40	4	2.2	0.1	0.2	164
Epiphyas postvittana light brown apple											
Mean (N=3)	7.7	10.1	0.9	61.3	37.5	90	9	3.2	0.3	0.7	410
Best		11	1	55	30	92	9	3.9	0.4	0.7	464
Crambus pascuella grass veneer											
Mean (N=2)	11.9	23.3	0.6	51.3	12.4	27	3	2.4	0.1	0.3	88
Best		23	0.9	49.9	18.8	37	4	4.3	0.2	0.4	157
Camptogramma bilineata yellow shell											
Mean (N=3)	14.6	19.7	0.7	66.2	24.1	37	4	3.9	0.2	0.5	135
Best		16	1	78.9	32.2	61	6	6.9	0.4	0.9	294
Xanthorhoe fluctuate garden carpet											
Mean (N=2)	17.4	17.8	0.9	75.1	36.9	50	5	6.9	0.4	0.9	223
Best		18	1	75.2	30.7	57	6	9.2	0.5	1	295
Udea olivalis olive pearl											
Mean (N=2)	19.1	21.8	0.9	61.5	37.5	43	4	8.4	0.4	0.8	203
Best		24	1	69	41.9	42	4	9.6	0.4	0.8	208
Apamea lithoxylaea light arches											
Mean (N=2)	220.9	25.3	0.7	64.7	25.2	26	3	48.1	1.9	5.8	86
Best		26	0.8	67.9	26.6	29	3	62.1	2.4	6.4	108

The jumping performance of nine species of moths analysed, arranged in ascending order of their masses. Data in the five columns on the left are the mean of means for the performance of (N) individuals of each species (±s.e.m. is given where N>5); the best performance (defined by the fastest take-off velocity) of a particular individual is also given. The calculated values in the six columns on the right are derived from these measured data.

and in a second jump by *Eudonia mercurella* in which the wings moved before take-off (strategy 3) (Fig. 5B). At the start of such jumps, the dorsal surface of the body was almost parallel to the ground but when the propulsive legs moved, the front of the body was progressively raised more than the rear (Figs 4 and 5). The result was that the angle of the body increased relative to the horizontal (compare angle α at frames −7 ms and −1 ms in Fig. 4), effected in large part by extension of the femoro-tibial joints of the front legs. The first propulsive movements of the middle legs marked the start of the acceleration phase of the jump and were followed a few milliseconds later by propulsive movements of the hind legs. Both of these pairs of legs depressed about their coxo–trochanteral joints and extended about their femoro–tibial joints. They then continued to straighten until they reached their fully depressed and extended positions just before take-off. The front legs lost contact with the ground a few milliseconds after the start of the propulsive movements of the middle legs so that they could not make any further contribution to changes in body angle or to the forces propelling take-off. The middle legs were the next to lose

contact with the ground. Finally, 1–2 ms later, the hind legs lost contact with the ground, marking take-off and the transition from the acceleration phase of the jump to the aerial phase. In *H. pseudospretella*, the acceleration period of a jump lasted 11.8±1.1 ms (mean±s.e.m. for five jumps by each of 10 individuals) and in *C. unitella*, the mean acceleration period for six jumps by one individual was 8±1.7 ms (see Table 2 for values for another eight species).

The relative timing of the propulsive movements of the middle and hind legs could most readily be resolved when the ventral surface was visible either as the result of the body rotating in the roll plane during take-off from the horizontal (Fig. 2), or as viewed from underneath when jumping from the front glass surface of the experimental chamber (Fig. 3A,B). In this latter jump, the middle legs moved 9 ms before take-off, followed 6 ms later by a similar movement of the hind legs. This was the longest time difference seen between the movements of the two pairs of legs and may have been exaggerated by the rapidity of the hind leg movements as they slipped on the glass surface. The grand mean latency between the initial movement of the middle and hind legs
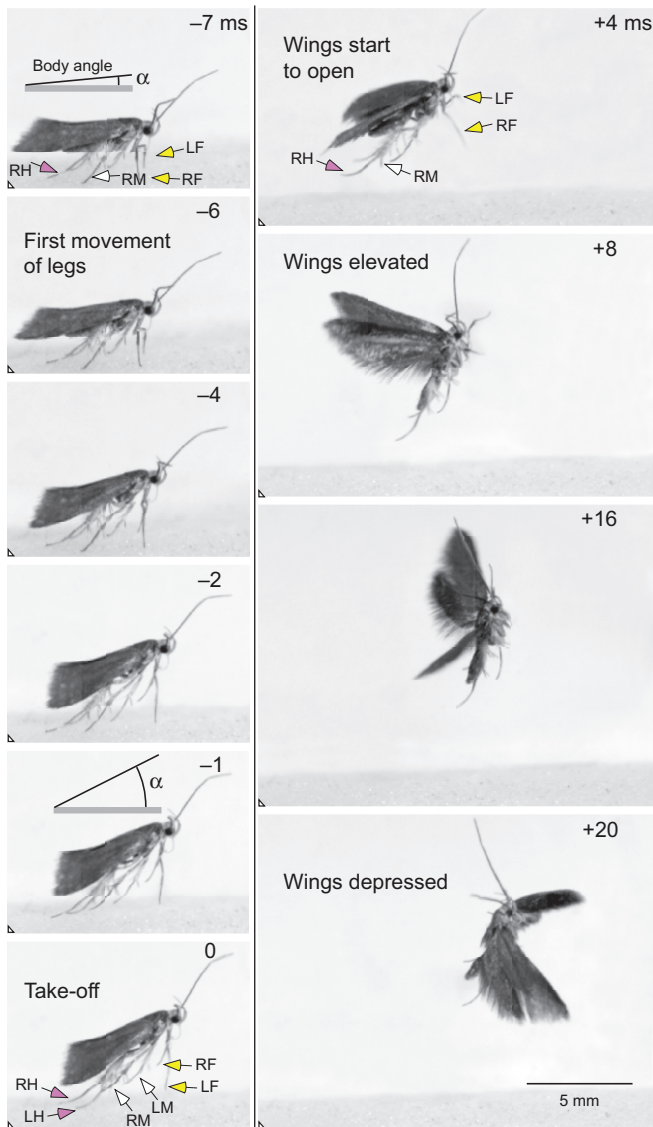
Fig. 4. Jump by the golden-brown tubic *Crassa unitella* in which the wings opened after take-off. The jump was from the horizontal floor of the chamber and was viewed from the side. The wings remained folded during the propulsive leg movements of the jump and only started to open 4 ms after take-off when flapping flight then ensued.

in five jumps from the foam surface of the floor or side walls of the experimental chamber by each individual of six species was 3.1±0.2 ms.

Wing movements

In the second strategy of jumping movements, the wings remained folded during the propulsive phase of the jump and only opened a few milliseconds into the aerial phase (Fig. 4 and Fig. 5A, supplementary material Movie 2). Once fully airborne, the wings moved upwards to reach the almost fully elevated position that they would attain in subsequent wing beat cycles. They then moved downwards in the depression phase of the wing beat cycle so that once airborne there was a smooth transition into forward flapping flight which enabled more height and distance to be gained. The jump propelled by the legs was therefore responsible for the launch into the air with the wings making no contribution.

In the third strategy of jumping, the wings opened and began to elevate before the propulsive movements of the middle and hind legs had started (Fig. 5B, Figs 6 and 7, supplementary material Movie 3). During the depression and extension of the propulsive legs, the wings moved downwards in the depression phase of their wing beat cycle that was completed only after take-off. The form of the leg movements, as viewed from underneath in jumps from a horizontal (Fig. 6) or vertical surface (Fig. 7), followed the same pattern as in the first two strategies of jumping. The relationship between the wing and leg movements was analysed in detail for a jump made by *Crambus perlella* from a vertical surface and facing the camera (Fig. 8). This orientation allowed the positions of the wing tips (Fig. 8A) to be determined at the same time as the angular changes of the joints between body and femur (representing depression of the trochanter about the coxa), and the femur and tibia of the middle (Fig. 8B) and hind legs (Fig. 8C). In this particular jump, the wings opened and began to elevate 12 ms before the first movements of the middle legs started. In other jumps, this timing between the first movement of the wings and the subsequent movements of the propulsive legs was variable. The initial movements of the hind legs then followed 2 ms later. The wings continued to move upwards, reaching their maximum elevation about 5 ms before take-off. They then began to depress so that at the point of take-off they were moving at their fastest rate. These initial movements of the wings continued into a regular pattern that powered flapping flight. In these jumps both the wings and legs were therefore moving before take-off. The combination of the propulsive movements of the middle and hind legs, which lifted the body sufficiently into the air, and the timing of the phase of the wing movements ensured that the wings did not contact the ground during their first depression (Fig. 5B and Fig. 6).

From the first two strategies of jumping, it is clear that the leg movements themselves can launch a moth into the air. Two assessments were therefore made of the contribution that the wings make to take-off, when in this third strategy of jumping they are moved at the same time as the legs during the propulsive phase of a jump. First, the time to take-off (acceleration time) and the take-off velocity were compared in the same individual brown house-moth *Hofmannophila pseudospretella* which generated a series of eight jumps over a period of 25 min, some with and some without the wings moving before take-off. There was no statistically significant difference (t-test: t_6=0.140, P=0.893) in the acceleration time of a jump when the legs alone propelled the moth to take-off (9.80±1.02 ms, mean±s.e.m., N=5 jumps) compared with jumps where the wings moved before take-off (10.00±0.58 ms, N=3 jumps). For this same but very small data set there was, however, a statistically significant difference (t-test: t_6=3.209, P=0.018) in the take-off velocity achieved; jumps propelled by the hind legs alone had a take-off velocity of 1.04±0.03 m s^{-1} compared with a velocity of 0.88±0.04 m s^{-1} when the wings also moved. The movements of the wings thus appeared to reduce take-off velocity. Of the 86 moths studied, we could not encourage a larger number of jumps of both strategies to be performed by the same individual. Pooling data from different moths of the same species, and pooling data from different species showed that wing movements made no significant difference to take-off velocities.

A second comparison was made between the mass of a moth and the jumping strategies that it used (Figs 9–12). In all 14 jumps performed by the lightest moth analysed, *Leucoptera laburnella* (Fig. 9), take-off was propelled only by movements of the legs (strategy 1); sometimes the wings were opened but only when the moth was airborne
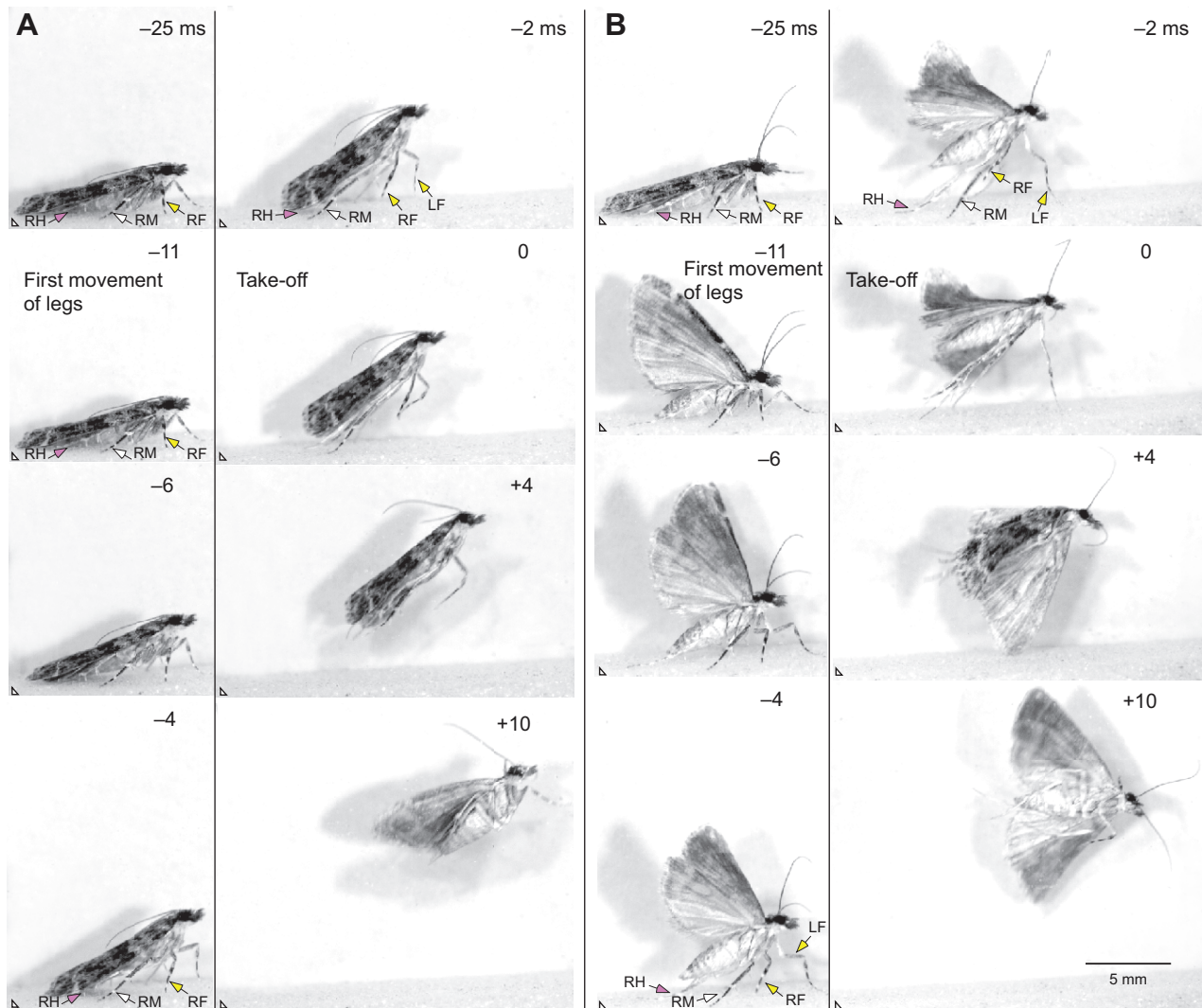
Fig. 5. Two jumps by same individual small grey moth *Eudonia mercurella*. (A) Jump propelled entirely by the legs in which the wings did not move until the moth had been airborne for 10 ms. (B) The seventh jump later, in which the wings opened before the legs began their propulsive movements (−11 ms) and at take-off (0 ms) were in the depression phase of their first wing beat cycle.

(strategy 2). By contrast in the heaviest moth analysed, *Apamea lithoxylaea* (Fig. 10, supplementary material Movie 3), wing movements began either before or at the same time as the leg movements in all of its jumps, so that at the time of take-off they were at various stages of performing a down stroke (strategy 3). Plotting body mass against the percentage of jumps with wing movements before take-off (strategy 3) for all 58 species analysed showed a clear relationship with an $r^2=0.4$ for the linear regression line and $P=2.0\times10^{-8}$ (Fig. 11A). If the different species were divided into two groups in the first of which <20% of their jumps involved wing movements before take-off and a second group in which >80% of their jumps used wing movements before take-off, a box plot showed strong correlations with body mass (Fig. 11B). For the lighter moths, the majority of their take-offs were propelled only by the legs and without the participation of wing movements. By contrast, for the heavier moths, the majority of their take-offs were preceded by movements of the wings. For moths with masses between these two extremes, wing movements could occur either before or after take-off, with the lighter moths more likely to use strategies 1 and 2 and the heavier ones, strategy 3. There were notable exceptions to this relationship, with, for example, some light geometrid moths usually moving their wings

before take-off from their horizontally open position at rest. Illustrative examples of the predominant position of the wings at the point of take-off are given for 39 of the species analysed (Fig. 12).

Jumping performance

From the analysis of all the jumps made by moths of different sizes and masses the following aspects of performance were calculated (Table 2). Mean acceleration times were correlated with body mass, and ranged from 10 ms in some of the smaller moths to 25 ms in the heaviest ones. By contrast, peak take-off velocities were not correlated with body mass and were similar across all species ranging between 0.6 to 0.9 m s^{-1}. The fastest velocity achieved by an individual moth was 1.2 m s^{-1}. The energy required to produce the fastest jumps was only 1.1 µJ in the lighter moths but to generate similar take-off velocities the heaviest moths had to expend up to 62.1 µJ. Mean accelerations ranged from 26 to 90 m s^{-2} and a maximum force of 9 **g** was experienced by some moths in their fastest jumps. On the basis that the muscles powering the movements of the middle and hind legs comprised approximately 10% of body mass, as found in other jumping insects (Burrows, 2006), the fastest jump would
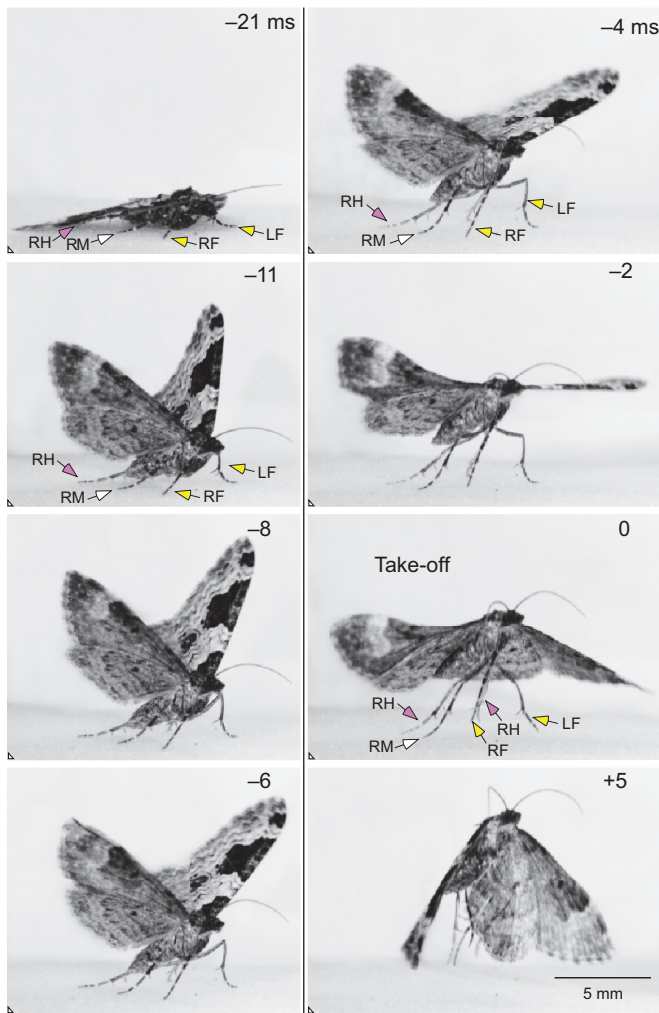
Fig. 6. Jump by the garden carpet moth *Xanthorhoe fluctuata*, in which the wings opened before take-off. Wing movements accompanied the propulsive movements of the legs. At take-off, when middle and hind legs were fully depressed and extended, the wings were being depressed.

require a power output of 106–464 W kg^{-1} in the different species. These values would be halved if the use of the two pairs of legs requires the estimates of the mass of the jumping muscle to be doubled. The values from the heavier moths in the lower part of the right hand column of Table 2 are also likely to overestimate the power output of the leg muscles in jumps where the wings are moved before take-off, because the calculations do not take account of the contribution of the muscles that power the movements of the wings.

The trajectories of jumps had a grand mean angle relative to the horizontal of 56.7±2.2° (*N*=68 moths). The grand mean angle subtended by the body relative to the horizontal at the point of take-off was 32.5±2.2 for the same moths.

DISCUSSION

This paper shows that moths use three strategies for launching into the air and that all involve the same propulsive movements of the middle and hind legs. First was a strategy for jumping in which the wings remain folded along the body so that propulsion was provided only by the rapid movements of the middle and hind pairs of legs. The wings did not move either before or after take-off. Second, was a strategy in which movements of the middle and
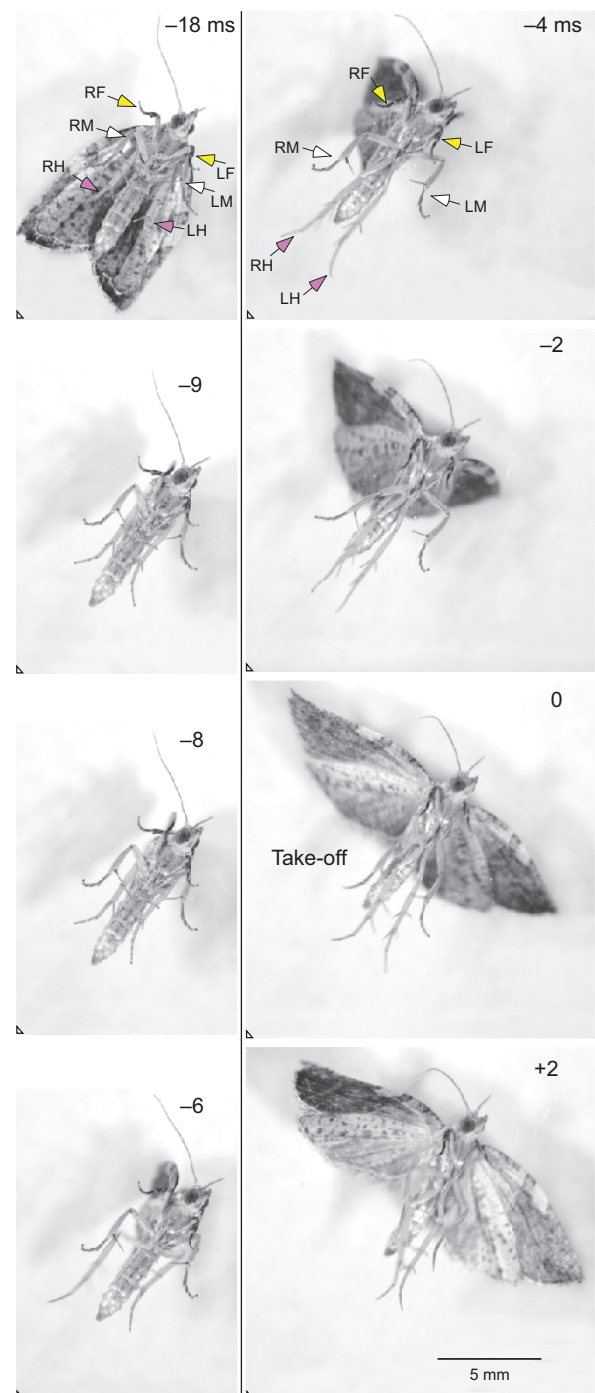
Fig. 7. Jump by the light brown apple moth *Epiphyas postvittana*, in which the wings opened before take-off. The jump was from the front glass surface of a chamber allowing the movements of the legs to be related clearly to the movements of the wings. At take-off, the middle and hind legs were fully outstretched and the wings were beginning their depression phase of their first wing beat cycle.

hind legs were solely responsible for the launch but when the moth was airborne the wings opened and then began to flap. Take-offs using strategies one and two are thus pure jumping movements. The third strategy involved wing movements that began either before, or at the same time as those of the middle and hind legs, so that all these appendages contributed force to take-off.
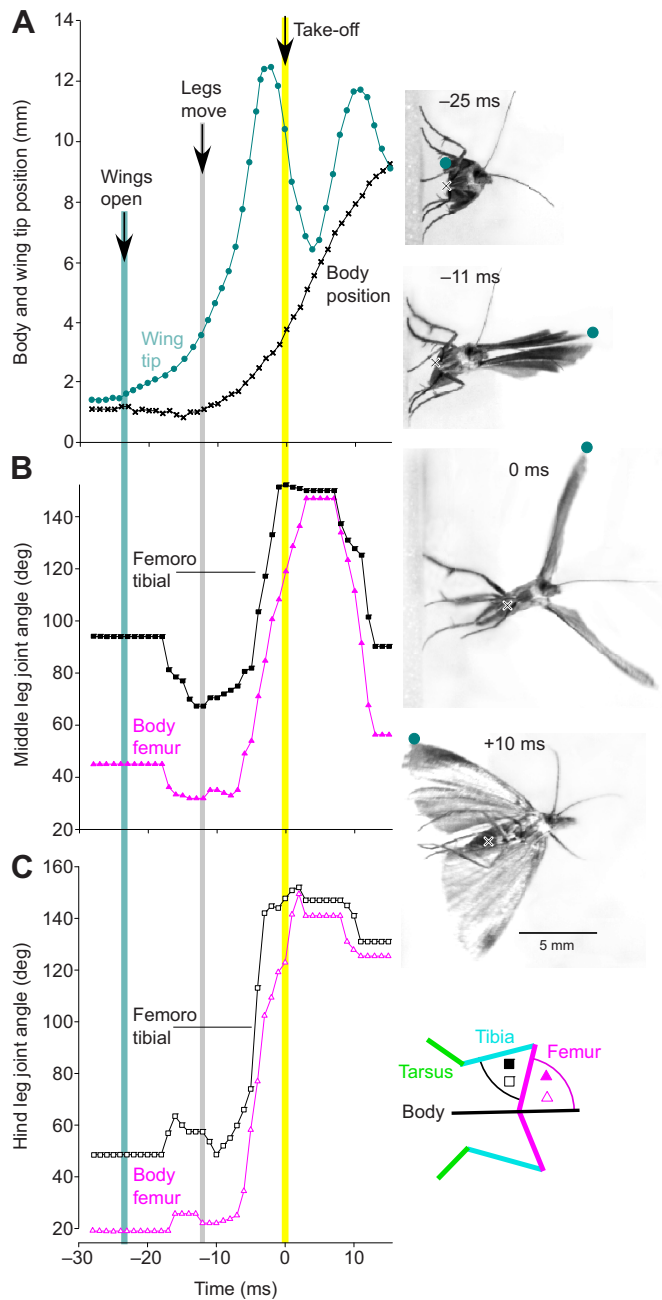
Fig. 8. Relationship between leg and wing movements in a jump by the yellow satin veneer moth *Crambus perlella*. (A) The positions of the tip of the right front wing (blue circles) and of the ventral thorax (black crosses) plotted against time. (B,C) Joint angles of B, the middle legs (filled symbols) and C, hind legs (open symbols) during the jump. The angle between the body and femur is shown by pink triangles; the angle between the femur and tibia by black squares. Individual frames from the jump at the times indicated are shown in the column at the right. The diagram at the bottom shows the leg angles that are plotted.

Mechanism of jumping

The middle and hind legs acted together to lift the moth into the air but their movements were not tightly synchronised. Across different species, the middle legs began to move approximately 3 ms before the hind legs, but lost contact with the ground 1–2 ms before take-off, which only occurred when the hind legs lost ground contact. The propulsion provided by both pairs of legs was produced by depression movements of the trochantera and their
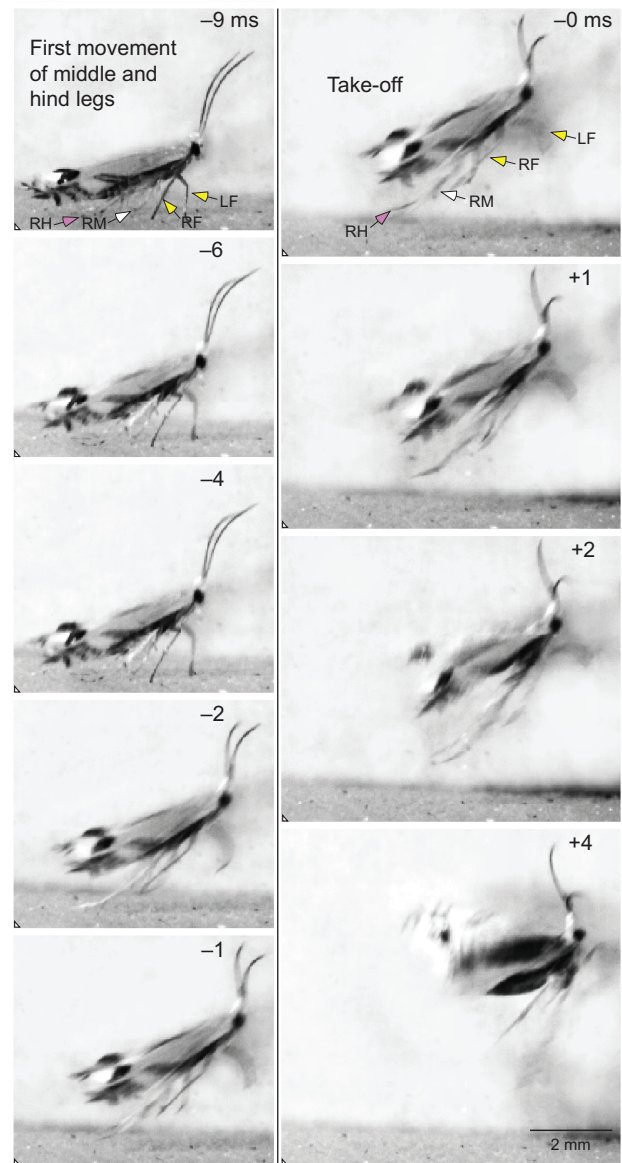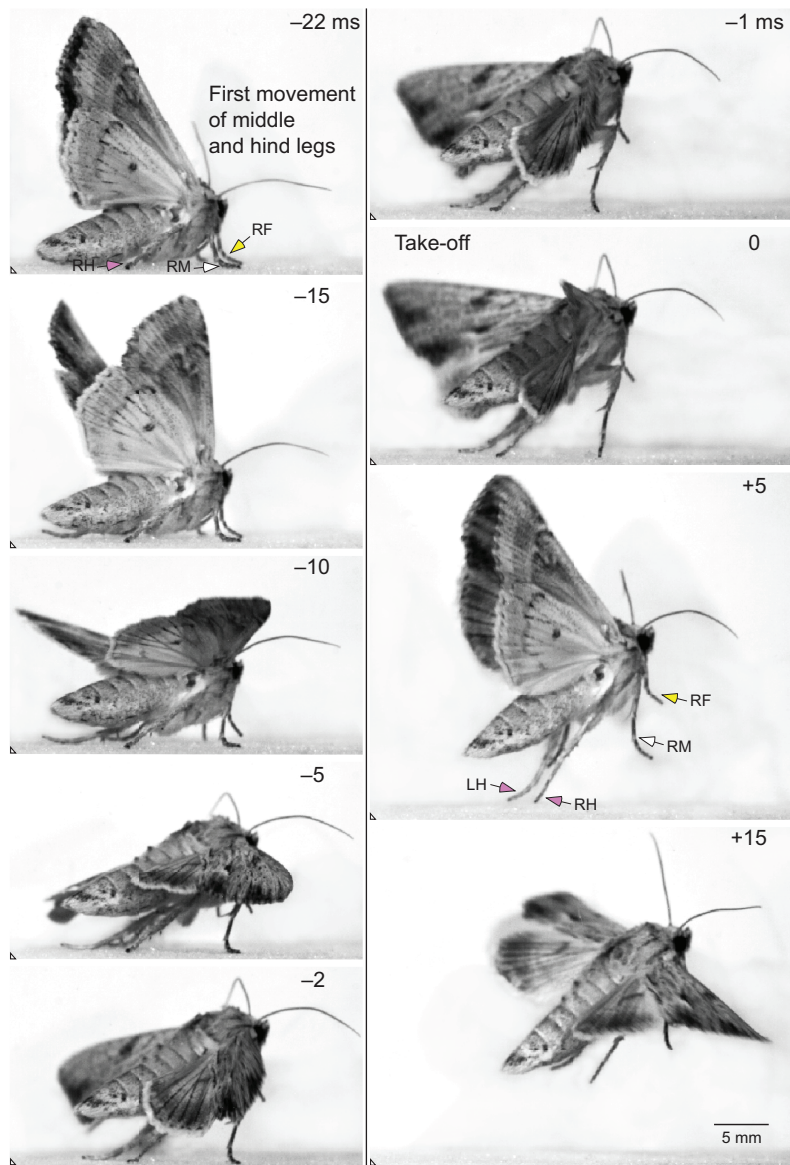

Fig. 9. Jump by the lightest moth analysed, the laburnum leaf miner *Leucoptera laburnella*. This moth had a mass of only 0.1 mg and a body length of 2.5 mm. This jump was propelled only by the legs as the wings did not open until the moth was airborne.

closely associated femora and by extension of the tibiae about the femora. The larger muscles powering these movements came from the trochanteral depressors located in the thorax; the narrow cylindrical femora offered little space for large extensor tibiae muscles. The front legs set the angle of the body relative to the substrate and by being lifted from the ground soon after the first movements of the middle legs could contribute little to propulsion.

Calculations from the kinematics show that even in the fastest jump, the power requirements of the muscles were well with the maximum active contractile limits of muscle from different animals that has been shown to range from 250 to 500 W kg⁻¹ muscle (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977). The propulsive movements of the middle and hind legs could therefore be produced by direct muscle contractions so that there is no need to invoke the action of a catapult

Fig. 10. Jump by the heaviest moth analysed, the light arches *Apamea lithoxylaea*. This moth had a mass of 235 mg and a body length of 18 mm. The wings and the middle and hind legs all began to move before take-off.

mechanism. This is further supported by the finding that the pairs of middle and hind legs started to move at different times, indicating that there was no single release mechanism that synchronised the movements of these legs in their propulsive depression and extension movements.

Contribution of the wings

The wings could only contribute to the take-off forces in the third strategy for jumping when they opened and began to move before the moth became airborne. In the other two strategies the wings either remained folded throughout both the propulsive and aerial phases of the jump, or only opened and began to flap once airborne. A comparison of jumps using any of the three take-off strategies indicates that the early involvement of wing movements before take-off had no effect on the acceleration time or take-off velocity. This would indicate that particular phases of the wingbeat movement, such as the upstroke, may add to the drag rather than providing lift and forward momentum and would therefore be detrimental for an escape response. Advantages to the use of wings must lie in a quicker transition to flapping flight and increased lift for moths with heavier bodies.

Jumping strategy and behaviour

Do the different strategies for jumping underlie different behavioural uses of launching into the air? Many jumps analysed here were in response to gentle mechanical stimuli imposed by the experimenter, but some also occurred spontaneously or at least in the absence of any apparent stimulus. The experimental process was designed to reveal the mechanisms of take-off rather than relate behavioural strategies to demands of different environmental contexts. For example, when taking-off to move to another source of food, or to follow the scent trail of a potential mate, would the use of wing movements predominate because the need for a rapid movement is less pressing? In flies, for example, different stimuli clearly lead to different types of jumping behaviour (Card, 2012), so that the three strategies may be expected to be used by moths in different circumstances.

Do moths of different masses use different launch strategies? Moths have a wide range of body sizes, which is reflected in a common division into micro-moths and others (larger moths). In this study, the masses varied by a factor of 2000 but still did not include the largest and heaviest moths. Many of the lightest moths either did not open their wings at all or only after take-off,
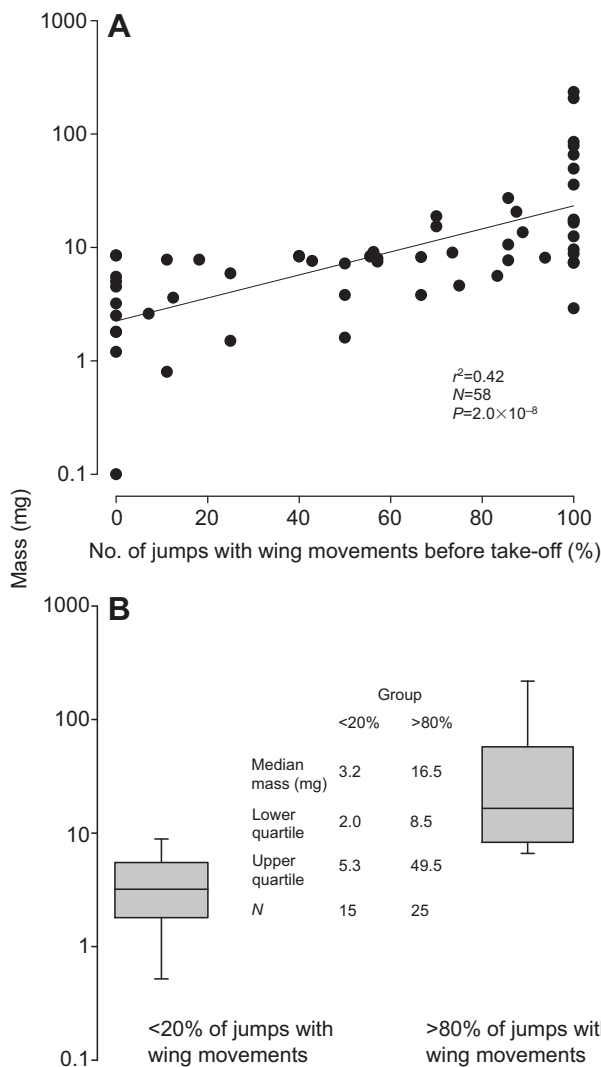
Fig. 11. Jumping strategies used by moths for take-off. (A) Plot of the log of body mass against the percentage of jumps in which wing movements occurred before take-off (strategy 3) for all 58 species analysed. Each point is the mean percentage for an average of 10 jumps (minimum of five) by an individual of each species. For those species where several individuals were analysed, the points represent the grand means. Details of the regression line are given. (B) Box plot in which species were separated two groups; first, <20% of jumps with wings movements preceding take off; second, >80% of take-offs were preceded by wing movements. A Wilcoxon rank-sum test shows that the probability of the two groups being different at $P=5.3\times10^{-6}$.

so that strategies 1 and 2 dominated. By contrast all of the jumps by the six heaviest moths used strategy three, suggesting that forces contributed by the wings are needed to generate the requisite lift. In the still heavier moths that were not studied here, is there a possible fourth strategy for launching into the air? With enlarged size, the body mass would increase as the cube while the length of the legs would increase only as the square, so that it might be expected that the wings would then play an increasingly dominant role in providing propulsion relative to the legs. In this strategy, even several cycles of wing movements might be expected to occur before take-off to generate the propulsion needed to raise the heavier body. Any extension of the legs would then assume the role of raising the body sufficiently to allow the full downward movements of the wings while contributing little propulsion.

What other insects jump in this way?

When propelling a jump, most insects analysed so far use just a single pair of legs. Small flies such as *Drosophila* use the middle pair of legs (Card and Dickinson, 2008; Zumstein et al., 2004), whilst most other jumping insects from locusts (Bennet-Clark, 1975) to fleas (Bennet-Clark and Lucey, 1967) and jumping bugs (Burrows, 2006) use only the hind legs.

The moths analysed here join a small group of diverse insects that includes lacewings (Burrows and Dorosenko, 2014), snow fleas (*Boreus hyemalis*) (Burrows, 2011), a fly (*Hydrophorus alboflorens*) (Burrows, 2013) and an ant (*Myrmecia nigrocincta*) (Tautz et al., 1994) in using both the middle and hind pairs of legs together to propel jumping. What advantage do moths get from such a mechanism? Two reasons can be suggested. First, the ground reaction forces will be distributed over a larger area provided by the four tarsi and over a longer time because acceleration times are slower, compared with insects of a similar mass using a catapult mechanism. This distribution of ground reaction forces allows moths to jump from delicate leaves or petals of plants, snow fleas to jump from snow (Burrows, 2011) and the fly *H. alboflorens* to jump from the surface of the water (Burrows, 2013). Second, moths, like snow fleas, *H. alboflorens* and lacewings, all have thin legs so that using two pairs of legs, and thereby doubling the muscle mass used for jumping, should generate more power to launch into the air. In *H. alboflorens*, jumps powered by both legs and wings have a take-off velocity that is much faster and an acceleration time that is much shorter than take-off powered only by the wings. In moths, the use of wings has no significant effect on take-off velocity. In larger moths, however, a combination of leg and wing movements should enable the requisite lift to be generated while avoiding the wings being banged on the substrate and thus being damaged.

MATERIALS AND METHODS

Moths were attracted to a light trap placed outdoors from 21:00 h to 23:00 h (dusk to early night) during July–September 2012 and 2013 in Girton, Cambridge, UK. House-moths were caught in M.B.'s house. Moths were identified by reference to Waring et al. (2003), Sterling et al. (2012) and http://ukmoths.org.uk/.

Sequential images of jumps were captured at rates of $1000\ \text{s}^{-1}$ and an exposure time of 0.2 ms, with a single Photron Fastcam SA3 camera (Photron Ltd, High Wycombe, UK). The images, with a resolution of 1024×1024 pixels, were saved directly to a computer for later analysis. Jumps occurred spontaneously, or were encouraged by delicate mechanical stimulation with a fine paintbrush or a 100 μm diameter silver wire, in chambers of three sizes depending on the mass and size of the moth to be analysed; first, 30 mm wide, 30 mm tall and 12 mm deep; second, 80×80×27 mm; third, 100×120×50 mm. All chambers were made of optical quality glass and the floor, sides and ceiling were lined with high density foam (Plastazote, Watkins and Doncaster, Cranbrook, UK). Moths would jump from any of these surfaces and from the glass front or back. Cold and uniform light to a whole chamber was provided by three Schott KL1500 light sources each fitted with two flexible arms and focusing lenses at their ends. The camera, fitted with a 100 mm micro Tokina lens, pointed directly at the middle of a chamber.

Image files were analysed with Motionscope camera software (Redlake Imaging, Tucson, AZ, USA) or with Canvas 14 (ACD Systems International Inc., Seattle, WA, USA). The time at which the hind legs lost contact with the ground and the insect therefore took-off and became airborne was designated as time $t=0$ ms, so that different jumps could be aligned and compared. The period from the first detectable propulsive movement of the middle legs and the time at take-off when the hind legs lost contact with the ground defined the acceleration phase of a jump. Measurements of changes in joint angles

Fig. 12. Position of the wings at take-off. The frame at take-off from jumps by 39 species of moth arranged in 7 rows according to mass; the heaviest moth analysed, *A. lithoxylaea* is at the top left and the lightest *L. laburnella* is at the bottom right.

and distances moved were made from jumps that were parallel to the image plane of the camera, or as close as possible to this plane. Jumps that deviated from the image plane of the camera by more than 30 deg were not included in the analysis. Peak velocity was calculated from the distance moved in a rolling three point average of successive images just before take-off. A point on the body that could be recognised in successive frames and was close to the centre of mass was selected for measurements of the trajectory of the moth. The angle subtended by a line joining these initial positions after take-

off, relative to the horizontal, gave the trajectory angle. The body angle at take-off was defined as the angle subtended by the longitudinal axis of the moth relative to the horizontal at the point of take-off. A total of 749 jumps by 86 moths (minimum three jumps by each individual) belonging to 58 species and 13 families were captured and analysed. Measurements are given as means± s.e.m. Laboratory temperatures ranged from 23 to 25°C.

The anatomy of the middle and hind legs and metathorax was examined in intact moths and in those preserved in the following ways: fixation in 5%

buffered formaldehyde and subsequent storage in 70% alcohol; fixation and storage in 70% alcohol or 50% glycerol. Individual colour photographs were taken with a Nikon DXM1200 digital camera attached to a Leica MZ16 microscope. To determine the lengths of the legs, enlarged images of fixed specimens were captured with a digital camera attached to the same microscope and projected onto a large monitor. These images of individual leg segments (trochanter, femur, tibia and tarsus; Fig. 1B) were then measured against a ruler and the sum of these parts gave the length of a particular leg to an accuracy of 0.1 mm. Body masses were determined to an accuracy of 0.1 mg with an analytical balance (Mettler Toledo AB104, Beaumont Leys, Leicester, UK).

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Movie 1. Side view of *Hofmannophila pseudospretella* captured at 1000 frames s^{-1} and replayed at 10 frames s^{-1}, as it jumped from the floor of the experimental chamber. This is a jump belonging to strategy one. See also Fig. 2.

Movie 2. Side view of *Crassa unitella* captured at 1000 frames s^{-1} and replayed at 10 frames s^{-1}, as it jumped from the floor of the experimental chamber. This is a jump belonging to strategy two. See also Fig. 4.

Movie 3. Side view of *Apamea lithoxylaea* captured at 1000 frames s^{-1} and replayed at 10 frames s^{-1}, as it jumped from the floor of the experimental chamber. This is a jump belonging to strategy three. See also Fig. 10.