Quantifying the Landing Reaction of Cockroaches

Final Report

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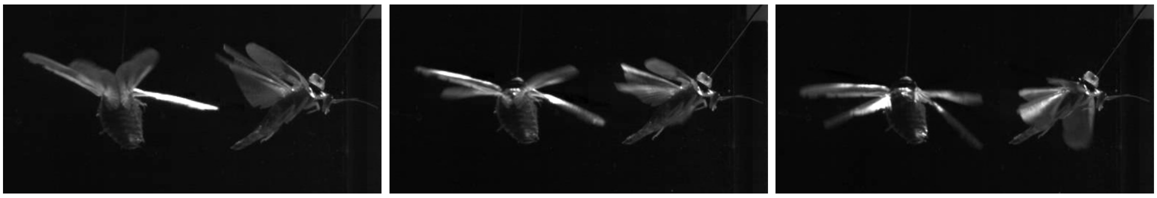

QUANTIFYING THE LANDING REACTION OF COCKROACHES

– FINAL REPORT FOR ARIADNA STUDY 08/6302 –

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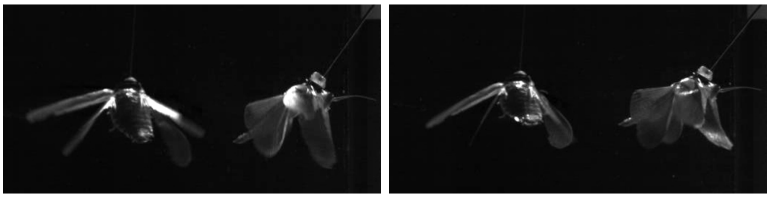

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1 Abstract

Cockroaches – however capable of flight they are – are largely ground-dwelling insects and one can assume that flight will always be a non-preferred form of locomotion. Specific adaptations are expected to be present, allowing for optimized landing strategies and transitional phases between aerial descent and terrestrial locomotion. Although the flight apparatus is developed in most representatives, little is known of both flight abilities and aerial performance in cockroaches.

In order to validate the potential arising for future technical applications in unmanned planetary exploration, a first step toward understanding aerial performance in cockroaches was undertaken. Flight experiments were performed on individuals of *Blaptica dubia*, which were launched from a ramp in 2.5 m height. Three-dimensional video sequences of *B. dubia* were recorded for whole flight trajectories and additionally starting and landing phases were analysed using high-speed video equipment. Decisional strategies in cockroach flight were mapped as ehtogramms.

Free Flight experiments showed that male specimens of *B. dubia* are capable of stabilizing their aerial descent by attaining a dorso-ventral righted position and deploying their wings. The descent process mainly consists of 3 distinct phases: a ballistic phase, a body righting and wing deployment phase and a stabilized flight and landing phase. Female *B. dubia* only display a ballistic fall.

The aerial descent in male *B. dubia* seems to be controlled and directed as in other wingless arthropods as well as vertebrates. As however no highly specialized transitional phases or landing precautions were observed, it remains unclear whether or not cockroaches are appropriate model organisms for a biomimetic approach to landing control in unmanned planetary exploration.

Keywords: insect flight, flight control, landing strategies, Blattaria, *Blaptica dubia*

2 Introduction

2.1 Diversity of Animal Flight

Speaking in evolutionary terms, the development of locomotor modes plays an essential role in the invasion of new habitats. Extreme habitat transitions (aquatic - terrestrial, terrestrial - aerial) will result in the necessity of structures and processes required in both habitats. The transition from terrestrial locomotion to aerial locomotion has independently been performed several times in biological evolution and flight is most prominently displayed in three extant clades: birds, bats and winged insects (Dudley et al., 2007). Apart from these apparent examples in animals which are highly specialized with regard to actively powered, flapping flight, aerial locomotion occurs in a much wider range of animals, which are more or less capable of a controlled transitory, aerial movement either with or without wings.

Non-flapping aerial movement is historically classified in two modes of aerial manoeuvres: gliding and parachuting (Dudley et al., 2007).

Classical gliding is usually associated with actively controlled drag and lift forces during an equilibrium gliding phase, following after an initial downward acceleration. Active flight control is obtained through the regulation of aerodynamically active surfaces, such as wings or wing-like appendages and is commonly understood to lead to a "shallow" gliding angle of less than 45°. In parachuting the aerial descent is passively slowed down without an active regulation of drag and lift magnitudes, usually resulting in a "steep" gliding angle above 45°. As both classical gliding and parachuting are related to the presence of aerodynamically active surfaces, the mechanisms that regulate both aerial manoeuvres descent are most often the same in both cases.

Additionally animals lacking apparent airfoils have also been observed to influence their flight trajectories. Therefore, in order to extend the classical (limited) definitions of flight and to further include animals lacking flight appendages, the term directed aerial descent (DAD) has been introduced (Dudley et al., 2007; Yanoviak et al., 2005)

It is assumed that the phenomenon of DAD to intentionally control an animals body trajectory during a fall is far more widespread in both vertebrate and invertebrate taxa than it is currently recognized. Amongst the known and described lineages capable of controlling their aerial route, DAD with a glide angle below 45°is observed in lizards of the genus *Draco*, flying squirrels within the family *Sciuridae* (Dudley et al., 2007) as well as in flying snakes of the

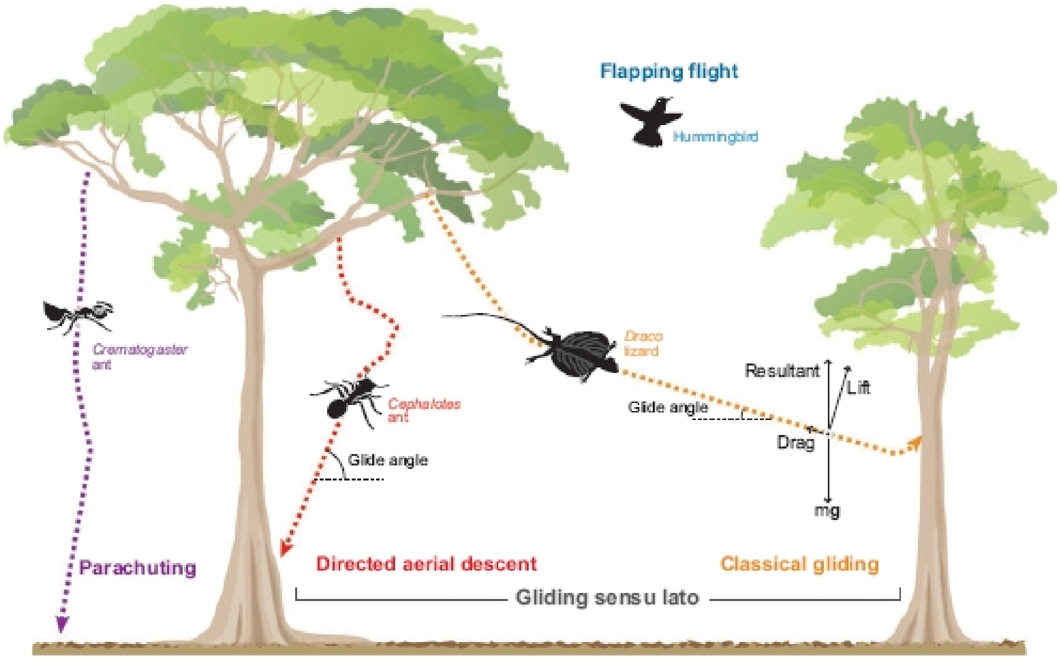


Figure 2.1: Flight in biological systems is foremost divided in flapping flight and non-flapping flight, the latter thereby historically being subdivided in parachuting and gliding. As however parachuting and gliding cannot be strictly separated by means of specific criteria applying to all organisms, the term directed aerial descent (DAD) is introduced, (Dudley et al., 2007).

genus *Chrysopelea* (Socha et al., 2005). An equilibrium gliding phase is missing in these animals and accordingly it is not surprising that in these same taxa a DAD with glide angles of above 45°can also be observed under different behavioural constraints. The range of animals displaying DADs with glide angles above 45°further includes frogs of two families (Hylidae and Rhachophoridae) (McCay, 2001), flying marsupials of the genus *Petaurus*(Nachtigall, 1979) as well as wingless insects such as ants (Yanoviak et al., 2005; Yanoviak and Dudley, 2006) and bristletails (Yanoviak et al., 2009).

Glide angle alone is however not sufficient enough to define the term "control" in DAD, let alone how control is achieved during DAD. As demonstrated for frogs by McCay (2001) DAD in a complex environment requires controlled agility around torsional and rotational axes which not only provides for a "stable flight" but also precedes landing.

Landing is the final and most critical phase of flight. Apart from the risk of encountering potential predators, (wingless) animals can suffer severe injuries or maiming if appropriate measures are not undertaken in order to reduce flight speed by decelerating. Such distinct landing manoeuvres are present in certain animals and have been qualitatively described for gliding marsupials (*Petaurus*)(Nachtigall, 1979) and flying squirrels (Dudley et al., 2007). Deceleration in e.g. *Petaurus* is induced by rapidly increasing the angle of attack and hence drag forces acting on the animal (Nachtigall, 1979).

2.2 Aerial Performance in Winged Insects

For as far back as the 15th century insect flight has been a fascination for biologists, physicists and engineers alike (Nachtigall and Wisser, 2003). Advances in high-speed video technology, flow visualization and measurement techniques such as digital particle image velocimetry (DPIV), as well as computational fluid dynamics (CFD), have led to considerable progress in understanding the aerodynamics of winged insect flight. Numerous reviews on insect aerodynamics are available (e.g. Nachtigall and Wisser, 2003; Sane, 2003; Wang, 2005) and will not be discussed here.

2.3 Cockroach Morphology and Flight Behaviour

Compared to other insect groups, little is known of the aerial performance in cockroches. Cockroaches (Blattaria) are a member of the largest group of insects, the neopteran or modern winged insects. As such they possess a pair of veined wings on both the mid and hind thoracic segments, with fore- and hindwings varying in design. While forewings have an elliptical shape and are sclerotized (hardened) to a certain extent, hindwings are larger, fan-like and have a soft, membranous design. Although there is a general presumption that cockroaches are not good fliers, aerial manoeuvrability is present in various species and is seen as a strategy mainly for predator evasion (Bell et al., 2007). Flight kinematics and the production of aerodynamic forces are dominated by the hindwings. During flapping flight the fore and hindwings operate independently and slightly out of phase, with hindwings showing a large stroke amplitude and the forewings merely oscillating around the horizontal plane. The dominance of hindwings during flapping flight increases with both increasing flight stability and speed. Due to these characteristics, cockroaches are generally termed as "hind-motor" insects. (Brodsky, 1994).

Cockroach flight is controlled by a central rhythmic programme or CPG (Central Pattern Generator) as in most flying insects (Delcomyn, 1971; Fraser, 1977; Goldsworthy and Wheeler, 1989) and further modified by cephalic and thoracic receptors, which again rely on multiple afferent sensory input. A main source of sensory input comes from the cerci, a pair of wind sensitive sensory extensions located at the very end of the abdomen which are mainly associated with an escape response from predators (Ritzmann, 1984; Rinberg and Davidowitz, 2000). Experiments have shown that cerci sensitivity can be specifically tuned to flight specific situations (Libersat and Camhi, 1988). Further the removal of single cerci results in asymmetrical wing movements and the entire removal of both cerci leads to the complete stop of wingbeat activity (Fraser, 1977). Although it is known that the antennae and the compound eyes play a role in cockroach locomotion (Harley et al., 2009) this has not specifically been documented for flight.

However in contrast to the above mentioned, cockroaches show clear morphological adaptations towards a concealed lifestyle (Brodsky, 1994). As in many other groups contained in the Neoptera, numerous cockroach species have lost the ability to fly. Consequently, the most visible morphological adaptation is wing reduction or the entire loss of wings. Accordingly cockroaches have been arranged in three categories: **(i)** forewings and hindwings developed in males and females, **(ii)** sexual dimorphism present: wings short or absent in females only, **(iii)** wings short or absent in both males and females (Bell et al., 2007). Even if wings are present this does not always seem sufficient for predicting flight abilities in cockroaches. The presence and specification of thoracic flight musculature may therefore additionally indicate flight ability. Cockroaches which are capable of enduring flight usually possess pink, pigmented flight muscles, whereas white muscles which are not sufficient for providing enough energy for flight power output are found in flightless species (Bell et al., 2007).

In summary, reports on flight behaviour in cockroaches are contradictory. It is assumed that arboreal species are good fliers (Bell et al., 2007) and this might correlate with the risk of being knocked out of arboreal habitats or evading predators in this habitat (Dudley et al., 2007). Here, we assume that flight in cockroaches, however capable of flight a species may be, will always be a non-preferred mode of locomotion and that behavioural adaptations will be present in order to ensure a safe landing and a quick transition from aerial to terrestrial locomotion. In accordance with the ESA Advanced Concepts Team (Seidl, pers. comm.) it is further assumed that the control architecture underlying cockroach DAD is simpler than in other insects. Therefore, a potential for implying behavioural patterns in cockroach landing in space exploration may arise.

2.4 Biomimetic Approaches for Space Exploration

In planetary exploration the design and deployment of unmanned robotic systems is crucial (Thakoor, 2000; Thakoor et al., 2004). Unmanned exploration missions to planets within the solar system involve a critical descending and landing procedure, where the spacecraft descends in an almost vertical trajectory to the planetary surface. At this time, landing systems decelerate and minimize impact during landing by employing a combination of retrorockets, parachutes and airbags.

Due to the communication round-trip delay time between the spacecraft and ground control this phase of planetary exploration is largely uncontrolled and therefore highly critical (Seidl and Girimonte, 2007). Appropriate counteractions cannot be undertaken in the encounter of unstable conditions (e.g. planetary crosswinds or heavy vibrations). A desirable approach to minimize potential risks during this phase are drafted toward the implication of autonomous landing strategies. Bio-inspired approaches include vision-based guidance, navigation and control systems, as well as prototype flyers presented in Thakoor et al. (2004). However, only limited research has been conducted on aerial vehicle flight control and stabilization.

In part this is lies in the fact that the simplest forms of aerial deceleration systems are passive gliders. Plant seeds often imply self-stabilizing parachute-like designs (e.g. dandelion seeds) or rotational propeller designs (e.g. maple seeds) in order to decelerate or or obtain a constant vertical speed. Although they may serve as inspirations for such bio-inspired landers (Seidl and Girimonte, 2007) planet-inherent limitations (e.g. a thinner atmosphere or lower gravitational forces) may lead to a decreasing effectiveness of passive spacecraft stabilisation systems (Thakoor et al., 2004). Actively controlled yet autonomous planetary descending systems would therefore prove to be beneficial (Seidl and Girimonte, 2007).

2.5 Project Objectives

The current study aims at providing insight into flight behaviour and landing strategies in cockroaches. It is further to be assessed in how far cockroach landing behaviour can provide a possible model input in the development of planetary exploration systems.

In general behaviour can be considered as hierarchically structured from a top category terming the broadest level of classification down to a single component of a behavioural act (Lehner, 1996). Within this given interpretation, flight is defined as behavioural pattern, flight phases (see 2.5.1) are defined as behavioural acts and the movement of aerodynamic active surfaces or postural changes during flight are defined as behavioural components. Accordingly general considerations can be equally addressed in a hierarchical structure as follows:

1. Is a directed aerial descent present in cockroaches?
2. If so: Is a distinct flight/landing trajectory distinguishable in cockroaches?
3. If so: Are distinct flight/landing phases present in the directed aerial descent of cockroaches?
4. If so: Are there any stereotypical reactions and/or behavioural patterns that characterize these distinct phases?
5. If so: How do stereotypical reactions influence the aerial descent?

The consecutive answers to each addressed issue will lead to a general characterization of aerial behaviour in cockroaches. If present, flight phases (behavioural patterns) and body movements during flight (behavioural components) will be analysed. In this context, flight phases will be analysed with respect to flight parameters, which are the adequate temporal and spatial determinants of flight.

2.5.1 Characterization of Flight Phases

A typical flight trajectory is likely to to be composed of several phases:

1. **Ballistic dive phase:** This initial phase is characterized by a projectile-like fall of the animal with unfolded wings (Dudley et al., 2007). The phase will be analysed regarding its duration: How long is this initial phase/how long do animals take to react to the flight situation?
2. **Wing deployment phase:** Following the initial dive, wing deployment and flight initiation are expected (Krämer and Markl, 1978). This phase includes the unfolding of the wings and the first complete wing-beat cycle (i.e. unfolding, downstroke, upstroke). The duration of wing deployment will be analysed from its beginning until the first wing beat cycle is completed.
3. **Stabilization phase:** This phase comprises the main stabilization reactions and body alignment behaviours to reorient the body and to slow the descent. In order to characterize this phase it is essential to verify which body alignment manoeuvres occur and how long it takes until the cockroach attains a stable flight.
4. **Equilibrium flight phase:** The equilibrium flight phase is characterized by both a constant glide angle and air speed. The phase includes the transition point which indicates the end of the initial acceleration of the descent. Further, constant drag and lift forces are usually associated with equilibrium flight (Dudley et al., 2007). The most essential question which arises, is whether or not equilibrium flight is present in cockroaches.
5. **Landing phase:** In order to prevent a massive and potentially hazardous impact, landing procedures are expected. These are associated with a deceleration before ground contact, which characterizes this final phase. Along with potential flight manoeuvres which are to be analysed (e.g. body alignment leading to increased drag), it is of further interest to know when landing is initiated (time after take-off, time before ground impact) and whether or not landing is guided by visual cues (Srinivasan et al., 2000; Srinivasan and Chahl, 2001; Franceschini et al., 2007).

In order to characterize a typical flight trajectory, we intend to distinguish the described phases. If present, phase specific considerations will be addressed via the assessment of phase specific parameters.

2.5.2 Characterization of Flight Parameters

In order to characterize and quantify the general trajectory of the aerial behaviour of cockroaches multiple flight parameters can be considered:

- **Duration of the flight [s]:** The duration of the flight is the time from take-off to ground impact.
- **Total track length [m]:** The total track length is the length of the flight track, measured along the entire path from the point of take-off to the point of ground impact.

- **Horizontal distance travelled [m]:** The horizontal distance travelled is the cumulative length of the three dimensional flight trajectory projected on the ground plane.
- **Start-to-finish distance [m]:** The start-to-finish distance is the straight-line distance between the take-off point and the ground impact point, i.e. the length of the start-to-finish vector
- **Horizontal start-to-finish distance [m]:** The horizontal start-to-finish distance is the length of the start-to-finish vector projected on the ground plane.
- **Linearity index [-]:** The linearity index is a dimensionless quantity and is calculated by dividing the total track length by the start-to-finish distance.
- **Speed [m s^{-1}]:** Speed can be subdivided into several components:
    1. **Airspeed:** An the individual's speed along its trajectory path.
    2. **Lateral horizontal speed:** An individual's sidewards speed component.
    3. **Forward horizontal speed:** The speed in direction of an individual's longitudinal axis.
    4. **Vertical speed:** The speed at which an individual vertically descends.
- **Descent angle γ [°]:** The inclination angle of the local flight path with respect to the horizontal.
- **Horizontal body angle α_H [°]:** The horizontal body angle is the angle between the longitudinal body axis and the horizontal plane. It indicates the inclination of the cockroach's body with regard to the ground.
- **Body angle of attack α_B[°]:** The body angle of attack is the angle between the cockroach's longitudinal axis and its local flight path. Here two possibilities may be encountered:

$$\alpha_B = \gamma + |\alpha_H| \quad \text{when animals are head upward and} \tag{2.1}$$

$$\alpha_B = \gamma - |\alpha_H| \quad \text{when animals are head downward.} \tag{2.2}$$

- **Wingbeat frequency f [Hz]:** Frequency of the fore- and hindwing flapping movement. Propulsion is provided by wing movement, steering reactions are induced by differences in contralateral wing movements.

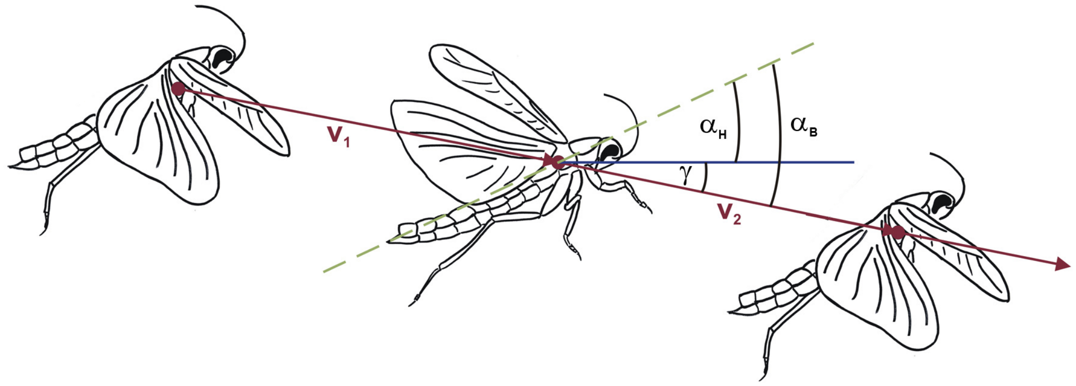


Figure 2.2: Behavioural components during aerial descent in cockroaches, which can be determined spatially and temporally include the horizontal body angle α_H (between specimen longitudinal axis (green) and horizontal plane (blue)), the body angle of attack α_B (between specimen longitudinal axis and trajectory path (red)) as well as the wingbeat frequency which is given by the completion of a wingbeat cycle including both a downstroke and upstroke. γ = descent angle; v_1, v_2 movement vectors between two consecutive position.

2.5.3 Characterization of Flight Behaviour

Body movements and body postures are defined as single behavioural components that will characterize and influence flight phases. Such components are foremost reflected in spatial and temporal parameters such as body angles or wingbeat frequency, which are already mentioned above. Further body righting manoeuvres may exist which cannot directly be assessed by certain parameters, but which can be described and categorized, e.g. turning and banking manoeuvres (McCay, 2001).

In order to describe behaviour, ethograms are a standard method (Lehner, 1996). Ethograms provide an integrative overview and understanding of behavioural patterns defined on an operational basis. It is a clear project objective to provide possible model concepts for implication in unmanned planetary exploration. Based on the operational definition of flight components, flight parameters and flight phases, these model concepts may ultimately be derived from ethograms delineated due to the experimental outcome.

3 Methods

3.1 Test Animals

The Dubia cockroach (*Blaptica dubia*, Serville 1839) is a medium sized cockroach (bodylength $30-50$ mm) which is native to Central and South America. It is therefore commonly known as South American Dubia cockroach or, according to its appearance, as "Orange spotted roach". This species is sexually dimorphic – males and females show distinct sex-specific differences. Whilst male cockroaches have a fully developed wing apparatus with both a pair of fore- and hindwings as well as according pigmented flight musculature, females are only equipped with rudimentary forewings and lack muscles required for flight.

Adult males and females were purchased from pet store supplies (Zoo am Hulsberg, Bremen, Germany) and reared in a glass vivarium (Temperature $= 25-30\,^{\circ}\mathrm{C}$; Relative Humidity $= 30-50\,\%$). Animals were fed on a diet of cereal, carrots and apples. Food and water were provided *ad libitum*.

Free flight experiments were performed with (fully) winged adult males. A control experiment was performed with wingless females of *B. dubia*. Morphological data for both males and females was obtained from each animal prior to each experimental trial. Morphological data included body mass, body length, body width (pleural width) taken for all animals and additionally wing length and chord length in males only. Only animals with visibly intact antennae, eyes, cerci and wings (in case of males) were used for experiments, as sensory feedback for insect flight is heavily dependent on these structures (Goldsworthy and Wheeler, 1989).

As flight performance in cockroaches has been observed to be dependent on environmental conditions (Yagodin and Kovbasa, 1984), near identical environmental conditions (Temperature $= 24-26\,^{\circ}\mathrm{C}$; Relative Humidity $= 35-50\,\%$) were ensured throughout all experiments. Each cockroach was used only once per experimental trial.

Experiments were approved by the "Senatorin für Arbeit, Frauen, Gesundheit, Jugend und Soziales" of the Hanseatic City of Bremen, according to §7, §8 and §9 of the German Tierschutzgesetz.

Figure 3.1: Male (left) and female (right) specimens of *B. dubia*. Males are equipped with both fully developed fore and hindwings, with the latter being folded underneath the forewings when animals are not in flight. Females entirely lack hindwings and possess only rudimentary forewings.

3.2 Experimental Set-up

Free flight experiments were performed in a custom built flight arena located at the Biomimetic Innovation Centre (B-I-C). Aluminium beams (Rexroth/Bosch; cross section 40 mm×40 mm) were mounted together, thereby providing the framework of the arena (6 m × 3 m × 3 m; W×D×H). White curtain sheets (1.5 m×3.3 m; W×H) were draped from the upper bars of the framework and the floor of the arena was laid out with white polystyrene foam. Lighting from above was provided by neon tubes, mounted above the median axis of the arena. These measures ensured a uniform surrounding and lighting in the arena, devoid of any visual cues which could possibly influence the aerial behaviour of the tested cockroaches.

Experiments were initiated by releasing animals into an elevated launching ramp consisting of a perspex tube (l= 1 m; ⌀= 75 mm) which was mounted to a wooden panel. Holes drilled into the panel allowed for the perspex tube to be tilted and fixed at angles from 0 – 90° (35° standard tilting angle, unless indicated otherwise). Cockroaches were placed in the upper third section of the launch tube and allowed to slide down the ramp, thereby accelerating. For stereo recordings cockroaches were oriented feet downward in the launch tube. For 2D high-speed recordings of flight initiation, cockroaches were placed on their backs prior to release, in order to verify whether dorso-ventral righting manoeuvres are included in flight control. After exiting the tube in 2.5 m height, cockroaches were defined as "flying freely" and video recordings were obtained.

3.2.1 3D Video Recordings – Flight Overview

Whole flight sequences were simultaneously recorded using two 14 bit digital CCD cameras (pco.1600 camera, PCO Imaging AG, Kelheim, Germany) equipped with Nikon wide angle lenses (AF-S DX Zoom-Nikkor 18 – 55 mm, 1:3.5-5.6; AF Nikkor 20 mm, 1:2.8) at 28.3 fps and a frame resolution of 1600×1200 pixels. Both CCD cameras were mounted perpendicular to each other, with one camera recording flight sequences from the side (lateral view) and

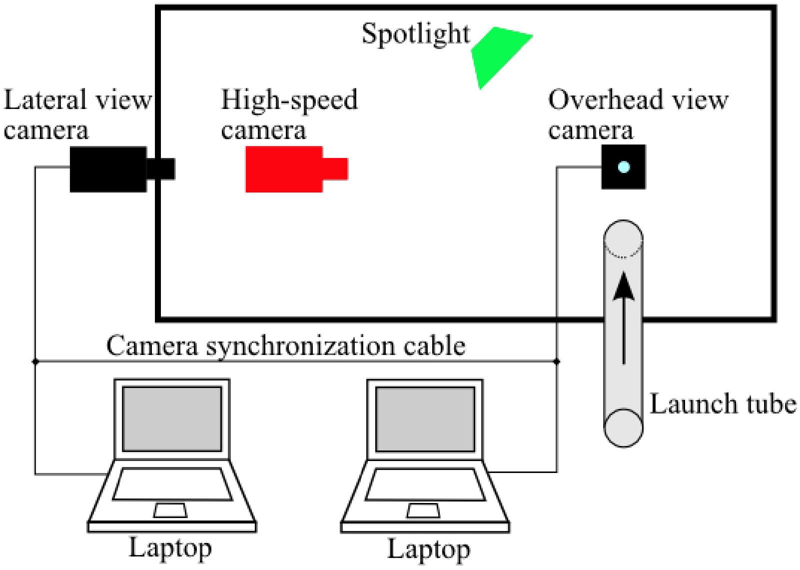


Figure 3.2: Diagram showing the experimental flight arena set-up (topview). A tilted launch tube was used to initiate flight by releasing cockroaches into the flight arena. For 3D flight analysis an overhead camera (black with blue dot) and a lateral camera (black) were operated, synchronized and connected via separate laptops placed outside of the arena. Illumination was provided by neon tube lights positioned above the median axis of the arena (not indicated). For high-speed recordings the overhead and lateral cameras were replaced by a high-speed camera (red) which was placed within the arena. Additional illumination during high-speed recordings was provided by a spotlight (green) situated next to the camera. The high-speed camera was manually operated by a laptop positioned outside the arena.)

the other camera recording flight sequences from above the launching tube (dorsal view). The field of observation resulting from the overlapping field of view of both cameras was 1.8 m × 2.4 m × 2.5 m (W×D×H). Both cameras were placed outside the flight arena (see figure 3.2). Simultaneous/stereo recordings were obtained by externally (manually) triggering both cameras from a computer equipped with camera operation software (pco.camware, PCO Imaging AG, Kelheim, Germany). Recordings began once cockroaches started accelerating within the launching tube. Flight sequences were saved as bitmap image sequences.

Camera calibration was performed prior to flight experiments by recording an image of a 3-dimensional object of known measures (0.56 m × 0.39 m × 0.45 m; W×D×H) placed within the flight arena and the visual field of both cameras.

3.2.1.1 Flight Trial Variables

A subset of experiments with actively varied parameters was performed within the three dimensional analysis of whole flight trajectories.

Influence of Visual Cues

Visual cues heavily influence locomotion and navigation in insects. As this has also been shown for cockroaches (Harley et al., 2009) the experimental set-up was re-arranged in order to verify whether the aerial descent in cockroaches is also influenced by the presence of visual influences. For this purpose the flight arena was equipped with 2-dimensional landmarks ($0.16\,\mathrm{m}\times 0.16\,\mathrm{m}$), which were laid out on the white floor in a random pattern. Previous studies have shown that cockroaches of the genus *Periplaneta* have optical receptors that are sensitive to a wavelength of $507\,\mathrm{nm}$, however show no reaction to wavelengths of $630-700\,\mathrm{nm}$ (Mote and Goldsmith, 2005). As this might also be expected for *B. dubia*, trials were conducted with green and red landmarks respectively.

Added Mass / Payload Variation

In order to verify how the controlled descent of cockroaches is altered by additional payload, mass was added to test animals by applying weights to the pronotum, which is approximately located near (yet anterior of) the animals' centre of mass. Mass was added in 3 consecutive steps: 10% body mass, 30% body mass and 50% body mass.

Variation of Starting Angle

Essential flight parameters such as horizontal and vertical flight speed are assumed to be heavily influenced by starting conditions. In order to assess cockroach flight behaviour with respect to different starting conditions, the launching tube was adjusted to tilt angles of 25° and 45°.

3.2.2 2D High-Speed Video Recordings – Flight Detail

In order to obtain detailed time-resolved recordings of cockroach flight, high-speed video sequences were recorded. For this purpose a high-speed video camera (Fastcam Ultima APX-RS, Photron Europe Ltd. U.K.) equipped with a Nikon normal focus lens (AF Nikkor $50\,\mathrm{mm}$, 1:1.2) was placed within the flight arena at a distance of $3.5\,\mathrm{m}$ from the launching tube, providing a 2D side view of the launching ramp plane (lateral field of view approx. $1.2\,\mathrm{m}\times 1.2\,\mathrm{m}$). Additional lighting was provided by a halogen spotlight positioned next to the high-speed camera (see figure 3.2).

Starting and landing sequences were separately recorded at $500\,\mathrm{fps}$ and a shutter speed of $1/1500\,\mathrm{s}$. Image recording was externally (manually) triggered from a computer equipped with camera operation software (Photron Fastcam Viewer, Photron Europe Ltd. U.K.) and began once cockroaches started accelerating within the launching tube. Flight sequences were saved as bitmap image sequences.

Camera calibration was performed prior to flight experiments by recording an image of a 3-dimensional object of known measures (0.56 m × 0.39 m × 0.45 m; W × D × H) placed within the flight arena and the visual field of the high-speed camera.

3.2.3 Video Analysis and Data Processing

Bitmap image sequences from both 3D and 2D recordings were cut and converted to uncompressed AVI-video files using the programme ImageJ (Image Processing and Analysis in Java; National Institutes of Health, USA).

3.2.3.1 3D Analysis – Flight Overview

Pairwise image motion analysis was performed by tracking and digitizing cockroach body positions along the flight path using motion analysis software (SkillSpector version 1.2.4, Video4coach, Svendborg, Denmark). Positional data were digitized by preferably tracking the test animals' centre of mass (COM) which was visually estimated along each individual's longitudinal axis as the hind wing insertion point.

SkillSpector uses the direct linear transformation (DLT) method to resolve the raw coordinate data obtained from complementary views into a single 3-D space. After reconstructing the 3-D flight trajectory spatial points were smoothed by SkillSpector using a quintic spline. This technique of data smoothing produces results similar to those of applying a low-pass filter (Hedrick et al., 2004). The advantage of the quintic spline method is that velocity can be directly calculated from the spline curves, which proves to be the most accurate method for calculating derivatives on the basis of positional data (Walker, 1998).

3D data digitized with SkillSpector including axial positions, horizontal and vertical velocities, as well as horizontal and vertical accelerations were subsequently processed with Microsoft Office Excel and Matlab (Version 7.1, The MathWorks Inc., USA).

3.2.3.2 2D Analysis – Flight Detail

High-speed motion analysis was performed by tracking and digitizing cockroach body positions and cockroach body angles for starting and landing phases using ImageJ. For landing phases hindwing positions were additionally tracked and digitized in order to obtain information on wingbeat frequencies.

Horizontal and vertical velocities were calculated using a sampling frequency of 100 Hz, i.e. only every fifth image was used for analysis.

2D data digitized with ImageJ was further processed using Microsoft Office Excel, Matlab and SciDAVis (http://scidavis.sourceforge.net/).

3.2.3.3 Data Selection Criteria

Only image sequences that met certain criteria were included in data analysis. General criteria for the inclusion of flight sequences were:

- Sufficient image quality.
- Headfirst exit of cockroaches from the launching tube.
- Aerial descent (or in case of high-speed recordings: specific flight phase of interest) entirely captured by video recording equipment.

Further, during stereo recordings, the moment when the cockroaches just made ground contact was usually not resolved temporally due to the to the sampling frequency of 28 Hz. Therefore the last image prior to impact was used to determine final flight positions in 3D analysis.

The influence of cockroach body alignment with respect to the image plane was taken into consideration for 2 dimensional high-speed recordings, especially when recording landing sequences. Only image sequences showing cockroaches in full or near-full side view (cockroach longitudinal axis perpendicular to camera axis and in image plane) were considered for motion analysis. Near-full side view was defined as a maximal visible length difference of 3.5% body length in images and actual body length. Considering the length of a cockroach as radius in a unit circle, this corresponds to a maximal horizontal angle diversion of 15°.

4 Results

4.1 3D Analysis – Flight Trajectory

The analysis of stereo recordings revealed that male individuals of *B. dubia* were capable of controlling their aerial descent. Aerial descent thereby generally consisted of two phases which could clearly be distinguished: an initial ballistic dive followed by a controlled descent phase which lasted until ground impact (fig. 4.1). Both a rapid wing deployment and stabilization phase were present. After wing deployment and stabilization, flapping flight was initiated. Neither wing deployment, stabilization or flapping flight sequences were resolved in flight trajectories. Wing deployment and stabilization are overlapped by the dominance of ballistic behaviour, active powered flight did not result in a gain in height. It was not possible to further subdivide the controlled descent phase into further distinct phases either by visual assessment or flight trajectory / flight parameter analysis. An equilibrium flight phase was neither observed in trajectories, nor by analysing flight parameters (see below). A specific landing phase was not present as such (see 4.3), the entire controlled aerial descent must rather be seen as a landing preparation.

Throughout all observed flights vertical speed was the most dominant velocity component (fig. 4.2). Airspeed as the resultant speed vector from vertical and horizontal velocity components clearly followed the pattern displayed by vertical speed (figs. 4.2a, 4.2b). Vertical speed always increased throughout the initial phase of descent (ballistic dive) and began to gradually decrease once individuals had entered the controlled descent phase. The onset of the descent phase usually coincided with wing deployment (also see section 4.2). As airspeed does not display any constancy throughout flight, equilibrium flight is clearly absent. Horizontal speed (presented as resulting vector from forward and sidewards velocities in the horizontal plane in all boxplots) remained near constant during the initial ballistic sequence and also began to vary with the onset of controlled descent (fig. 4.2c). Finally, the descent angle as well displayed a dependency on wing deployment and the onset of controlled descent. After rapidly increasing to maximum values of almost 90°, the descent angle steadily decreased to angles ranging from 50°- 70°(fig. 4.2d).

During the controlled descent phase, a variety of flight path trajectories was displayed (fig. 4.1). These flight path trajectories were visually assessed in 3 categories:

1. Near ballistic flight trajectories.

2. Helical flight trajectories.
3. Shallowed flight trajectories.

Near ballistic flight trajectories were observed in a small amount of male individuals only. Although these flight trajectories closely resembled passive fall with respect to vertical and forward velocities, clear sideward movements were observed. Helical trajectories were most remarkable with respect to vertical speed. In these trials, the slowest final vertical speeds (and as such airspeeds) were observed, with vertical velocities remaining up to $1\,\mathrm{ms}^{-1}$ below vertical velocities in other flight trials. Shallowed flight trajectories usually displayed a clear lateral component throughout descent. This is most evident in those flight trajectories with curvilinear motions $< 90^\circ$, which also involved large start-to-finish distances.

The fact that male individuals are at least moderately capable of controlling their flight is most apparent when comparing male and female flight trajectories. In contrast to males, females only showed a single flight trajectory which was that of a ballistic dive (fig. 4.3). Accordingly this was reflected in all flight parameters with vertical speed and descent angle constantly increasing and horizontal speed not varying at all (fig. 4.4).

Flight parameters for reference experiments with male and female *B. dubia* are summarized in tables 4.1 and 4.2 (values for 35°).

4.1.1 Influence of Visual Cues

In flight trials performed with visual cues overall flight and landing behaviour did not essentially differ from that observed without landmark patterns, although there were seemingly fewer helical flight trajectories (fig. 4.5). Neither red nor green landmarks were preferred as targeted landing sites by *B. dubia*. The observed flight parameters also showed no essential differences between animals provided with visual input and those without (fig. 4.6). The only obvious difference in the presence of visual cues seemed to be the prolonged duration of flight (fig. 4.6a). However this impression was put into a different perspective when looking at mean values which did not differ significantly (Student t-test, two-sided, $\alpha = 5\%$, tables 4.1 and 4.3 (values for 35°)).

4.1.2 Influence of Added Mass / Payload Variation

Trials with additional payloads showed that *B. dubia* males were capable of compensating added mass during flight. However, in our experiments only payloads amounting to an additional bodymass of 10% were tolerable. In fact additional payloads of 10% bodymass seemed to have little effect on aerial descent. Similar to flight trials in unloaded cockroaches clear forward and sideward movements in the horizontal plane were observed (fig. 4.7a, b). Also as observed in unloaded individuals, the controlled aerial descent phase started approx. 0.3 s after launch, with similar speed components and descent angles occurring respectively throughout this phase (figs. 4.8a, b). Due to the greater total mass the length of the ballistic dive (in metres) was larger, leaving less height for controlled actions. Nevertheless, cockroaches were able to pull put of the dive phase and achieve a stable flight. This is especially reflected in the dorsal view, revealing the amount of movements in the horizontal plane, as well as the descent angles which showed a great variation and a gradual decrease after 0.3 s (4.9a, b). As far as flight paths are concerned, mainly curved trajectories were observed. Interestingly, loaded individuals (10% bodymass) hardly displayed helical flight trajectories in contrast to unloaded specimens.

Trials with an additional payload of 30% body mass showed a near ballistic behaviour in most individuals. Although the side view indicates a certain amount of divergence from a ballistic flight path after a fall of approximately 1 m, the view from above (dorsal view) displays virtually no movement at all in the lateral horizontal direction (fig. 4.7c, d). Airspeed in these trials reached the same maximum values as in those without or with less additional mass, however in comparison velocities increased for a longer period of time. The sharp decrease in both airspeed and descent angle once maximum speed was reached, reflects that single animals had already made ground contact once v_{max} was reached (fig. 4.8c, d; fig. 4.9c).

Only test animals loaded with an additional 50% bodymass showed a more pronounced uncontrolled flight, which heavily resembled that of female cockroaches (fig. 4.7e, f). In these trials only a single individual proved to diverge from a projectile-like fall. Accordingly, all flight parameters reflected this fact, with airspeed steadily increasing until v_{max} and abruptly falling back to $0\,\mathrm{ms}^{-1}$ (fig. 4.8e, f), as well as descent angle showing the same abrupt reduction to 0°after around 0.5 s (fig. 4.9d)

4.1.3 Influence of Starting Angle

Flight trajectories varied considerably with respective starting angles. Curved trajectories were present at all starting angles, however curve radius seemingly increased with increasing angle, leading to trajectories which were elongated in forward flight direction. This coincides with the fact that helical trajectories were more often observed at angle of 25°compared to the other two angles of 35°and 45°. At 35°helical trajectories were still observed, however no longer at 45°(fig. 4.10).The elongation of flight trajectories in launch direction and the reduction of helical descent manoeuvres are reflected in the total track length as well as horizontal flight distance. With increasing starting angle horizontal flight distance increases, while total track length decreases (table 4.1). Flight trajectory elongation is further indirectly reflected in horizontal velocity components. Horizontal velocity shows a larger variation with increasing starting angle (fig. 4.11b, d, f).

Both horizontal and vertical velocity components indicate that initial speeds are higher when cockroaches leave the launch tube at higher angles. This can be directly linked to greater acceleration in the launch tube, due to the steeper tube inclination. What seems remarkable in this context though, is the fact that at 45°inclination, cockroaches show little variation for vertical speed which is almost constantly low in comparison to 35°trials (fig. 4.11c, d).

As can be taken from table 4.1 the initial descent angle is heavily influenced by starting angle, the final descent angle however is not.

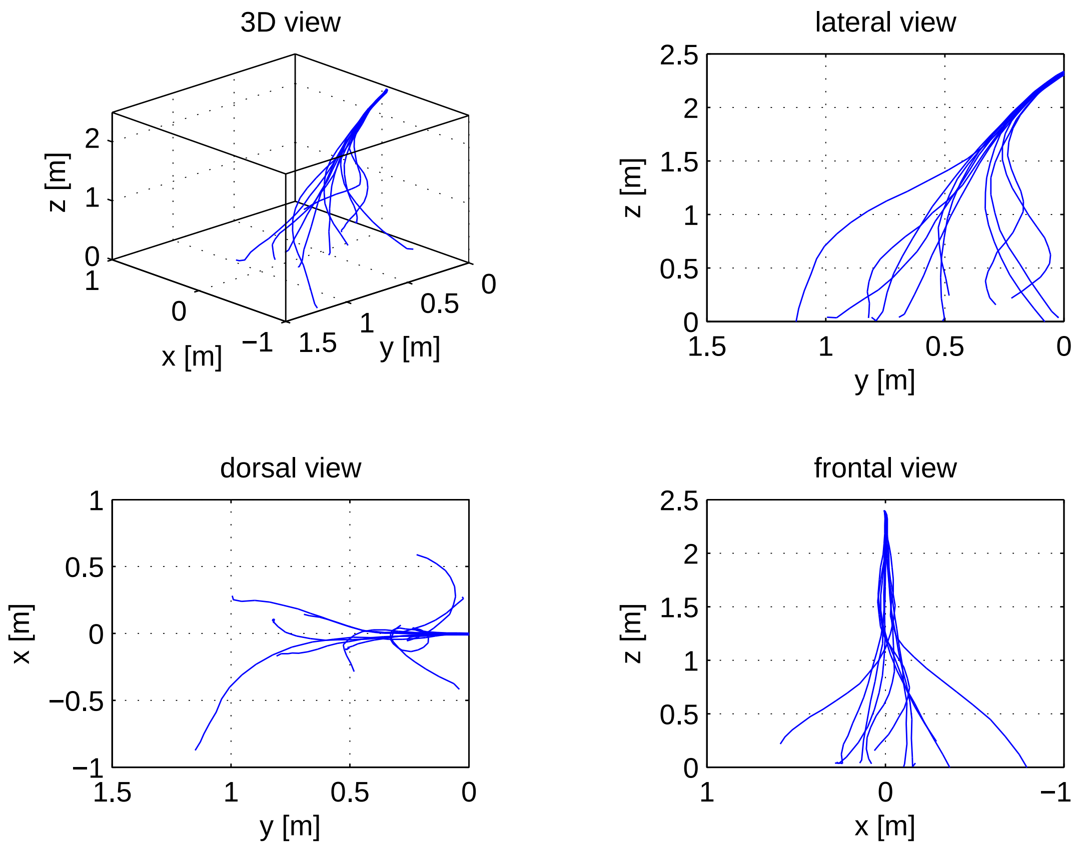
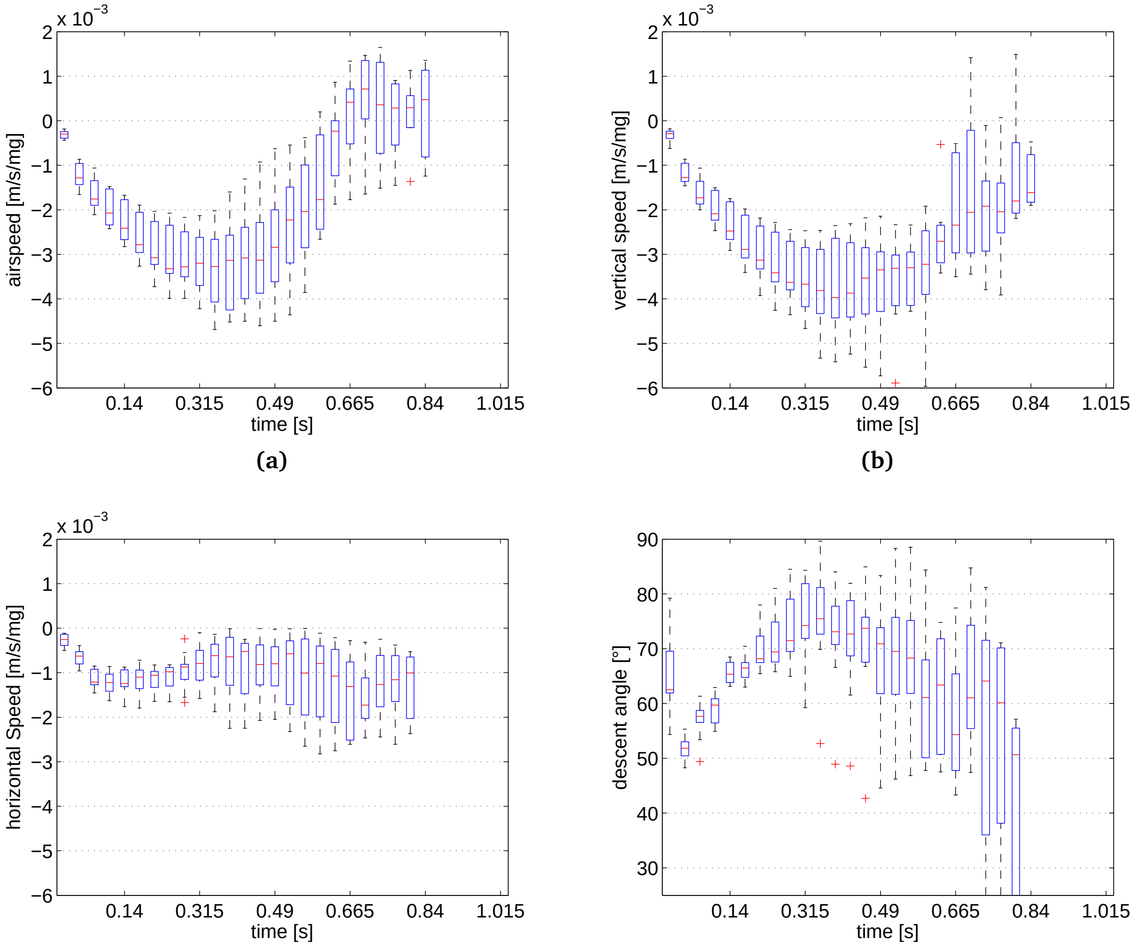


Figure 4.1: Flight trajectories for male *B. dubia* launched from 2.5 m height and a starting angle of 35° (reference experimental procedure). After a ballistic phase of 0.5 – 1 m most test animals deviated from the ballistic trajectory. However no standard trajectory was differentiated. Aerial descent trajectories included curved and helical flight paths as well as straight flight paths with pronounced levelling sections. n=11



(a) (b)

(c) (d)

Figure 4.2: Flight parameters for the aerial descent of male *B. dubia* plotted against flight duration (height of release 2.5 m, starting angle 35°, n=11). Boxplots are consistent with flight trajectories, showing an initial increase for airspeed, vertical speed and descent angle until approximately 0.3 s after launch. At around 0.3 s airspeed and vertical speed gradually decrease as does the descent angle. Also, horizontal speed varies to a greater extent. This indicates an active control behaviour of male cockroaches during flight. For means of a better inter individual comparison all velocities are standardized with regard to individuals mass (mg).

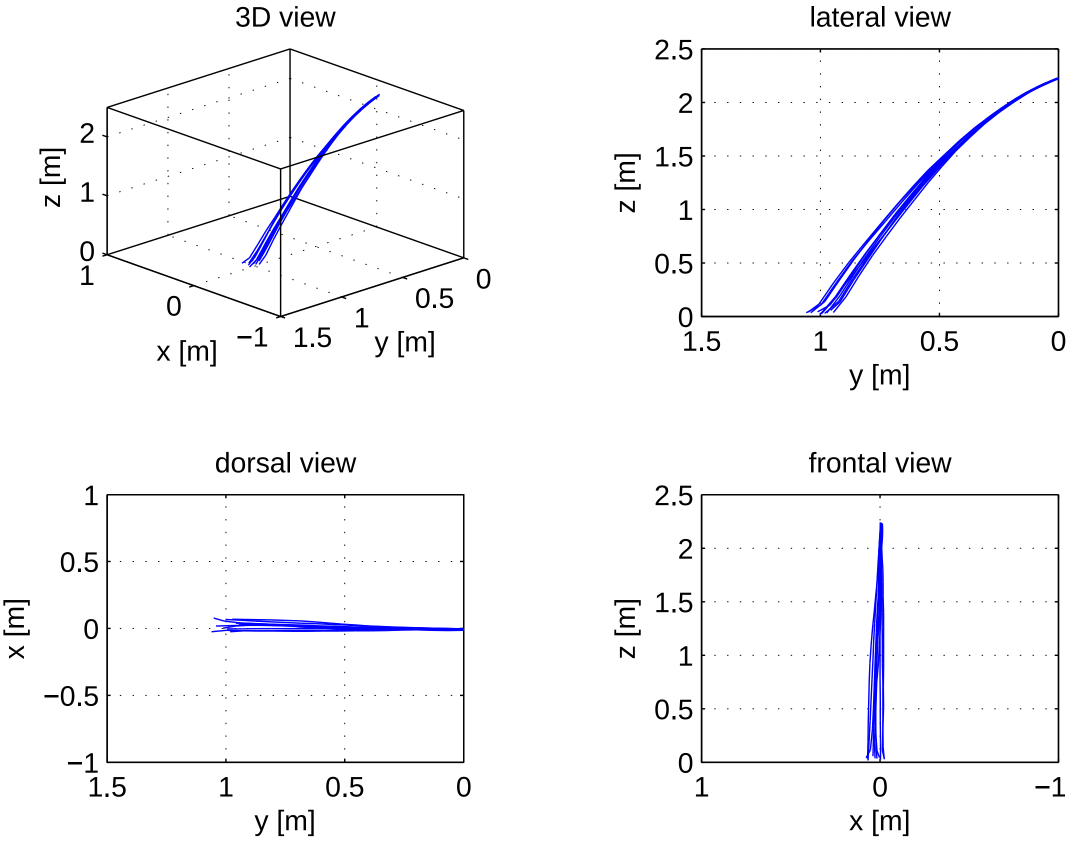
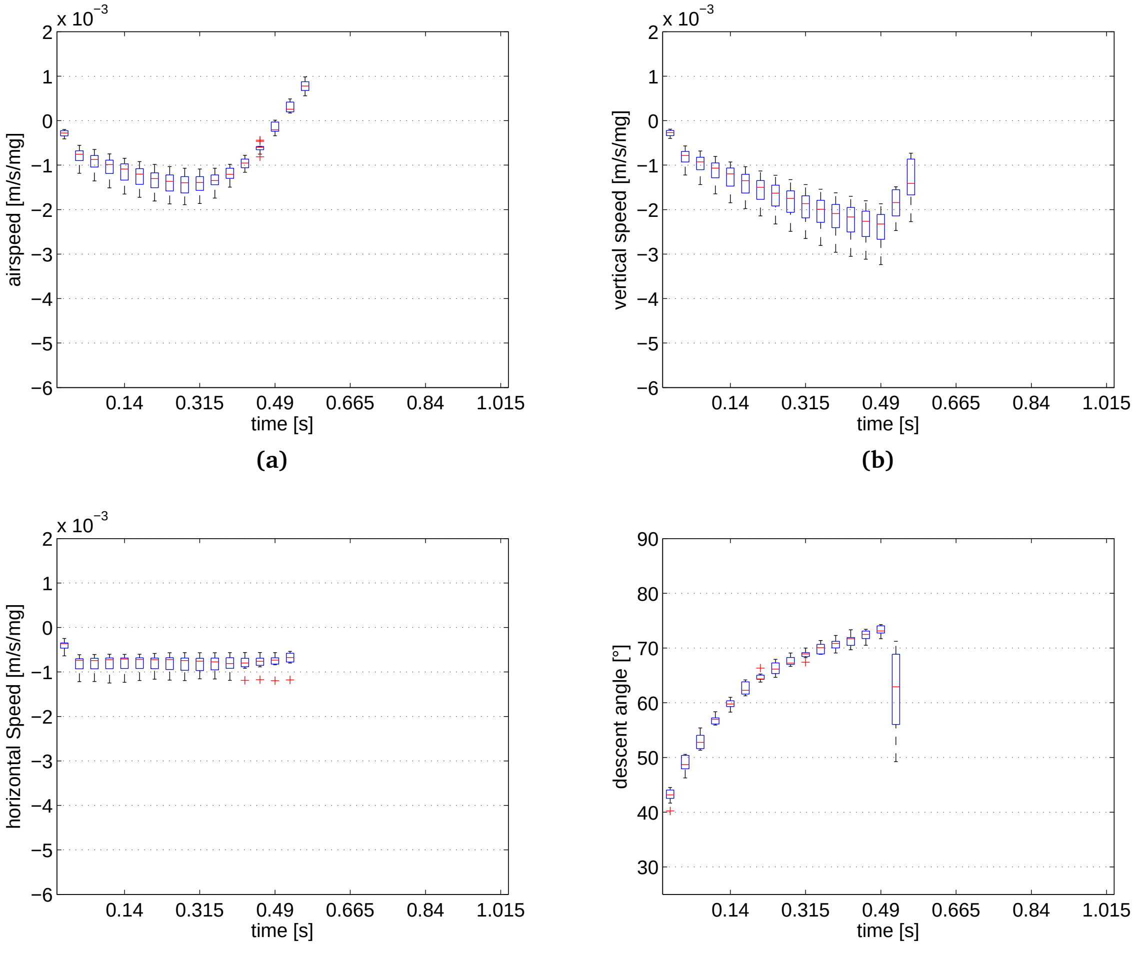


Figure 4.3: Flight trajectories for female *B. dubia* launched from 2.5 m height and a starting angle of 35°. Flight trajectories follow the path of a ballistic projectile. In contrast to male trajectories (fig. 4.1) not a single female deviated from this path (n=10).



(a) (b)

(c) (d)

Figure 4.4: Flight parameters for the aerial descent of female *B. dubia* plotted against flight duration (height of release 2.5 m, starting angle 35°, n=11). Boxplots underline the uncontrolled ballistic nature of female descent as airspeed, vertical speed and descent angle constantly increase during the entire flight, whereas horizontal speed shows no variation. For means of a better inter individual comparison all velocities are standardized with regard to individuals mass (mg).

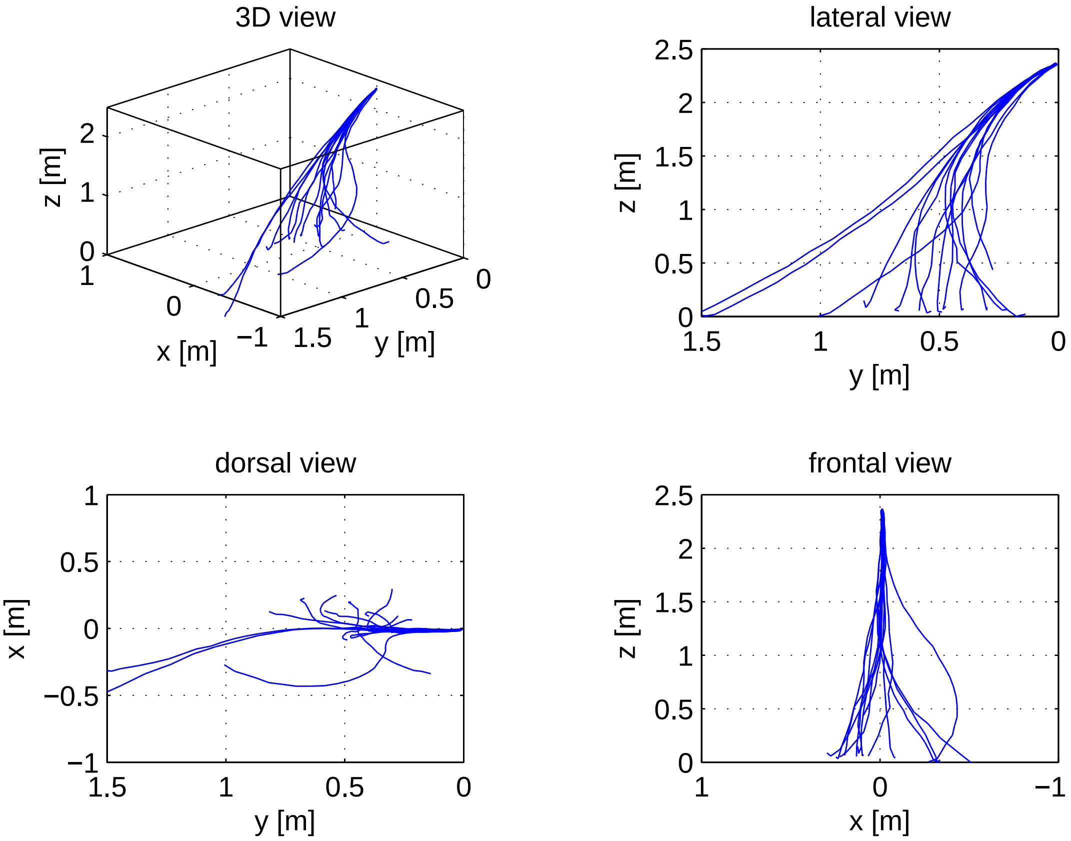
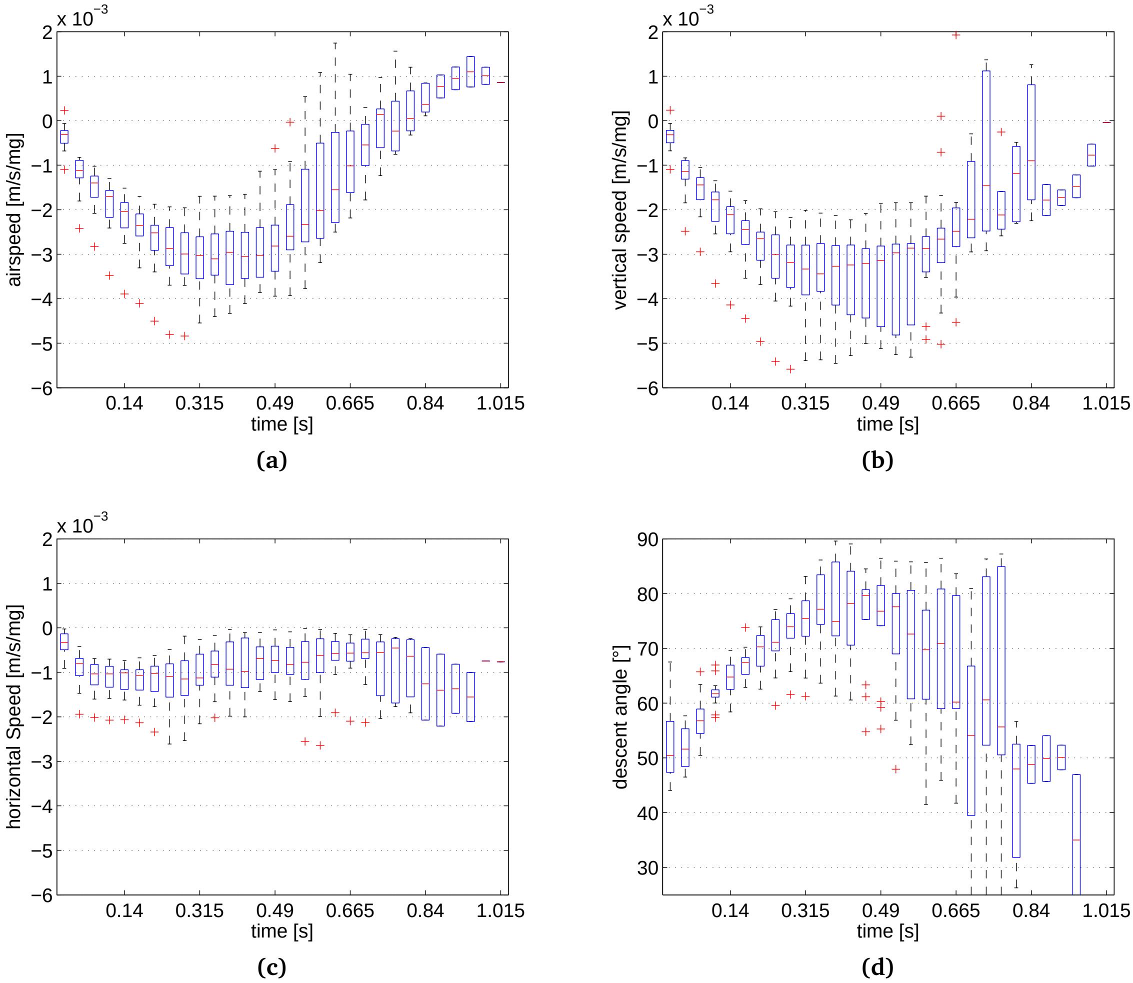


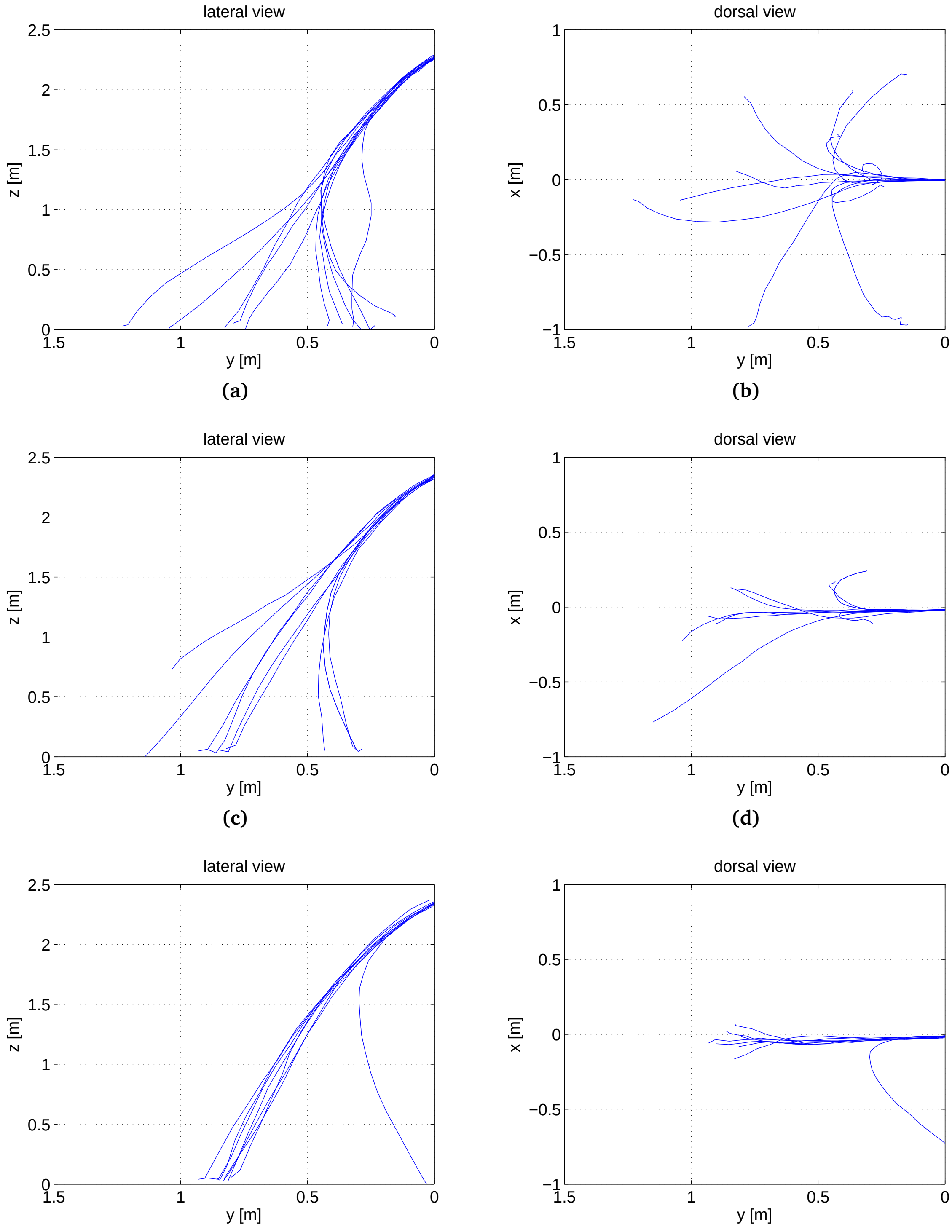
Figure 4.5: Flight trajectories for male *B. dubia* provided with visual landmark patterns (height of release 2.5 m, starting angle 35°, n=14). Flight patterns do not strongly differ from those observed in animals without visual guides.



(a) (b)

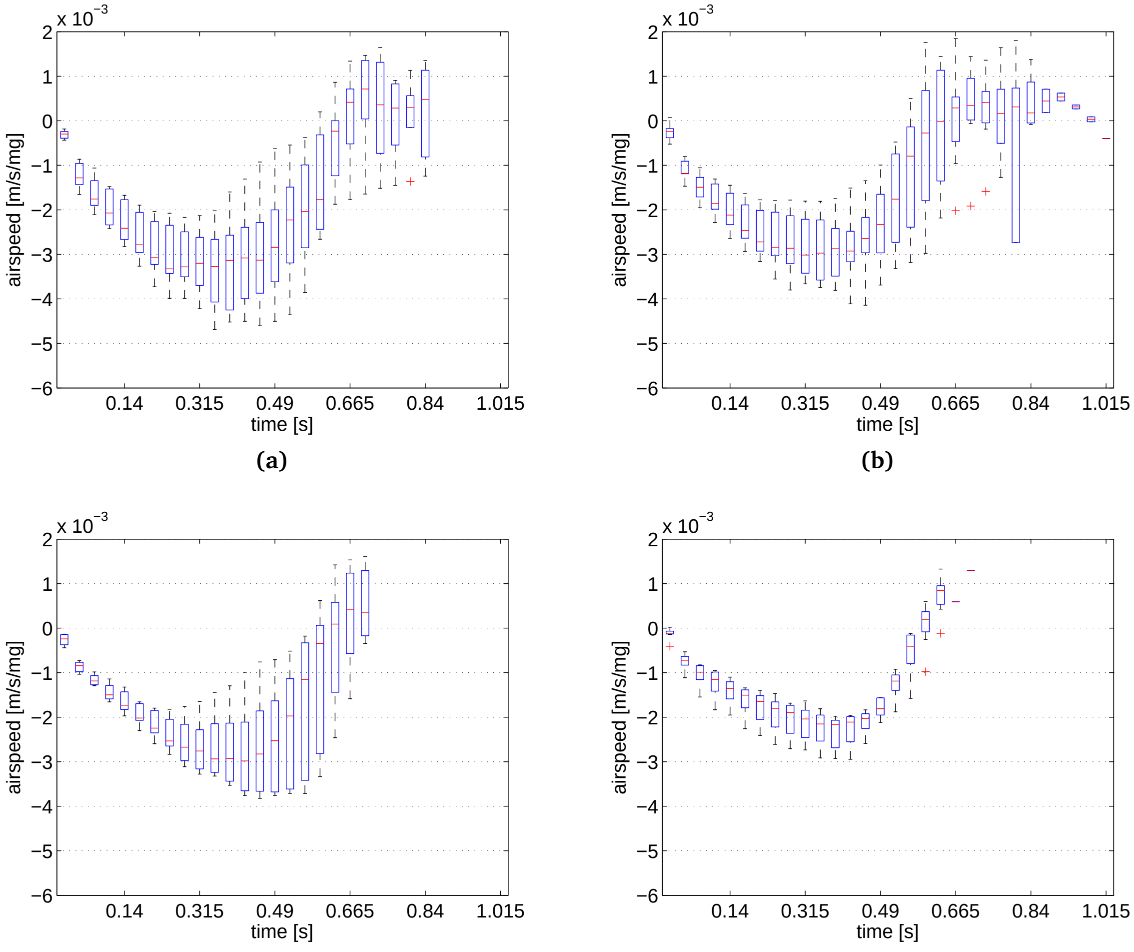
(c) (d)

Figure 4.6: Parameters for the aerial descent of male *B. dubia* provided with visual input (height of release 2.5 m, starting angle 35°, n=14). Neither any velocity component, nor the descent angle pattern differs from those observed in flight lacking visual cues. For means of a better inter individual comparison all velocities are standardized with regard to individuals mass (mg).



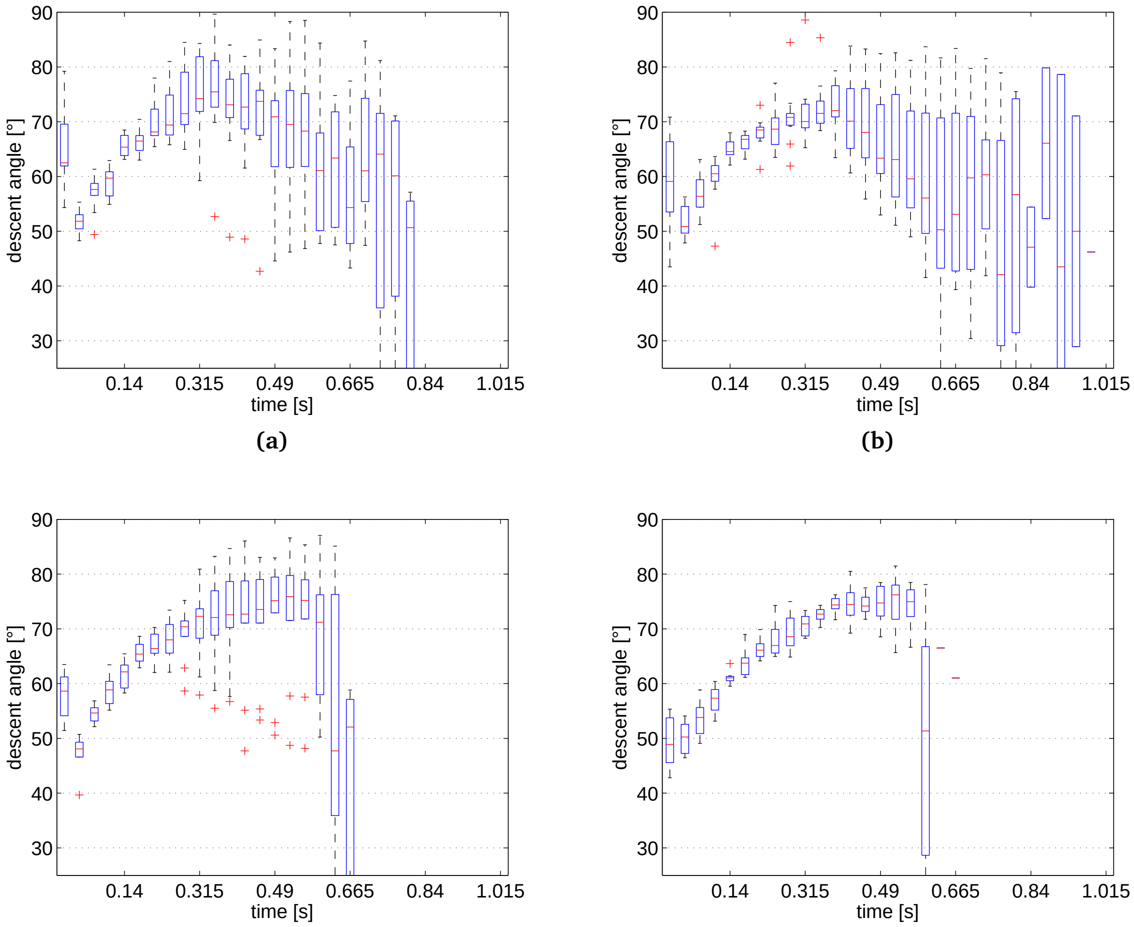
(a) (b) (c) (d) (e) (f)

Figure 4.7: Flight trajectories for male *B. dubia* with additional payloads (height of release 2.5 m, starting angle 35°). **a, b:** With an additional payload of 10% bodymass test animals were still able to control their descent and successfully pull out of a ballistic dive (n=11). **c, d:** With an additional mass of 30% bodymass, little sideward movement in the horizontal plane was observed. Trajectories show little influence of control by test animals (n=10). **e, f:** With an additional payload of 50% bodymass male trajectories resemble those of females i.e. ballistic curves (see fig. 4.3). Males cannot compensate this amount of payload (n=8).



(a) **(b)** **(c)** **(d)**

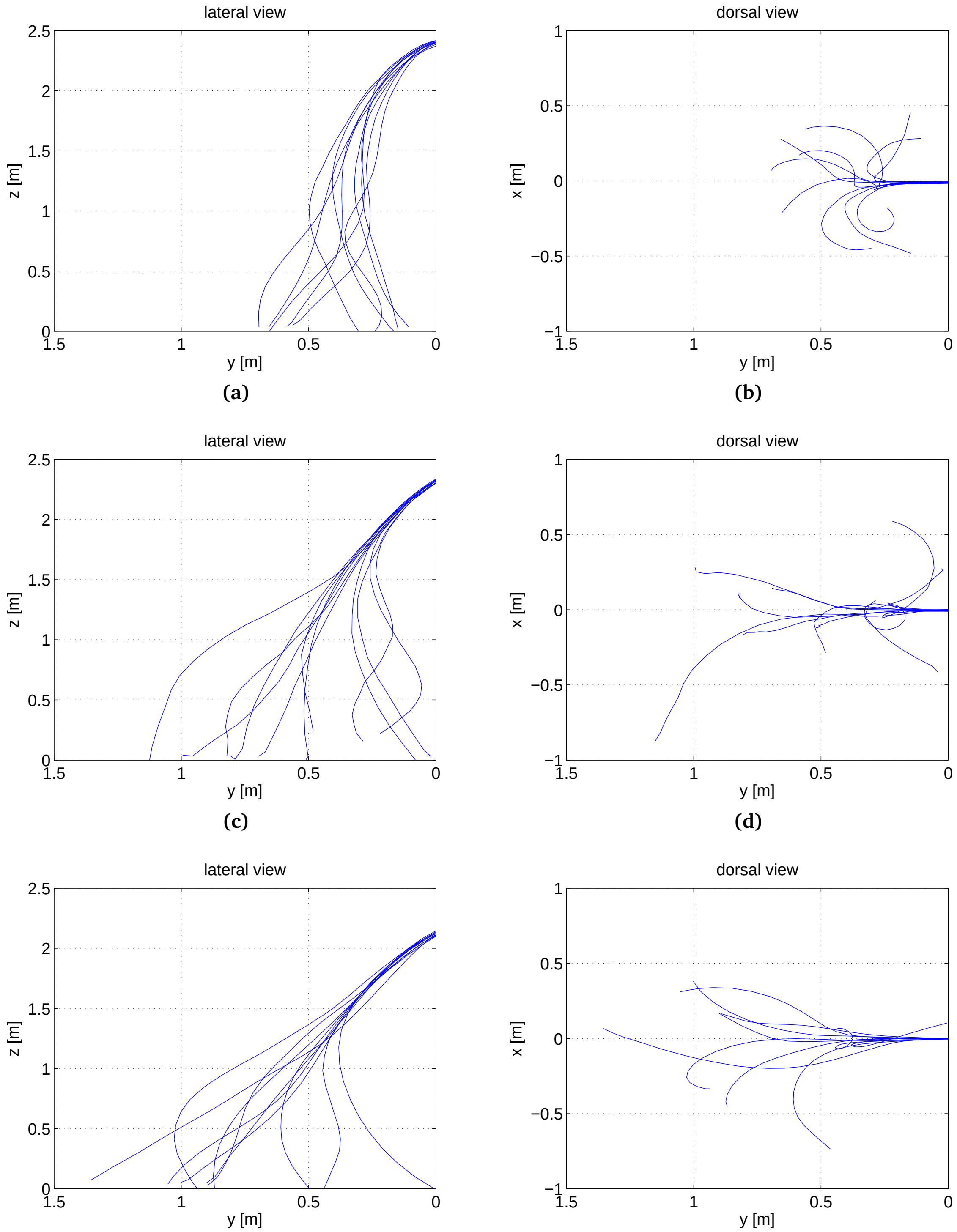
Figure 4.8: Influence of additional mass on airspeed throughout the aerial descent of male *B. dubia*. Airspeed behaviour (with vertical speed as dominant component) reflects the trajectories influenced by additional payload. Airspeed in reference trials without payload (a) and trials with an added 10% bodymass (b) showed similar curve progressions with initially increasing values up to approx. 0.3 s and subsequently a gradual decrease in velocity, indicating a certain amount of aerial control. Flight duration in both cases was nearly equally long. In trials with an additional 30% (c) and 50% (d) bodymass however, graphs for airspeed steadily increased until approx. 0.5 s and then rapidly decreased again, indicating that some individuals had already hit ground without gaining control of flight. Flight duration in these cases was considerably shorter. For means of a better inter individual comparison all velocities are standardized with regard to individuals mass (mg).



(a) (b)

(c) (d)

Figure 4.9: Influence of additional mass on descent angle throughout the aerial descent of male *B. dubia*. Descent angle in reference trials without additional payload (a, n=11) and with 10% additional bodymass (b, n=11) increased during the first 0.3 s of flight and showed great variation and gradual decrease afterwards which shows characteristics of stable and controlled flight. In flight trials with additional masses of 30% (c, n=10) and 50% (d, n=8) bodymass the descent angle also steadily increases until approx. the same max. values as in (a) and (b), however it remains at these max. values until it suddenly drops to zero due to the end of flight.



(a) (b)

(c) (d)

(e) (f)

Figure 4.10: Flight trajectories for male *B. dubia* at varying starting angles. At a starting angle of 25°(**a,b**) both side and top views show curved and helical characteristics. Flight paths deviate early from a ballistic trajectory, the landing zone is well defined. At a starting angle of 35°(**c, d**) helical and curved descents are still observed, however less pronounced than for 25°. At 45°(**e, f**) trajectories do not vary greatly in sideward directions, but are elongated in forward direction. Curved, yet no helical trajectories were observed.

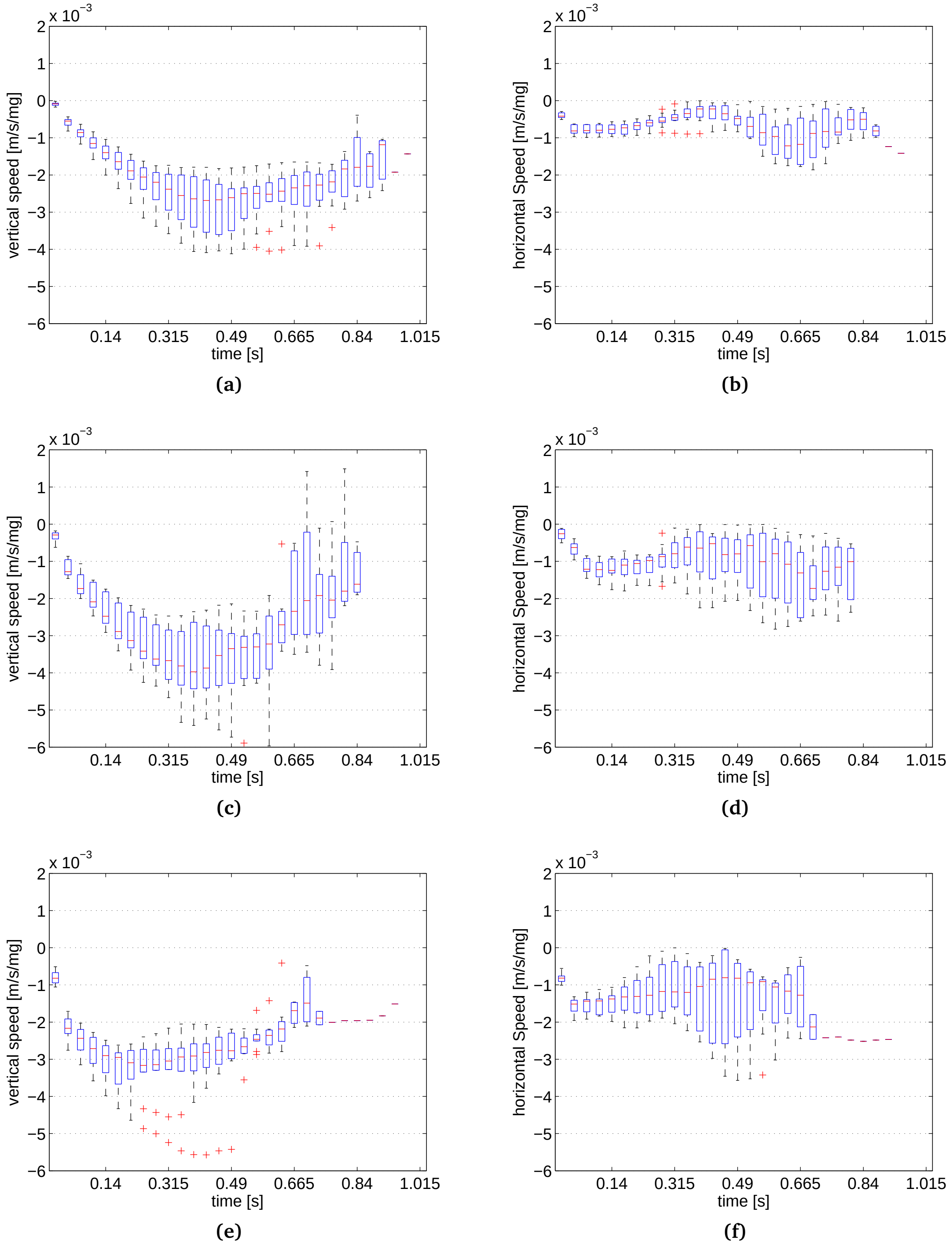


Figure 4.11: Influence of starting angle variation on vertical and horizontal velocity components during the aerial descent of male *B. dubia*. From 25° (a, b; n=10) to 35° (c, d; n=11) to 45° (e, f; n=10) horizontal speed increases. This is due to the steeper tube inclination leading to a faster forward acceleration during the launch phase. The greatest variation as well as the greatest total values in vertical speed however are displayed at 35°, whereas at 45°vertical speed is kept almost constant throughout cockroach flight. All velocities are standardized with regard to individuals mass (mg).

Table 4.1: Summary of flight parameters in *B. dubia* male individuals. Experiments were either performed at varying starting angles (25°, 35°, 45°) with no additional mass or at a fixed angle of 35° with varying additional masses (+10%, +30%, +50% bodymass).

	Starting angle			Added mass		
	25°	35°	45°	10%	30%	50%
	n=10	n=11	n=10	n=11	n=10	n=8
Flight Duration [s]	0.90±0.06	0.78±0.09	0.72±0.11	0.83±0.13	0.71±0.02	0.68±0.02
Total track length [m]	2.59±0.04	2.57±0.19	2.42±0.11	2.62±0.23	2.46±0.20	2.53±0.06
Horizontal flight distance [m]	0.85±0.08	0.95±0.29	1.09±0.24	1.08±0.32	0.89±0.27	0.90±0.07
Start-to-finish distance [m]	2.47±0.03	2.45±0.19	2.33±0.11	2.48±0.18	2.38±0.20	2.48±0.03
Linearity index [-]	1.05±0.02	1.05±0.03	1.04±0.03	1.06±0.04	1.03±0.02	1.02±0.01
Descent angle $\gamma_{initial}$[°]	41.01±2.95	51.70±1.91	56.25±1.86	51.78±2.80	46.85±4.01	50.09±2.95
Descent angle γ_{final}[°]	67.33±7.64	62.20±21.33	62.62±11.51	61.58±19.64	66.03±16.94	74.20± 3.92
$V_{air-initial}$ [ms^{-1}]	1.41±0.14	1.93±0.30	3.14±0.15	1.97±0.25	1.80±0.24	1.98±0.24
$V_{air-final}$ [ms^{-1}]	3.22±0.52	3.60±1.57	3.35±0.77	2.39±1.71	4.24±1.77	5.65±0.90
$V_{vert-initial}$ [ms^{-1}]	0.92±0.09	1.52±0.25	2.61±0.11	1.55±0.21	1.31±0.23	1.52±0.18
$V_{vert-final}$ [ms^{-1}]	2.94±0.43	3.24±1.72	2.94±0.81	2.13±1.70	3.92±1.85	5.42±0.83
$V_{hor-initial}$ [ms^{-1}]	1.06±0.13	1.19±0.17	1.75±0.14	1.22±0.16	1.22±0.14	1.27±0.19
$V_{hor-final}$ [ms^{-1}]	1.25±0.53	1.29±0.57	1.49±0.58	0.94±0.62	1.37±0.80	1.55±0.52

Table 4.2: Summary of flight parameters in *B. dubia* female individuals.

	Starting angle		
	25°	35°	45°
	n=10	n=10	n=10
Flight duration [s]	0.71 ±0.01	0.6±0	0.54±0.02
Total track length [m]	2.55±0.04	2.44±0.02	2.33±0.03
Horizontal flight distance [m]	0.80±0.1	1.01±0.04	0.94±0.04
Start-to-finish distance [m]	2.52±0.03	2.41±0.03	2.31±0.02
Linearity index [-]	1.01±0.002	1.01±0.001	1.01±0.001
Descent angle $\gamma_{initial}$ [°]	41.40±2.81	48.72±1.52	54.46±1.59
Descent angle γ_{final} [°]	78.51±1.47	73.23±0.81	72.56±1.66
$V_{air-initial}$ [ms^{-1}]	1.53±0.23	2.76±0.12	3.28±0.16
$V_{air-final}$ [ms^{-1}]	5.88±0.16	5.92±0.18	5.97±0.17
$V_{vert-initial}$ [ms^{-1}]	1.01±0.17	2.07±0.11	2.67±0.16
$V_{vert-final}$ [ms^{-1}]	5.76±0.16	5.67±0.18	5.69±0.17
$V_{hor-initial}$ [ms^{-1}]	1.14±0.18	1.82±0.09	1.90±0.1
$V_{hor-final}$ [ms^{-1}]	1.17±0.15	1.71±0.08	1.79±0.18

Table 4.3: Summary of flight parameters in *B. dubia* male individuals, provided with visual landing marks. Starting angle 35°, n=14.

Flight duration [s]	0.83 ±0.11
Total track length [m]	2.53±0.27
Horizontal flight distance [m]	0.89±0.42
Start-to-finish distance [m]	2.41±0.26
Linearity index [-]	1.05±0.02
Descent angle $\gamma_{initial}$ [°]	51.87±3.64
Descent angle γ_{final} [°]	59.97±22.99
$V_{air-initial}$ [ms^{-1}]	1.93±0.31
$V_{air-final}$ [ms^{-1}]	2.24±0.71
$V_{vert-initial}$ [ms^{-1}]	1.52±0.25
$V_{vert-final}$ [ms^{-1}]	1.92±0.96
$V_{hor-initial}$ [ms^{-1}]	1.19±0.22
$V_{hor-final}$ [ms^{-1}]	0.88±0.40

4.2 2D Analysis – Flight Initiation and Stabilisation Phase

During high-speed records all cockroaches slid down the launch tube in a head-first position on their back, and subsequently dropped into the flight arena in this body position. The resulting initial flight path was primarily characterized by ballistic dive, body reorientation, wing deployment manoeuvres and attitude stabilization.

After an initial dive phase in which no reactions of the test animals were observed, body reorientation manoeuvres began and concurrent wing deployment started. This was considered as the end of the passive ballistic dive. The wing deployment procedure marked the beginning of body stabilization, essentially leading to a more or less constant body posture. This attitude stabilization again was the prerequisite for a stable and controlled aerial descent. This process was observed throughout all trials at all starting angles ($25-45°$). A general shift in behavioural pattern depending on starting angle was not indicated (fig 4.12).

Body reorientation was performed by means of dorso-ventral righting, i.e. the test animals re-orientated themselves from a position with feet facing upwards, to a position with feet facing downwards. Two manoeuvres for dorso-ventral righting were observed: Whereas some cockroaches performed a downward outside half loop to recover from inverted postures other insects passed over to normal flight through a half roll.

The two flight manoeuvres half loop and half roll were performed depending on the cockroaches' horizontal flight attitudes α_H when initiating the stabilization reactions (fig. 4.13). Although α_H displayed negative values for both half loops and rolls, values were considerably more negative for the former. According to the definitions given in equations 2.1 and 2.2this had a strong influence on the body angle of attack. In case of negative body angles of attack (α_B), indicating an extreme head down posture and the descent angle being smaller than the body angle of attack ($\gamma < \alpha_B$), outside half loops were initiated. If α_B was positive, indicating a less extreme head down posture and the descent angle being greater than the body angle of attack ($\gamma > \alpha_B$), cockroaches banked into a half roll.

Which dorso-ventral righting manoeuvre was initiated, was neither dependent on starting angles nor on the initial descent angles at which body reorientation occurred. Whereas the former was varied from 25°- 45°, the latter remained constant and did not differ significantly between trials with mean values ranging from $46 \pm 15°$ to $57 \pm 4°$ (Student t-test, two-sided, α = 5%) (fig. 4.13).

At the end of body righting α_B was positive in all trials, independent of the performed manoeuvre and regardless of α_H. With mean values for α_B ranging from $66 \pm 16°$ to $77 \pm 21°$ the body angle of attack was considerably greater than at the beginning of aerial descent, as were all descent angles with values for γ ranging from $76 \pm 7°$ to $81 \pm 5°$ (fig. 4.14). A single difference remained between half loop and roll flights, with α_H showing negative mean values for half loop trials and positive values for roll trials. However, due to the large variation these differences were not significant (fig. 4.14).

Wing deployment started as early as 0.004 s after start (observed for angles of 45°) and as late as 0.18 s after start (observed for 35°). On average wing deployment started after 0.063 ± 0.04 s and due to the large variation showed no difference between half roll and half loop trials although there seemed to be a tendency for wing deployment starting earlier in half loops (fig. 4.12 and table 4.4). Additionally due to the large temporal variation between individual behaviour, no dependency of wing deployment initiation on start angle was identified.

Attitude stabilization started as early as 0.046 s after start and was observed for angles of 45°and half loop trials. The slowest reactions with regard to attitude stabilization were observed after 0.13 s in test animals launched at 25°and performing roll manoeuvres. Mean values did show that the time lapse until attitude stabilization was initiated was shortest for starting angles of 45°. However no general pattern revealing a dependency of reaction time on starting angle was made out.

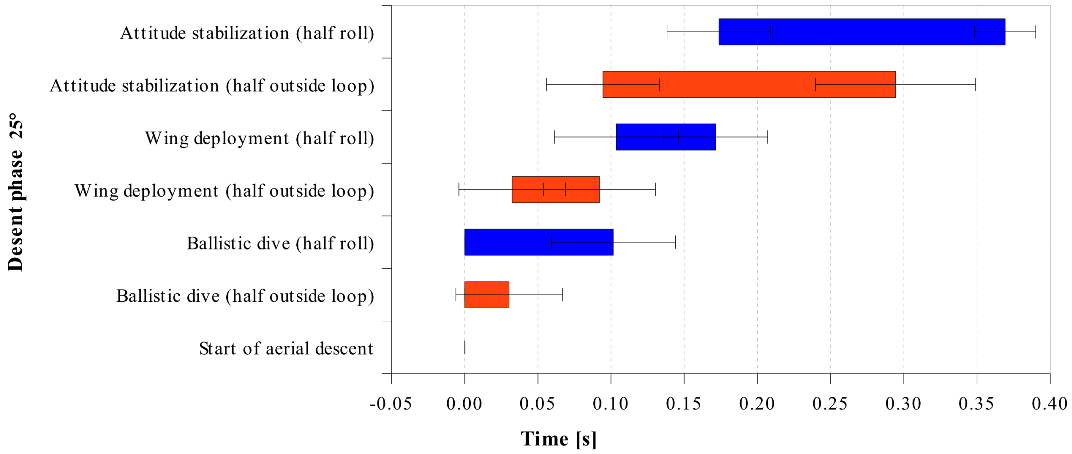
Stable descent was achieved after 0.394 s at the latest (start angle 25°) and was earlier observed in half loop trials than in roll trials. Although roll trials indicated that the time lapse between start and stable descent was dependent on starting angle, this could not be generally shown. On average it took 0.303 ± 0.036 s for cockroaches to pull out of the ballistic dive and start a stable descent.

After wing deployment and attitude stabilization all cockroaches were in a stable head-up position with regard to their flight path trajectory. Legs and feet always faced downward and were stretched out laterally. This posture was considered as the controlled aerial descent phase.

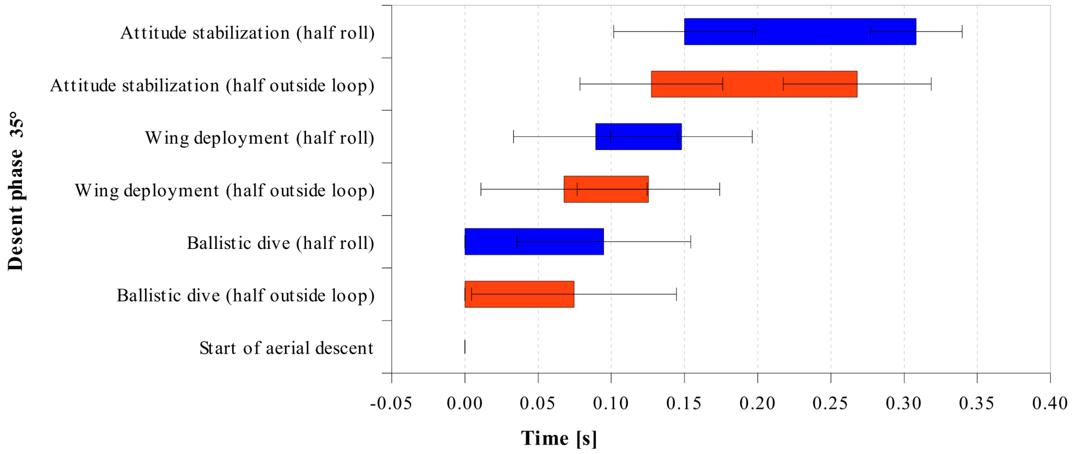
In summary , high-speed recordings reveal that wing deployment is the essential critical manoeuvre relevant for flight control. A stable attitude and body posture devoid of pitch and roll movements is obtained when both fore and hindwings are fully deployed. A regular wingbeat commences once a steady body angle of attack is achieved.

Table 4.4: Temporal summary of events occurring during the initial phase of aerial descent in male *B. dubia* as recorded with high-speed video equipment.

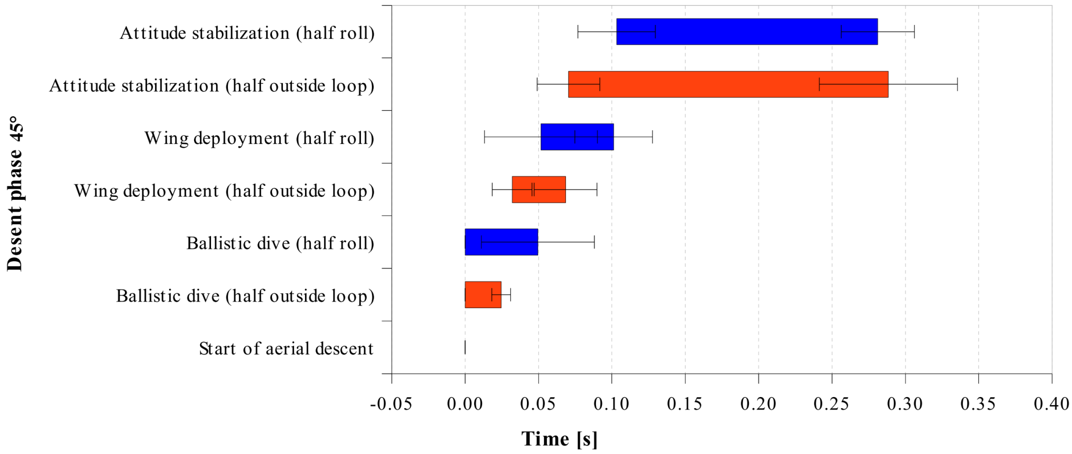
	Half roll			Half loop		
	25°	35°	45°	25°	35°	45°
	n=5	n=6	n=5	n=5	n=6	n=5
Duration of ballistic dive [s]	0.102±0.042	0.095±0.059	0.050±0.039	0.030±0.036	0.075±0.070	0.025±0.006
Start of wing deployment [s]	0.104±0.042	0.089±0.056	0.052±0.039	0.032±0.036	0.068±0.057	0.032±0.013
Duration of wing deployment [s]	0.068±0.008	0.059±0.015	0.050±0.020	0.060±0.041	0.058±0.028	0.036±0.019
Start of attitude stabilization [s]	0.174±0.035	0.150±0.048	0.103±0.026	0.094±0.039	0.127±0.049	0.070±0.021
Start of controlled descent [s]	0.371±0.021	0.310±0.031	0.283±0.025	0.296±0.055	0.270±0.050	0.290±0.047



(a)



(b)



(c)

Figure 4.12: Timelines of the "uncontrolled" descent phases at the three investigated tilt angles of the launch tube: 25°(a), 35°(b) and 45°(c). Trials are subdivided according to the observed flight manoeuvres half loop and half roll (see text, fig 4.13).

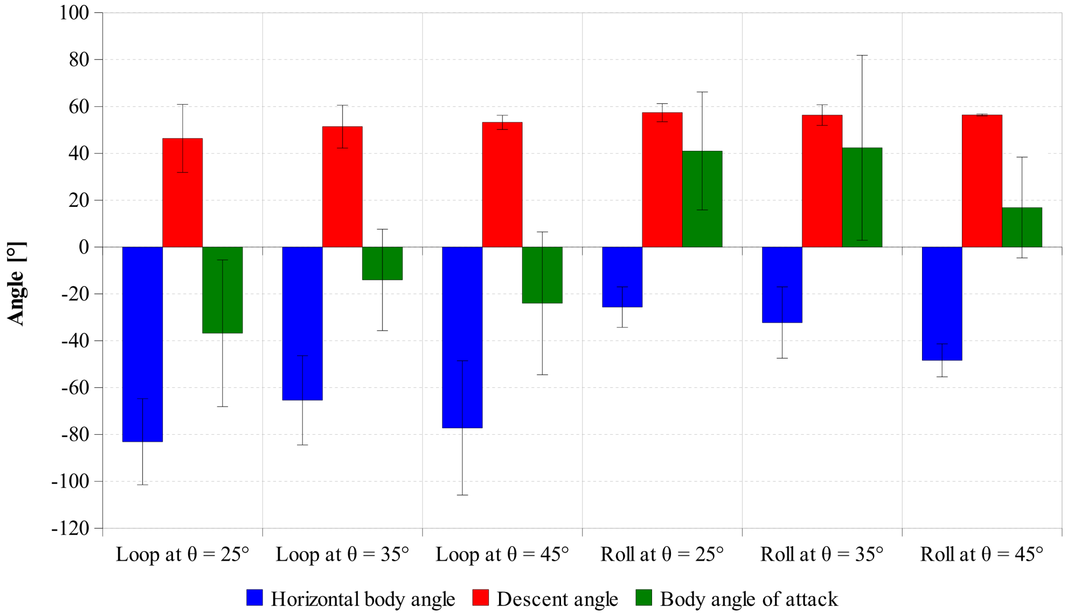


Figure 4.13: Initial body orientation in male *B. dubia* after launch tube exit, shows a dependency of the dorso-ventral righting manoeuvre on the body angle of attack (α_B). For positive values of α_B cockroaches bank into a half roll, for negative values of α_B outward loops are initiated. Interestingly, the initial descent angle (γ) does not differ between starting angles 25°-45°. Therefore, the cockroaches' orientation to the horizontal plane (horizontal body angle, α_H) is decisive for the outcome of α_B. (α_B, green), (α_H, blue)and γ, red) are represented as mean values ± s.d.error bars, n=11 with 5 rolls and 6 half loops.

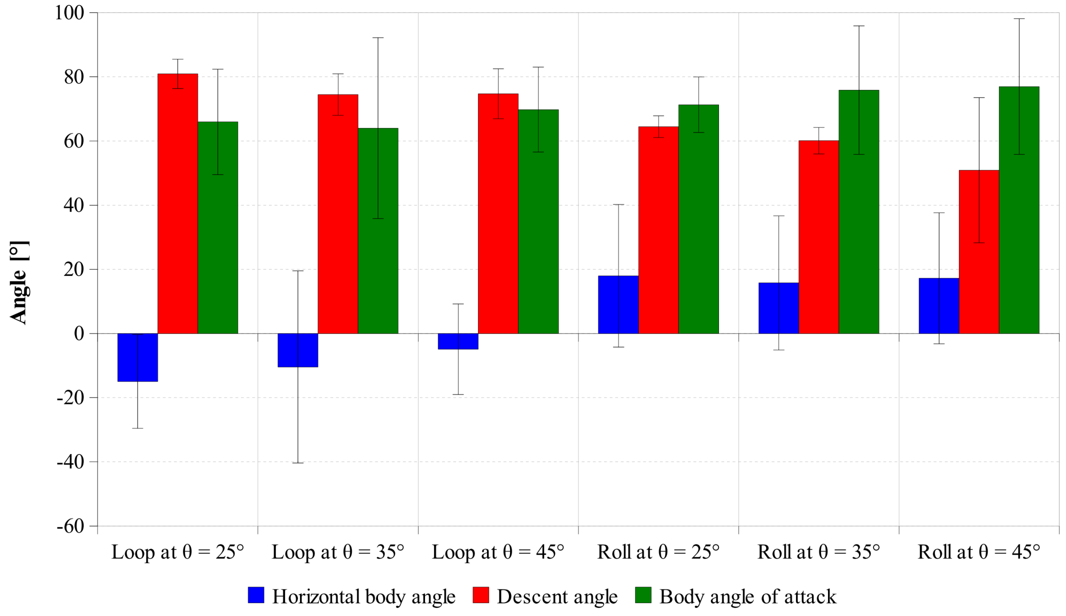


Figure 4.14: Final body orientation in male *B. dubia* after dorso-ventral righting manoeuvres and body stabilization. Only the final horizontal body angle α_H seems to differ between loop and roll trials. However, this is not significant. Both the body angle of attack α_H and the descent angle γ display large positive values for loop and roll trials, at the end of body stabilization.

4.3 2D Analysis – Landing Phase

High-speed recordings of the landing sequence provided information on approximately the last metre of descent, which could not be appropriately resolved by stereo recordings.

Flight parameters (see 2.5.2) between single individuals varied greatly, however showed only minor variation throughout individual flights (see table 4.5 and figure 4.15). Airspeed and vertical speed showed a minor tendency toward decreasing with decreasing height in as much as horizontal speed displayed a minor tendency toward increasing with decreasing height. Throughout the final metre a descent angle of $61.90 \pm 4.50°$ was attained.

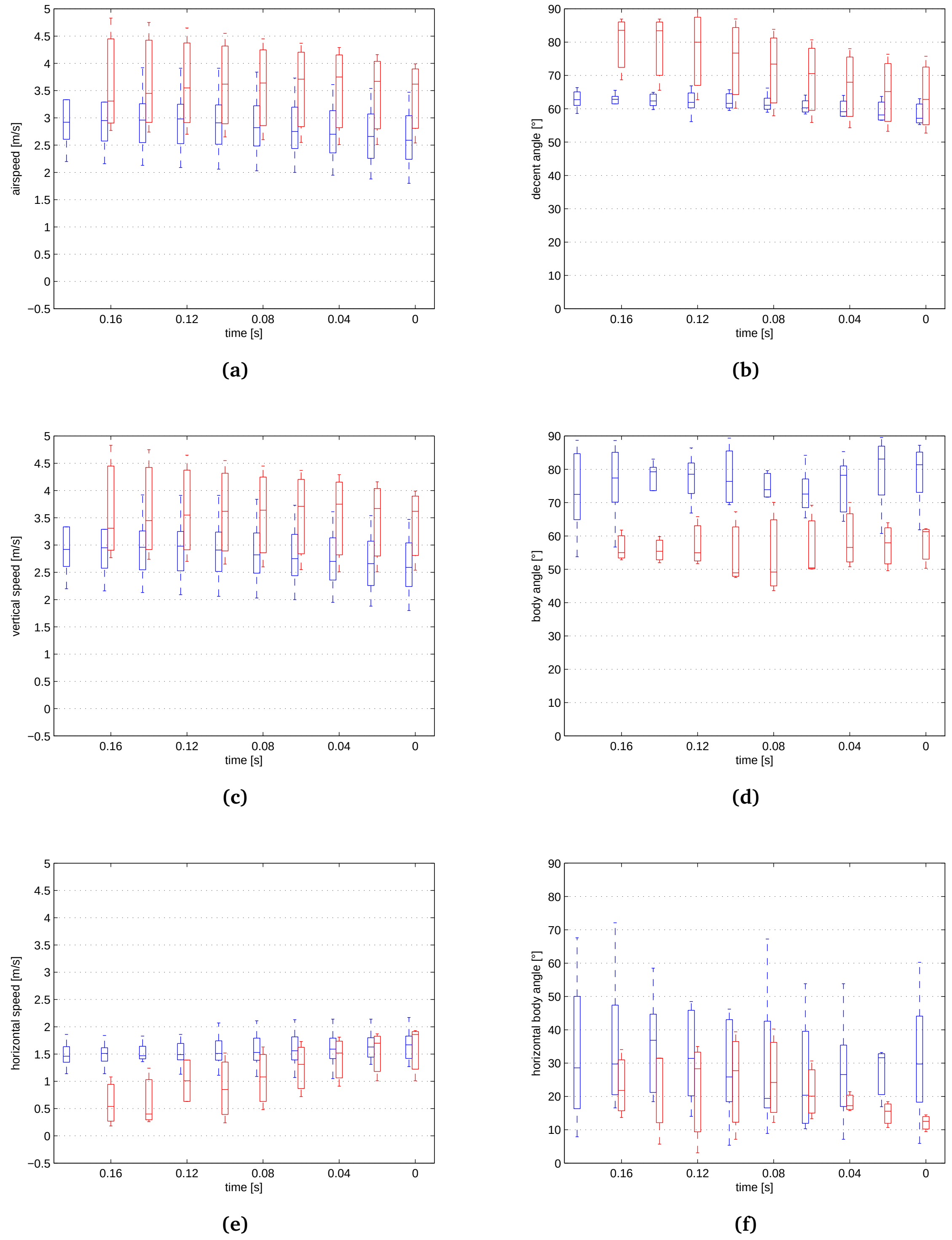
Neither of the behavioural components (see 2.5.3) showed a systematic adaptation in preparation of landing throughout tested individuals. Whereas both body angle α_B and horizontal body α_H seemed to slightly oscillate around an average value (see figure 4.15), wingbeat frequency remained nearly constant at 26.70 ± 1.80 Hz and showed no variation with decreasing height.

3 comparative trials performed with cockroaches that were released sliding down the launch ramp on their back did show a tendency towards a reduction of descent angle as well as an increase of horizontal speed throughout the last metre of flight. However due to the small sample size and the large inter-individual variation it remains unclear whether this in fact can be seen as a systematic landing approach.

Consequently, the analysis of high-speed recordings during the landing phase of male *B. dubia* only showed one stereotypic behaviour which can be fully accounted for: the animals' legs and feet always faced downward (dorso-ventral body orientation) and were laterally stretched out from the body. This body posture is already achieved at the beginning of controlled aerial descent (see section 4.2).

Table 4.5: Summary of flight parameters and behavioural components during the last metre of aerial descent in *B. dubia* male individuals, recorded with high-speed camera equipment; starting angle 35°, n=9.

V_{air} [ms^{-1}]	3.21±0.61
V_{vert} [ms^{-1}]	2.83±0.60
V_{hor} [ms^{-1}]	1.50±0.29
Descent angle γ[°]	61.90±4.50
Body angle α_B[°]	94.30±18.90
Horizontal body angle α_H[°]	32.50±18.70
Wingbeat frequency f [Hz]	26.70±1.80



(a) **(b)**

(c) **(d)**

(e) **(f)**

Figure 4.15: Timeline for flight parameters and behavioural components during the last metre of aerial descent in *B. dubia* male individuals, recorded with high-speed camera equipment (starting angle 35°;**blue:** feet-down start posture, n=9; **red:** feet-up start posture, n=3). In blue plots all parameters remain more or less constant. In red plots the horizontal speed seems to increase during landing approach, the descent angle seems to decrease. Due to the small sample size and the large variation it remains unclear whether this can be seen as a clear strategy.

4.4 Flight Behaviour Analysis

Both stereo recordings as well as 2D high-speed recordings provided input for the assessment of flight behaviour in cockroaches. As mentioned, certain flight parameters can also be seen as behavioural components, which ensure a stable descent. In sections 4.1, 4.3 and especially 4.2, these parameters have been described on a quantitative basis. As far as certain flight manoeuvres are concerned, a temporal assessment has also already been given in the aforementioned sections (see 4.2). Flight behaviour however, may also be assessed on an operational basis.

As such three operational procedures were defined for flight experiments: launch, descent and touchdown. A successful entire flight operation was defined when test animals landed on their feet and did not rebound from the floor. This accounts for the best possible transition from aerial to terrestrial locomotion. Accordingly, each operational level was categorized with respect to consecutive behavioural components)(e.g. change of body posture) and their respective influence on each other. The relationship of consecutive steps was delineated in ethograms and quantified with relative frequency.

High speed recordings showed that launch postures included cockroaches leaving the launch tube in a straight forward, head first orientation as well as two sideways orientations: a head first and an abdomen first launch tube exit. A straight forward orientation was usually preferred by cockroaches. During the descent procedure either an active stabilization took place or no stabilization occurred. Cockroaches predominantly stabilized their fall. Body reorientation, i.e. dorso-ventral righting was performed by rolls or loops. In such cases active stabilisation directly lead to either curved, helical or straight flight trajectories. To a great part, curved and helical trajectories were observed. Both strategies almost always led to a safe landing without rebound. In cases where no attitude stabilization was observed, the subsequent near ballistic drop nearly always lead to a head first impact and additional rebound (figs. 4.16, 4.17).

Summarizing and integrating both kinematic and behavioural analysis leads to the conclusion, that animals which actively stabilize their descent during an initial ballistic dive thereby attaining a feet down body posture, most commonly diverge into helical and curved flight paths. These paths seem most suitable for the reduction of the vertical velocity component, which is the predominant flight vector. As a result overall airspeed is reduced which in return leads to a softer ground impact and smoother transition between aerial and terrestrial locomotion.

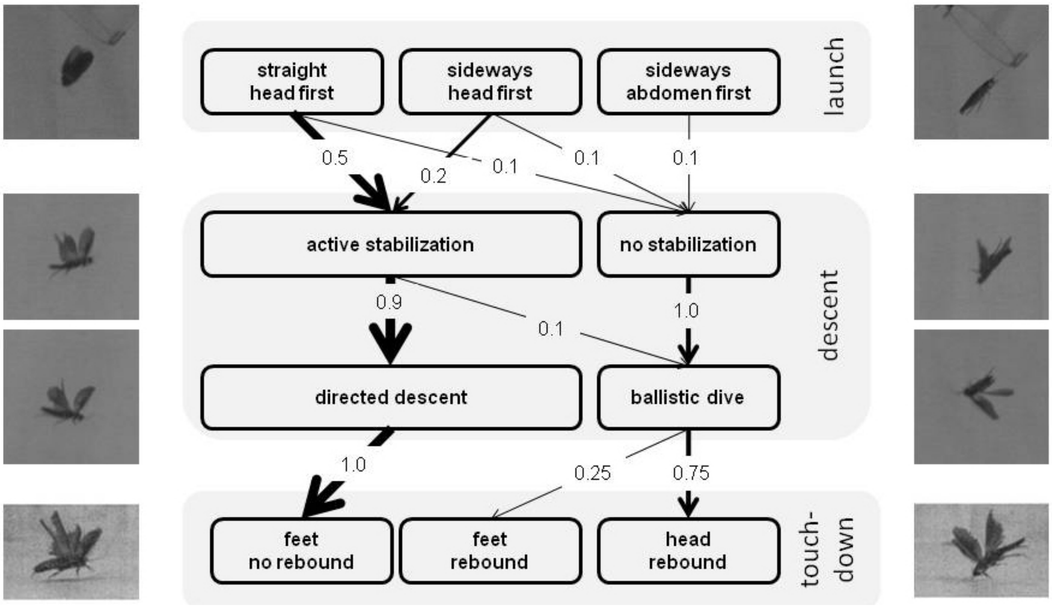


Figure 4.16: Ethogram depicting the operational development of aerial descent in male *B. dubia* (height of release 2.5 m, starting angle 35°, n=10). An active stabilization will lead to a controlled descent and subsequent successful landing, consisting of a single touchdown manoeuvre without rebound. Additional images taken from high-speed video sequences illustrate a successful descent manoeuvre (left) and an unsuccessful descent manoeuvre (right) with according body postures.

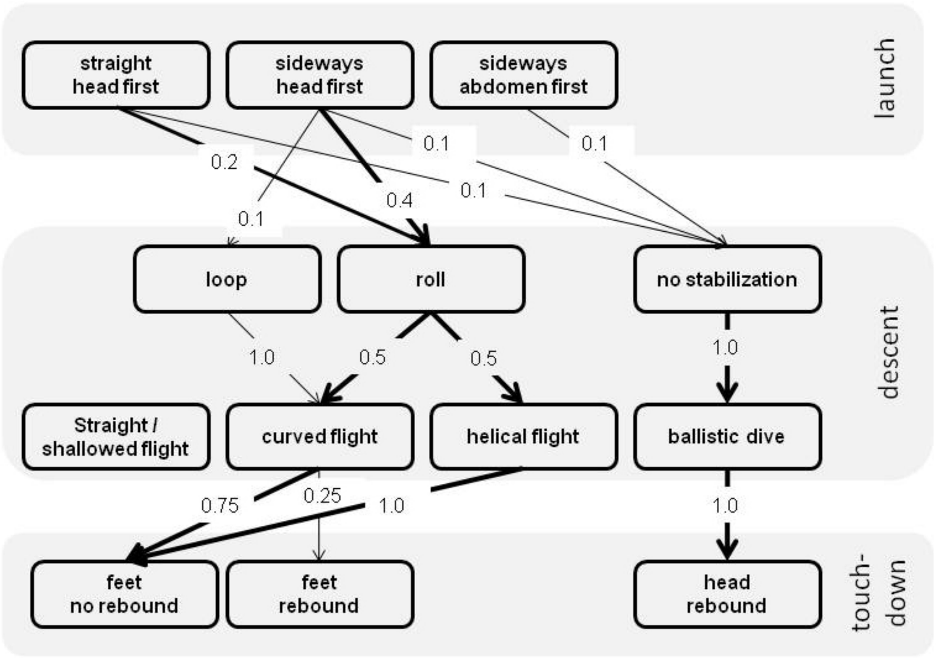


Figure 4.17: Ethogram depicting the operational development of aerial descent in male *B. dubia* on a more detailed level (height of release 2.5 m, starting angle 25°, n=10). Curved and helical flight paths are preferred and usually lead to successful landings.

5 Discussion

With respect to the chosen project objectives (see 2.5) the experimental outcome can be summarized as follows:

1. A controlled descent out of 2.5 m height can be observed in male specimens of *B. dubia*. This becomes apparent in direct comparison to wingless females of the same species. Whether or not this controlled descent is directed or not, could not be determined from experimental results.
2. No single distinct flight or landing trajectory was distinguishable. Rather, three types of landing trajectory which all potentially led to a successful landing were observed.
3. Of the potential flight phases (see 2.5.1) all were observed but an equilibrium flight phase which lacked entirely. The ballistic dive phase was most pronounced and clearly identifiable as an individual phase. Wing deployment and stabilization could not be identified in flight trajectories, but were observed in video recordings as transitory flight elements between the ballistic phase and controlled aerial descent.
4. Stereotypical cockroach behaviours observed after ballistic falling, included dorso-ventral righting either by performing a half outward loop or a half outward roll manoeuvre. Dorso-ventral righting and posture stabilization was supported by wing deployment. Legs were laterally extended throughout descent.
5. Foremost, stereotypical reactions result in a stable dorso-ventral body orientation. A sprawled posture is obtained throughout the entire aerial descent and provides for a successful aerial-terrestrial transition.

In the following this is discussed in detail.

5.1 Flight and Landing Kinematics

Each classical aerial form of locomotion (parachuting, gliding and powered flight) is characterized by specific morphological and aerodynamic features (Thomason, 1995). However, the aerial behaviour of *B. dubia* is not clearly classifiable within these categories.

The characterization of the flight paths and the quantification of flight phases during the aerial descent in *B. dubia* show similarities with both characteristics of the directed aerial descent of canopy ants as well as bristletails. As reported by (Yanoviak et al., 2005; Yanoviak and Dudley, 2006) workers of numerous arboreal ant species exhibit three distinct stages in their directed aerial descent. Initially, the ants drop vertically with extended appendages – flight resembles uncontrolled (ballistic) parachuting. Subsequently, ants rapidly turn in order to align the body toward the tree trunk. Finally, the aerial descent is accomplished with a steep and directed glide to the trunk. In arboreal bristletails an initial period of free-fall is also present, as is body reorientation and a targeted controlled glide (Yanoviak et al., 2009), the latter however greatly levelling off. A near vertical ballistic drop is present in *B. dubia*, as is body reorientation. Curvilinear trajectories are most common and seemingly not targeted. Herein lies the greatest difference to ants and bristletails as can be said by the outcome of our experiments.

While trajectory-averaged descent angles during the investigated aerial descent of cockroaches are $64.04 \pm 2.85°$, averaged descent angles in falling bristletails (69°) and equilibrium glide angles in canopy ants (75°) (Yanoviak et al., 2005, 2009) are higher and thus their general trajectories steeper. However, one must take in to account that at least the latter animals seemingly target their descent towards the nearest located tree trunk.

As release height in both ant and bristletail experiments was considerably higher than in our performed trials, it remains unclear whether trajectories in *B. dubia* will resemble those in ants and bristletails once release heights are identical. However as far as velocities are concerned, equilibrium glide speeds of falling canopy ants (Yanoviak et al., 2005) are comparable to the airspeed of the analysed cockroaches during stable descent (e.g. at $35°3.6 \pm 1.57\,\mathrm{ms}^{-1}$). Therefore we assume that at least near identical settings are achieved.

In comparison, glide angles in gliding marsupials *Petaurus* are considerably smaller (Nachtigall, 1979). For Mahogany Gliders (*Petaurus gracilis*) and Sugar Gliders (*Petaurus breviceps papuanus*) glide angles ranging between $20 - 30°$ have been reported. In contrast to cockroaches however, these mammals use gliding in order to cover longer distances and therefore show basically two-dimensional trajectories. Neither curves nor helical trajectories are performed and they do not seem desirable in order to reduce vertical velocities during flight. Glide angles displayed by the Southern Flying Squirrel (*Glaucomys volans*, $48 \pm 5°$) are substantially higher than those of other investigated gliding mammals. Bishop (2005) however trace this back to the fact that the squirrels did not reach their minimum glide angle during experimental trials, because the launch height was too low. Although similar effects may be present in our experimental results, these mentioned larger gliders clearly possess an equilibrium glide phase with pronounced controlled lift and drag forces. *B. dubia* can clearly not be classified within this context.

Only few winged insects are capable of a more or less pronounced and controlled gliding flight, among them dragonflies. For dragonflies maximum glide angles of approximately 30°have been reported (Wakeling and Ellington, 1997), which, is well below those observed in cockroaches as well as ants or bristletails. Wing morphology in dragonflies alone may enhance aerodynamic performance and allows for a control of lift and drag even under steady-state assumptions (Wakeling and Ellington, 1997; Kesel, 2000). Although other than ants or bristletails *B. dubia* males possess wings they are not capable of attaining a stable gliding flight let alone controlling their flight by wing deployment alone.

5.2 Flight and Landing Behaviour

During flight, body appendages such as legs and wings play an essential role as aerodynamically active surfaces, not only in insects. Yanoviak et al. (2009) e.g. states that body righting in falling bristletails is achieved by dorso-ventral and use of abdominal filaments as lateral rudders. Due to their substantial moment arm with respect to the bristletails centre of mass, the filaments are also used for other flight manoeuvres and targeting. In a broader definition of the term "aerodynamically active surface", other appendages may also play a vital role, especially with regard to postural orientation. When climbing geckos fall, air-righting is induced by swinging their tail. They even show the fastest body righting response reported with zero-angular momentum (Jusufi et al., 2008). Righting manoeuvres with the aim to land with the ventral side facing the ground are also found in non-flying mammals. Both tailed and tailless cats show identical body reorientation performance during fall with zero angular momentum. As typical for air-righting in mammals which is based on the instantaneous moment of inertia, even rats use twists and flexions of the spine in order to change shape (Hedrick et al., 2007).

High-speed records show that attitude stabilization in *B. dubia* does not take place before the wings are deployed. It is concluded that even the observed righting manoeuvres (half loops and half rolls) are induced by the wings and not by other appendages such as the legs. It further seems unlikely that in cockroaches – which are considerably larger than ants or bristletails – legs, antennae or the rather short cerci will solve any instability issues or serve as rudders for targeted flight. Especially with regard to half loops, a greater stabilizing mechanism around the pitch axis seems desirable. As discussed by Wootton and Ellington (1991) wings may provide for this required stability and control. As performed here, appendage (leg) abduction will however have a certain function and reflect a certain behavioural strategy during the aerial descent of cockroaches. In wind tunnel experiments with tethered individuals of *B. dubia*, test animals drew their legs towards their body instead of laterally abducting them (personal observation). This is in agreement with wind tunnel experiments performed on *Periplaneta americana*, which also display the same behaviour (Ritzman et al., 1980). Abducted appendages will certainly increase drag forces acting on individuals, which has experimentally been shown for a range of insects (Nachtigall and Wisser, 2003). Accordingly in falling cockroaches, drag will decelerate fall and reduce airspeed. Other flying insects such as bees and flies, extend and stretch out their legs directly before landing which is widely accepted as landing behaviour (Goodman, 1960; Srinivasan and Chahl, 2001).

It is difficult to assess whether cockroaches extend their legs intentionally to increase drag and slow down their descent, or if they instead are in a behavioural "landing mode" once airborne in our experiments.

Personal observations showed that when flight was initiated as a result of an escape response, cockroaches displayed a different flight performance compared to release via the launch tube. As escape response cockroaches were observed to jump from elevated locations for take-off, immediately unfolded their wings and began flapping. Compared to the flight presented in this study, the flight was more prolonged, yet nevertheless with at least a moderate in altitude.

5.2.1 Influence of Visual Cues

Although cockroaches may generally be influenced by visual stimuli, it seems as if this does not apply to the experimental flight conditions induced here. This may be due to the fact that cockroaches are unresponsive to visual stimuli as long as they are not in a state of migration i.e. migratory flight. Similar behaviour has previously been reported for aphids (Hardie and Powell, 2002), which do not show any behavioural response to their otherwise preferred wavelength of $\approx 550\,\mathrm{nm}$ until they have completed several minutes of flight. In an experiment showing a similar approach to assessing visual cues during directed aerial descent as ours, Yanoviak and Dudley (2006) report that canopy ants (*Cephalotus atratus*) show a colour-sensitive (or rather reflectance specific) aerial behaviour, preferring highly reflective surfaces as landing spots. However, besides the fact that the overall height of release ($> 10\,\mathrm{m}$) allowed for a longer re-orientation time in these experiments, essential flight parameters (e.g. descent angle) were also observed to be influenced by individual behaviour in the initial acceleration phase rather than by visual cues.

5.2.2 Influence of added mass - payload variation

Observations for bees by Feuerbacher et al. (2003) reveal that bees are capable of maintaining a stable hovering flight when pollen-loaded with an equivalent of 18% their own bodymass. This additional payload has no effect on wingbeat frequency, wing stroke amplitude, stroke plane inclination or body angle. However, in order to achieve these stable hovering flight conditions, bees increase their muscle power output and as such their natural metabolism significantly. The hawkmoth *Manduca sexta* does not increase wing beat frequency either and can reportedly compensate an additional payload of approx. 30-50% bodymass in free hovering flight. Reissman et al. (2008) describe this as feature as “stability robustness”.

In a classic study Marden (1987) compared the ability of 49 different insect species to cope with additional weight loading during takeoff. His findings demonstrate that there is a strong relationship between takeoff ability and flight muscle ratio, which he defined as the ratio of flight muscle mass to total flight mass, including additional payloads. Across all studied species (which additionally included several bird and bat species) he observed a maximal flight muscle ratio of 0.16 at which takeoff was still just barely achievable, stable flight not included.

However, comparable studies on the implications and limitations of additional weight loading as seen in the context of this study are rare. In the above mentioned cases, test animals are either capable of hovering flight (which cockroaches are not), or were tested in “classic” ground takeoff situations in contrast to the “drop-launching” conditions induced in this study.

Additionally, as mentioned by Bell et al. (2007) cockroach flight ability is most pronounced in species with pigmented flight musculature. Whether the amount of payload compensation observed for 10% additional bodymass in our experiments can be soley described by the flight muscle ratio defined by Marden (1987), is therefore difficult to assess.

5.3 Project Resume

The project outcome can be seen as utmost ambivalent. Except for neurophysiological tests, basically all major issues which were addressed in the study proposal were also addressed in experiments. Accordingly a large amount of data was successfully acquired, in return leading to initial insight into a biological model organism which previously had not been addressed under the given focal aspects of this Ariadna study. However, according to the innovative character of the study, only a first insight and evaluation of cockroaches as model organisms was acquired. These first insights can be addressed with regard to biomimetic implications (especially within the context of planetary exploration), as well as with regard to further general technical aspects. Finally, cockroaches can be evaluated as model organisms for purely biological and biomechanical considerations with regard to flight kinematics, flight behaviour and aerodynamics.

5.3.1 Biomimetic implications for space exploration

The direct application of cockroach-like mechanisms for attitude stabilization or descent deceleration seems rather limited under extraterrestrial conditions. Whereas small UAVs or MAVs may be considered as planetary explorers, great challenges are encountered for the use in spacecraft. The landing of a spacecraft requires to be well-directed preferably without deviations from the planned trajectory or the landing site. However, there is no guidance principle visible in descending cockroaches since their descent seems not t be target-directed. Control mechanisms in cockroaches focus on body and posture stabilisation rather than targeted descent. On the other hand, this can be seen as an essential prerequisite for safe landing, if a targeted surface approach is negligible. As such, an essential idea behind control architecture might lie not in the active control over a predestined flight path, but rather in a simpler control architecture focussing on active control of rotational stability and agility. As a result of axial orientation, landing trajectories will then passively be adjusted in a second step.

When considering cockroaches as possible biomimetic model organisms for space exploration missions, one might have to take another aspect into account: Cockroaches, however capable of flight they are, are foremost ground dwelling animals. As such it is not surprising that the specialisation in cockroach escape behaviour does not necessarily lie in the actual process of escaping, but rather in sensing and controlling when to escape e.g. switching into an escape mode, and then enduring the escape phase. One of the most essential outcomes of this study must therefore be seen in the fact that both volant males and nonvolant females both survive an enormous impact virtually unaffected. The magnitude of this impact can be taken from high speed recordings, which display a considerable amount of deformation in cockroaches accompanying ground impact.

5.3.2 Biological considerations

In contrast to other animals e.g. insects lack fossil evidence for the development of wings (Wootton and Ellington, 1991). The apparent lack of intermediate forms between wingless and winged insects leads to diverse hypotheses which account for the development of wings and the direct benefits arising from these appendages (Wootton and Ellington, 1991; Brodsky, 1994; Dudley et al., 2007; Yanoviak et al., 2009). Cockroaches remain an interesting model organism within these terms. In order to explain the evolution of wings on both a biomechanical and behavioural basis Yanoviak and Dudley (2006); Yanoviak et al. (2009) approached this complex in different insect groups. However, in their first studied insect group – (canopy) ants – the flight apparatus has been entirely reduced and as such explanations toward the evolutionary development of wings seem difficult to retrace. In their second study two insect groups – silverfish and bristletails – which have not developed wings throughout their lineage were observed. Here it also remains unclear how observations of directed aerial descent can account for the development of wings and their functional implication in evolutionary biomechanical terms. Additionally, test animals in both studies are small enough to account fur nearly purely passive aerodynamic behaviour.

Cockroaches on the other hand as primarily winged insect show a broad variety of morphological adaptations concerning both wing development as well as size (and mass) 2.3. Sexual dimorphism in winged males and wingless females of e.g.*B. dubia* as presented in this study may on the other hand provide comparative input towards understanding the benefits of aerodynamically active body appendages. Furthermore, experiments with added mass as performed here may show the performance limits of these appendages. Interestingly, in cockroaches the reduction of wings seems to coincide with increasing mass (Bell et al., 2007).

An adequate experimental set-up for determining actual flight activity and aerial control in descending cockroaches, can be taken from neuroethological studies as performed by Kutsch and co-workers (Kutsch et al., 1993, 1999; Fischer and Kutsch, 2000; Berger and Kutsch, 2003). By recording flight muscle activity whilst simultaneously applying radio telemetry on free flying cockroaches, one might possibly be able to evaluate in how far male cockroaches try to actively attain a stable flight attitude and in how far flight trajectories are directly related to actual flight muscle activation via neuro-motor feedback loops rather than passive aerodynamic effects. Previously designed radio telemetry devices lie within the required mass dimensions as far as design is concerned and therefore maybe considered as adequate with regard to the outcome of payload studies as performed here (Kutsch et al., 2003).

Acknowledgements

Two Master degree (MSc) projects were developed within this study. Experimental data gained and provided by Philipp Kloss and Joshua Tagoe within their Master degree projects greatly contributed to the success of this study and are included in this final draft report. We would like to thank Philipp Kloss and Joshua Tagoe for their equal contribution to this study.

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