Deciphering choreographies of elaborate courtship displays of golden-collared manakins using markerless motion capture

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Abstract
Courtship displays are complex behaviours that evolve mainly through sexual selection. Males of golden-collared manakins (Manacus vitellinus) gather in leks and perform very elaborate courtship displays in forest courts to attract females. The rapid movements of the display, that involve acrobatic jumps between saplings, are challenging to record and investigate. Here we describe the use of a combination of tools to quantify the choreographies of manakin displays and reveal previously unknown aspects of the courtship. To test the prediction that aspects of male jump trajectories vary among males and may be subject to female choice, we evaluated whether parameters including take-off angle and velocity vary between individual males and displays. We used a custom-built synchronized camera system to record courtship displays in the field, under highly variable lighting conditions. We then used automatic image pattern recognition software to track the movements of the birds and extract three-dimensional (3D) coordinates of the birds’ movements. After post-processing and cleaning of the raw 3D data, we compared automated and manually produced annotations to test the reliability of the 3D tracking methods. A subsequent analysis of tracked movements revealed that individual males performed their displays consistently across different recordings. We found that males express extreme values of force when they jump off saplings and the jump trajectory has a ballistic shape, confirming that no additional propulsion is provided by the wings. We also applied the analysis approach to non-jumping birds and found that they move at greater heights than jumping males. The acquired knowledge and the developed methods will allow us to compare different males in relation to courtship success in order to understand the role of choreographies in mate choice.

KEYWORDS
3D motion capture, automated animal tracking, ballistic motion, courtship behaviour, movement reconstruction, sexual selection
1 | INTRODUCTION

Besides extraordinary morphological traits, such as modified feathers and stunning colours, many animals perform elaborate displays whose exact function is often unknown. Previous studies suggest that these displays may indicate some qualities of the performer, such as vigour, neuromuscular coordination or cardiovascular function, which can be used by potential mates during mate choice (Byers et al., 2010; Fusani et al., 2014). The role of male and female movements during courtship are in most cases only superficially known, as is their impact on mate choice. One of the difficulties of conducting quantitative studies on courtship displays is to precisely record and analyse the movements involved, as they are often very fast or subtle, or the animals are very small, or both (Bostwick & Prum, 2003; Elias et al., 2006; Girard et al., 2011).

Video recordings do not allow straightforward analysis of the movements of most animal displays because of their two-dimensional (2D) nature, which limits precise measurements of movements to those occurring on a plane that is parallel to the recording camera’s image plane. A good example in this context is the tracking of movements of fish shoals in laboratory tanks to investigate collective behaviour and individuality (Jolles et al., 2017). Measuring movements in a three-dimensional (3D) space adds an order of complexity and requires dedicated hardware and software to allow several cameras to simultaneously record the subjects in 2D from different perspectives and subsequently reconstruct the movements in 3D. The methodology, which is generally known as ‘3D motion capture’, has seen considerable advances in the last decade and is widely used in biomechanics, sports science and the film industry (Fuller et al., 1997; Mündermann et al., 2006). Most commercial motion capture systems enable precise tracking in 2D or 3D of pre-defined physical markers placed on a moving object or animal. For example, Berg and Biewener (2010) used non-toxic, high-contrast paint to study the kinematics of take-off and landing during pigeons’ flight. Although markers allow efficient data collection, their use is not always practical to implement when studying animals, particularly in the wild. Some animals do not tolerate markers and simply remove them, while in other cases markers may limit behaviour (e.g., changed aerodynamics) or alter normal behavioural interactions (e.g., changed appearance affecting mating success). To avoid the use of markers, some studies can be carried out under laboratory settings where the environment and particularly the background can be optimized for maximal quality of video recordings, which simplifies later analysis (Mitoyen et al., 2021; Uhlmann et al., 2017). However, for many species it is not possible to conduct behavioural experiments in the laboratory as the behaviour of interest might change or might not be expressed (Egnor & Branson, 2016; Fisher et al., 2015). This is particularly the case for species known to perform the most spectacular and acrobatic displays, such as birds of paradise and manakins, as courtship in these species is shown only in specific locations or social contexts, that is large male aggregations called leks (Andersson, 1994). In these cases, recordings need to be conducted in the wild, where both the background content and dynamics and the lighting conditions cannot be controlled. Thanks to advances in machine learning applications to analyse unstructured data such as video recordings, markerless tracking of animals has recently become more possible. In particular, the introduction of deep learning algorithms, such as DeeperCut (Insafutdinov et al., 2016) has advanced the automated analysis of three-dimensional movements.

Our research group studies the elaborate courtship displays of golden-collared manakins (M. vitellinus) in the tropical forest of Panama. The males of this lek-forming species perform spectacular acrobatic dances and rely exclusively on courtship for their reproductive success. During the breeding season, each male prepares a courtship arena on the forest ground where they practice and perform their courtship display to attract females (Chapman, 1935). Females visit several male courts and may decide to enter a court to inspect a male closer. This initiates a ‘duo dance’ where both individuals move rapidly between the small saplings that delimit the courts. Previous work based on high-speed video recordings has revealed that during the courtship display (called jump-snaps display) males rapidly jump between the saplings of their court and produce wing-snaps in mid-air, ending with a final jump resembling a cartwheel to the ground (Chapman, 1935; Fusani et al., 2007). This final jump to the ground is always performed on the same sapling, called the mating sapling (Janisch et al., 2020). Previous studies showed that golden-collared manakins’ leg muscles are hypertrophic (Lowe, 1942) and express high levels of androgen receptors (critical in the pathway to activate skeletal muscles) compared to other bird species that do not engage in such extreme courtship behaviours (Feng et al., 2010). During each jump sequence males do not use their wings for self-propulsion and therefore rely fully on the initial jumping force to perform these elaborate movements. To the naked eye, females apparently perform similar movements, but in fact they fly between saplings and do not produce wing-snaps (Fusani et al., 2007). They also pace the dance: they take off and fly towards the male, which immediately jumps towards another sapling (Barske et al., 2015). Each male maintains a very precise jumping sequence between specific saplings, in a rehearsed choreography that resembles a stereotypical motor sequence pattern (Janisch et al., 2020). These studies strongly suggest that the spatial information contained in a male’s display, as well as its temporal dynamics, are likely to be important for communicating aspects of male quality to females searching for a mate. Even with high-speed cameras, however, we have not yet been able to capture the full spatial and temporal properties of the display, which requires a 3D description of the choreography.

Here, we developed methods to measure and study the movements of unmarked manakins performing their courtship display in 3D. Our aim was to derive kinematic features from the trajectories of the display, such as take-off velocity and take-off angle, in order to study whether these features are consistent between displays. As males jump between saplings, we hypothesised that male trajectories could be modelled as parabolic, ballistic motion. In contrast, females use additional force from their wings to fly the same routes, so we predicted that the parabolic fit would be better in males than females. We used a customized recording system composed of a set
of synchronized high-resolution, high-speed cameras and a commercially available semi-automated machine learning system to perform offline detection of birds in the recorded videos. We then used custom-written software to extract single jumps from the resulting 3D display coordinates and modelled the jumps as ballistic trajectories to quantify information about the movements of the birds. To understand how the choreography was shaped in relation to the propulsive mechanisms, we applied the same approach to sequences of juvenile males and/or female manakins that were recorded flying between saplings instead of jumping. We also compared manual and automated tracking results to test the reliability of automated tracking. In future studies, this methodological approach will allow us to investigate how display choreography is integrated together with other components of the courtship (such as plumage brilliance andlek position) to produce a holistic value that can be used by females to select their mates.

2 | METHODS

2.1 | Field sites and recording details

The behavioural data were collected in secondary rainforests around Gamboa (9°06′60″ N, −079°41′60″ W) in the Republic of Panama. For this study we chose three males from two different leks. Regarding STRANGE guidelines (Webster & Rutz, 2020), as this was a field study, the factors Social background; Rearing history; Genetic make-up; and Experience were beyond the scope of this work and cannot be addressed. Regarding Trappability and Self-selection, each male was individually trapped using mist-nets close to its court, marked with coloured leg bands to allow individual recognition, blood samples and physiological measurements taken and immediately released. By catching males individually we minimized any impact on the other males in thelek. Regarding Acclimation and habituation, after catching and marking, males were left alone for at least 2 days, after which we started to habituate them to our presence and the camera system. We only kept working with males that habituated well to our setup. In 2017, we collected recordings from the beginning of February until the end of April and in 2018 from mid-January to mid-May. Regarding their Natural changes in responsiveness, recordings took place during the peak of males’ activity in the mornings, from 6:30 to 9:30 and in the early afternoon, from 13:00 to 16:00 (Day et al., 2007).

2.2 | Mating system

Golden-collared manakins have a lek mating system, with leks containing between 2–20 males each defending a court where they perform their jump-snap displays (Chapman, 1935). Courts are clearings on the forest ground surrounded by 3–7 saplings which males actively maintain by removing leaves and dead wood. Females visit the leks regularly and a first level of mate choice involves the female entering a male court and joining him in a ‘duo dance’, where the female paces the male’s jump and observes him closely. Occasionally, the female accepts the invitation of the male and copulates with him within the court (Barske et al., 2015; Fusani et al., 2007).

2.3 | Recordings and automated analysis

For recordings we used a custom-designed camera system (Loopbio GmbH), composed of a portable computer that controls three small high-speed cameras (Basler ace cameras, type: acA1920-155uc) through a hardware synchronizer. The system can be controlled remotely with a wireless connection. The cameras were fixed on tripods approximately 1.5 m away from the centre of a male’s court to capture the scene from different viewpoints. We chose the height and angle of each camera in order to reduce occlusion from leaves or branches. Each time we set up the system, the zoom lenses were manually adjusted to bring the centre of the court into focus. At the end we hid the cameras under camouflage nets for minimal disturbance of the birds (Figure 1). Courtship displays were recorded at 60 frames per second (fps) and with a resolution of 1920 × 1200 pixels.

In order to combine multiple 2D video recordings into a 3D representation of space, additional video recordings are required to calibrate the cameras (calibration methods are reviewed by Hartley & Zisserman, 2004). First, intrinsic calibrations are used to correct lens distortions for each camera independently and require recordings of an object with known geometric structure such as a chequerboard, which must be recorded at different locations, distances and angles. Extrinsic calibrations are used to resolve the relative positions of the cameras in 3D space and require simultaneous recordings of a point that is visible from multiple cameras at the same time, recorded at different locations in the space. Finally, ground-level calibrations are used to map the recorded 3D space onto real-world space and require recordings of at least five non-coplanar points with known real-world 3D coordinates (e.g., in cm). Therefore, every time we set up the camera system we recorded intrinsic, extrinsic and ground-level calibration videos before recording courtship displays. A chequerboard was used for intrinsic calibrations and blue and red LEDs for extrinsic calibrations. For ground-level calibration (Jackson et al., 2016), we used a multi-arm calibration frame, which had markers at known relative distances and a spirit level to allow precise positioning relative to horizontal (Model QF-26, Firefly Instrument (HK) Co Ltd.). When weather conditions or arena size prevented use of the frame, we used five non-coplanar points on the saplings of the arenas as reference points (Jackson et al., 2016).

Camera calibrations and courtship videos were post-processed with the software Loopy (Loopbio GmbH) for the subsequent 3D reconstruction of a bird’s movement. Loopy also includes the Convolutional Neural Network ResNet50 to perform automated object tracking (He et al., 2016) which we trained with manual annotations (boundary box method) of over 150,000 frames of males performing alone. For female movement data (see below), we used manual annotation only, as we have not yet trained a female manakin detector. After acquiring
2D data from each separate video recording, we applied the 3D calibrations to combine the three synchronized video views into the final 3D coordinates of the tracked bird’s movement. X and y defined the position on a plane parallel to the ground, z defined the height above the ground and each point was associated with a frame number (see Figure 2a for an example 3D courtship display).

### 2.4 Processing of 3D position data

Position data were analysed using custom-written R scripts and functions (R version 3.6.3; R Core Team, 2020). 3D annotation files were pre-processed to remove spurious data points. First, we removed any frames with a displacement of precisely zero with respect to the previous tracked frame — these resulted from frames for which the annotation procedure could not estimate the bird’s location and instead copied the previous location. Second, 3D speed was calculated between subsequent frames (Euclidean distance between locations divided by the time elapsed) and a threshold of 7 m/s was iteratively applied to remove points with unreasonably high speeds. This threshold was chosen by visual inspection of speed histograms of manual and automatically annotated files, where a clear distinction could be seen between the distribution of jumping speeds and outliers.
In order to segment 3D locations into jumps, a speed threshold of 0.6 m/s (also chosen by visual inspection to estimate the border between speeds corresponding to jumps and perching intervals) was used to categorize frames in which the bird was likely to be at rest, that is perching on a sapling. Each of these locations was then associated with a sapling ID. In order to do this, the ground coordinates (x, y, estimated to the nearest centimetre) and numerical ID of each sapling were saved in a look-up table that we created manually by visual inspection of videos. The mating sapling in each court was defined as sapling ID 1, and numbering continued in a clockwise direction to include all available saplings. “G” was used to identify the ground. As saplings differ in their vertical orientation, we ignored the z dimension to simplify the perching assignment process. The x, y coordinates in each perching frame were compared to all sapling locations, and the sapling ID of the closest location (nearest neighbour method using Euclidean distance) was assigned to that frame (Figure 2a). Next, we cut the annotation sequence into jumps, defined as the series of coordinates beginning with the final perching frame before a sequence of non-perching frames and ending with the first subsequent perching frame (red and grey points in Figure 2). The IDs of saplings jumped from and to were also noted. Finally, we used simple linear algebra (Gram-Schmidt method, see Strang, 2016) to project each 3D jump trajectory onto the 2D plane described by the original z dimension and the horizontal line defined by the start and end positions of the jump. Jumps were additionally defined to start at horizontal position 0.

As male manakins jump from sapling to sapling (Fusani et al., 2007), we tested whether the jump could be geometrically described by a parabola and fitted each jump accordingly using polynomial regression (function lm, formula vertical ~ poly (horizontal, 2, raw = T)). Goodness of fit was quantified using adjusted $R^2$ in order to evaluate how well each male jump or female flight path was represented by a ballistic trajectory. We compared goodness of fit between males and females using a two-sample Wilcoxon rank sum test.

We then evaluated the quality of the automatic annotation process. To this aim, we manually annotated twelve videos from three different male arenas and compared them with the corresponding automated annotation results. In manual annotations we used every second frame and not every frame of the video, whereas in automated annotations all frames were included. We fitted parabolas to jumps between saplings, excluding any jump to or from the ground. In order to compare fitted trajectories of the same jump between automatic and manual annotations, we correlated the vertical values predicted by the two fitted models, using 50 horizontal values linearly spaced from the start to the end of the jump (same values used for each of the pair of fitted jumps being compared).

### 2.5 Behavioural variables

For the analysis of behavioural variables, we used 31 displays of three different males. For each jump, we used the parameters of the fitted parabolas (displacement trajectories):

$$y = \beta_0 + \beta_1x + \beta_2x^2$$  \hspace{1cm} (1)

and the equations of motion:

$$y = \tan(\theta)x - \frac{8}{2\beta_1\cos^2(\theta)}x^2$$  \hspace{1cm} (2)

to estimate the following parameters: take-off angle and take-off velocity, height at take-off, landing and vertex of the jump, and straight-line distance and curved distance (Figure 2b).

Take-off and landing heights were taken as the first and last fitted vertical values. Maximum height was the vertical value at the vertex of the parabola, which can be calculated from:

$$x = -\frac{\beta_1}{2\beta_2}$$  \hspace{1cm} (3)

Straight-line distance was the Euclidean distance between the first and last fitted points, and curved distance was the arc length of the fitted curve calculated using integration. The take-off angle and velocity are estimated using (2). Specifically, the take-off angle is estimated using:

$$\theta = \arctan(\beta_1)$$  \hspace{1cm} (4)

the inverse tan of the linear coefficient (atan), while the take-off velocity can be estimated using:

$$v_0 = \sqrt{\frac{-g(1 + \beta_2^2)}{2\beta_2}}$$  \hspace{1cm} (5)

where $g = 9.81 \text{ m/s}^2$. Take-off velocity was used to conservatively estimate the initial acceleration of each jump by assuming that two frames were needed for the bird to reach the estimated initial velocity, and therefore dividing velocity by 0.033 s. We also estimated the force exerted during each jump by multiplying acceleration by the average mass of a male manakin (0.018 kg). Note that using a smaller time interval would result in a larger acceleration, which means that our estimates of take-off force are conservative. For comparison, the force exerted by a standing manakin, calculated using the same average mass multiplied by gravity, is 0.177 N. To be able to compare jumps between different saplings or several individuals we standardized the distances of each jump by calculating the linearity (straight-line distance divided by curved distance). Finally, we calculated total speed of a jump by dividing the curved line distance by the time elapsed between the first and last tracked points of the jump.

We were also interested in comparing the trajectories of lekking males with those of juvenile males or females, who fly between saplings. In many manakin species, there is sexual dimorphism – females have a drab green plumage, which is remarkably different from that of adult males. Juvenile males of golden-collared manakins keep a female-like plumage during the first year. During previous field seasons, we observed banded, genetically sexed juvenile males joining adult males in courts during jump-display events (pers. obs.,...
Chapman, 1935; Lil, 1974). Therefore, without banding, it was impossible for us to discriminate between females and young males. For the present study, we used sequences in which the juvenile male/female was flying between saplings and did not analyse the simultaneous jumps of the court-owning male. We used eight such sequences recorded from six different courts. In two of the six courts we recorded two sequences spaced more than 15 min apart. As the juvenile males/females were not ringed, we assumed that they were eight different individuals. We estimated the same parameters for these birds as for males, except for take-off velocity, because juvenile males/females additionally use their wings to propel themselves and therefore violate the assumptions of ballistic motion used to calculate take-off velocity.

### 2.6 Ethical statement

All procedures were approved by the Smithsonian Tropical Research Institute and the Autoridad Nacional del Ambiente of the Republic of Panama (No. SE/A-118–17, 28th December 2017).

### 2.7 Statistical analysis

All statistical analyses were conducted using R (Version 4.0.3, R Core Team, 2020). We fitted linear mixed models (LMM) using the functions lmer and generalized linear mixed models (GLMM) using glmmTMB, respectively, of the package lme4 (Bates et al., 2015) and glmmTMB (Brooks et al., 2017). Bird ID was treated as a random factor to investigate changes in behavioural parameters across different displays and adult males/juveniles/females. As fixed effects we included the display number of each bird (ranging from 1 to 12 indicating the separate displays we sampled for each male) and the jump index as a scaled number (between 0 and 1, from first to last jump of a display to account for the different numbers of jump per display) as well as sex (male or female/juvenile male). We also included the squared term of the scaled jump index as an additional predictor to capture whether the animals reached an optimum in the middle of the display. We included additional random intercept effects for the display ID (a combination of display number and bird ID), date and time of display (morning or afternoon), all nested within the main random intercept effects factor bird ID. The random intercepts effect for the time of the day (morning/afternoon; nested within bird ID) controlled for recording differences that could occur due to different calibration sessions; display ID and date for possible day-to-day or display-to-display variation in the observed behavioural variables. We included random slopes for display number and jump index in the model to keep type I error rate at the nominal level of 0.05 (Barr et al., 2013; Schielzeth & Forstmeier, 2009). Model assumptions of LMM (normality and homogeneity of the residuals) were validated by visual inspection of the residuals plotted against the fitted values and QQ-plots of residuals (Field, 2005). We estimated model stability by excluding levels of the random effects one at a time, fitting the same model to the obtained subsets of data and comparing their estimates to those obtained for the full data set. This revealed the models to be of good stability. We obtained confidence intervals of the model coefficients by means of a parametric bootstrap (function bootMer, package lme4 or function simulate, package glmmTMB). Then we tested individual effects by comparing the full model with the null model lacking the respective main predictor jump index using likelihood ratio tests (Barr et al., 2013; Dobson, 2002).

The response variable take-off velocity was fitted for adult males only (163 jumps measured for three individuals) and therefore lacked the fixed effect sex. Full-null model comparison lacking jump index (jump index + jumpIndex^2) was significant. As the squared jump index revealed no overall significance in the fixed effects of the full model it was further excluded and a reduced model fitted, lacking the squared scaled jump index. In this model we excluded all correlations between random intercepts and slopes except for (1 + jump index | display ID).

For take-off angles we had a sample size of 231 jumps of 11 individuals and as they have a lower and upper bound, we scaled them to a range from 0 to 1 (scaled angle = (angle in degrees + 90)/180) and fitted a model with beta error distribution and logit link function (glmmTMB, Brooks et al., 2017). All correlations among random intercepts and slopes were excluded for model convergence. The null model lacking the main predictor jump index did not converge and therefore a full-null model comparison was not possible.

The response variable take-off height was fitted to 231 jumps of 11 individuals. Full-null model comparison lacking jump index (jump index + jumpIndex^2) revealed significance but as the squared squared jump index was not significant in the full model we excluded the term and fitted the model without it. All correlations between random intercepts and slopes were excluded. As an example, we provide the model description for the response variable take-off height for better understanding:

**Fixed effects:**

$$\text{Full} = \text{lmer}(\text{TOHeight} \sim \text{jumpIndex.s} + \text{l(jumpIndex.s^2)} + \text{sex} + \text{displayName.z} +$$

**Random effects with random slopes:**

$$\begin{align*}
(1 + \text{displayName.z} + \text{jumpIndex.s} + \text{l(jumpIndex.s^2)} | \text{daytime.date.birdCode}) + \\
(1 + \text{displayName.z} + \text{jumpIndex.s} + \text{l(jumpIndex.s^2)} | \text{birdCode}) + \\
(1 + \text{jumpIndex.s} + \text{l(jumpIndex.s^2)} | \text{displayID}).
\end{align*}$$

The fixed effects and random effects parts were the same for all models. We nested the variables daytime and date within the ID (birdCode) and created Daytime.date.birdCode. BirdCode and displayID (display number was nested in birdCode) are random intercepts and displayName.z (display number z-transformed), jumpIndex.s (scaled jump number) and l(jumpIndex.s^2) (scaled jump number squared) are the random slopes.

Finally, we fitted a LMM for the response variable total speed for males and females/juvenile males. In total we used 226 jumps of 11 individuals as some outliers had to be excluded due to measurement errors.
of the automated system (all jumps beneath a speed of 1.2 m/s were excluded). Full-null model comparison revealed no significance and therefore no reduced model was fitted. Correlations of random intercept and random slopes were excluded for all variables except birdCode.

3 | RESULTS

3.1 | Evaluation of the goodness of fit of the ballistic model for the trajectories

The trajectories of both court-holder males and plain green individuals were well described by a parabola. Goodness of fit was greater than 0.9 for 93.9% of the data. In more detail, 97.5% of the trajectories for males and 85.2% for females had a goodness of fit comprised between 0.9 and 1 (Figure 3). A non-parametric test revealed that average goodness of fit was larger for males than females (two sample Wilcoxon rank sum test, W = 7,368, p < .0001).

3.2 | Validation of the automated tracking

The comparison of the parabolas fitted to data from manual and automated annotations (see Figure 4 for an example) using Pearson correlation coefficients of the vertical values predicted by each fitted model yielded very high correlation coefficients (see Figure S1, all but five values lie above 0.9). Automated and manual annotations therefore reveal comparable results.

3.3 | Behavioural analysis

Take-off height significantly decreased from the first jump of a display until the last jump of a display (full-null model comparison: χ² = 15.17, p = .001) with no optimum in the middle of a display as the squared jump index was not significant in the full model. The reduced model lacking the squared jump index revealed also a clear difference of take-off height between males and females/juvenile males (χ² = 15.932, p < .001). Females/juvenile males stayed significantly higher on the saplings during the entire display (females = 0.31 ± 0.12 m (mean ± SD); males =0.17 ± 0.10 m, Figure 5a-b).

Using the linearity index to compare parabolas of the different trajectories across displays we found little variation (96% per cent of the data lie between 0.8 and 1). The take-off angle did not significantly vary between sexes or across different displays (sex: χ² = 1.524, p = .217, display number: χ² = 0.148, p = .700, jump index squared: χ² = 0.398, p = .528, Figure 5c-d).

A comparison of total speed between males and females/juvenile males revealed no significant results (Full-null model comparison: χ² = 0, p = 1, males/females/juvenile males: χ² = 2.538, p = .111, display number: χ² = 1.106, p = .293, Figure 5e-f). Take-off velocity significantly changed for males depending on the display number (χ² = 4.515, p = .034; Full-null model comparison χ² = 2.648, p = .104, Figure 6).

A correlation analysis of the parabolas of the jumps within individual males for the same sapling combination across all their displays revealed that two of the males (CAN03 and JUR12) are more consistent in their jumps. In the third male (CAN04) we find more variation (Figure 7). When looking at the mean and standard deviation of take-off heights of the males we also find that CAN03 and JUR12 are a bit more consistent than CAN04 (Table 1).

Finally, the average take-off acceleration was estimated to be 98.63 m/s² (range: 34.26–323.37 m/s², 98.63 ± 23.34, M ± SD). This equates to a force during take-off of 1.78 N for a manakin of mass 18 g (range: 0.62–5.82 N, 1.78 ± 0.42, M ± SD, Figure 8). This constitutes a leaping force of 9.6 times their body weight (force exerted by gravity, which is 0.177 N in this case).

4 | DISCUSSION

We successfully extracted 3D coordinates from videos of fast-moving birds recorded under challenging conditions in the field using a semi-automated 3D motion capture system. We presented an analysis pipeline using x, y, z coordinates and the known geometry of each male’s arena to segment tracked points into jumps with measurable spatial and temporal configuration. From there we derived jump parameters that serve as valuable variables to describe the birds’ movements. Based on goodness of fit results, we are confident that male manakins’ jumps are well described by parabolic motion, which confirms the observation that they are jumping ballistically among the saplings and that after taking off they are only subjected to gravity. Our comparison of fitted parabolas between manual and automatic annotated data of adult males also showed that the deep learning algorithm successfully tracked the birds in our videos and produced reliable data for further analysis. We can now measure these small and fast birds’ movements in three dimensions,
and while we previously relied on the distance between saplings to calculate jump speeds (Fusani et al., 2007), we can now calculate the curved distance traversed by the bird to achieve a more precise measure of speed. This is an important advance in the study of their elaborate courtship displays.

Intra- and inter-individual comparisons of the measured behavioural variables showed that in two of our three subjects there was little variation across individual birds’ displays. In accordance with previous results of our working group, consistency seems to play a role in such complex displays with males repeating a very precise jumping behaviour in order to increase speed and precision. Indeed, males follow a well-rehearsed motor sequence pattern that they practice and automatize throughout the entire mating season (Janisch et al., 2020). Future comparisons of courtship consistency between successful and non-successful males could indicate whether this feature is subject to female choice. In addition, a comparison between juvenile, inexperienced males and court-owners could shed light on the role of age and experience.

We found that take-off velocity of adult males significantly varied across the displays that we analysed. Displays vary mainly in the number of jumps that males perform, in our sample starting with a minimum of three up to 18 jumps. A higher number of jumps within one display could mean a higher power output, which likely results in muscle fatigue (Clark, 2012) and impacts take-off velocity. Barske et al. (2011) demonstrated that the heart rate of golden-collared manakins doubles during courtship displays compared to the daytime baseline, clearly showing that it is a physically demanding behaviour. This has also been found in other species, for example males of Anna’s hummingbirds (Calypte anna), which engage in highly powerful displays at the limit of their flight performance (Clark, 2012).

Furthermore, a leaping force of 9.6 times their body weight (average acceleration of 93.9 m/s²) was calculated. In comparison, previous studies reported an average take-off force of 1.7 times the body weight for pigeons (average mass 400 g and average acceleration 15.63 m/s²) and 2.6 times the body weight in starlings (average mass...
70 g and average acceleration 25.1 m/s$^2$ (Bonser & Rayner, 1996). Zebra finches with an average mass of 15 g and average acceleration of 47.8 m/s$^2$ can jump off with a force 4.9 times their body weight (Provini et al., 2012) (Figure 9). These studies calculated force either using mechanical force plates or ultra-high-speed photography of flights between fixed distance perches. Here, we tracked naturally behaving manakins in 3D and derived the forces from ballistic motion trajectories. Because we used a very conservative time constant to calculate acceleration, our acceleration and force estimates are likely to be lower than the actual values. Despite this, we demonstrated that golden-collared manakins excel in their performance and are at least twice as powerful as most other birds when jumping.

**Figure 5** The box plots show the data distributions of the different response variables (a: take-off height; c: take-off angles; e: total speed, which is the curved distance divided by the jump duration) for the three different males separately (blue boxes) and females/juvenile males together (red box). Box plots show median, quartiles and 1.5× interquartile range of the data. Outliers are shown as black crosses. On the right, all values of males (blue dots) and females (red dots) are plotted together with the fitted model for all data for each response variable separately (b: take-off height; d: take-off angles; f: total speed). The x-axis represents the scaled Jump Index which ranges between 0 and 1 [Colour figure can be viewed at wileyonlinelibrary.com]
between saplings. For future reference, it would be interesting to measure their acceleration using mechanical force plates and compare the results to findings from other species.

**FIGURE 6** Take-off velocity. (a) Data distributions of the three different males are shown as boxplots (details as in Figure 5). (b) All data are plotted with the fitted model, with different symbols depicting different males and a dashed line showing the fitted model [Colour figure can be viewed at wileyonlinelibrary.com]

**TABLE 1** Mean and standard deviation of take-off heights (m) for each sapling used by the three males

| ID   | Sapling | Mean | SD  |
|------|---------|------|-----|
| CAN03| 1       | 0.27 | 0.11|
|      | 2       | 0.20 | 0.08|
|      | 3       | 0.15 | 0.11|
| CAN04| 1       | 0.21 | 0.08|
|      | 2       | 0.23 | 0.10|
|      | 3       | 0.07 | 0.06|
| JUR12| 1       | 0.15 | 0.11|
|      | 2       | 0.09 | 0.03|
|      | 3       | 0.14 | 0.03|
|      | 4       | 0.12 | 0.03|
|      | 5       | 0.16 |    |

Note: For sapling 5 we could not calculate the standard deviation as there were not enough data available.

**FIGURE 7** Distributions of correlation coefficients for the pairwise comparison of different jumps between the same saplings are shown for each adult male separately. Boxplot details as in Figure 5, except outliers are shown as dots

**FIGURE 8** Distribution of leaping forces estimated for all tracked jumps of three male manakins (assuming a body mass of 18 g)

Future studies could focus on the analysis of the leg forces used by male manakins in different contexts, for example when they leave a branch in flight to find food. Another point would be the measurement of force in females. Feng et al. (2010) showed that males and females have comparable expressions of androgen receptors and therefore the legs’ muscles are not sexually dimorphic. However, females have less testosterone to activate androgen receptors and
Therefore they do not usually show the jumping and wingsnapping behaviour of males. Nevertheless, it is still an open question whether they use more force to jump off into flight compared to other species. Additional force data could also provide insights to the competing hypotheses of whether force will increase after an initial warm-up period or will decrease over time due to muscle fatigue. A recent study by Tobiansky et al. (2020) investigated the extraordinary muscle speed of golden-collared manakins during rollsnaps (clapping their wings together behind their back at a rate of 60 times per second). They found that their performance in terms of number of rollsnaps and their timing was a trade-off between speed and endurance, and that they reduced the number in order to avoid fatigue while maintaining an incredible speed. We hypothesise that this may be similar in their leg muscles, and that they vary the number of jumps within each display in order to avoid exhausting themselves while maintaining their jump speed.

When comparing court-holder males with females/juvenile males we discovered that the latter stayed significantly higher on the saplings during a duo dance. Taking into consideration a study from Stein and Uy (2006) that showed the crucial role of plumage brightness in males’ mating success, we speculate that females might from Stein and Uy (2006) that showed the crucial role of plumage brightness in males’ mating success, we speculate that females might form a large variety of other model systems, from other lekking species.

Studies of movement patterns in 3D could enable new possibilities to quantify differences between individuals in relation to age, sex and developmental stage and rank. Male manakins start practicing their courtship movements as juveniles (Chapman, 1935; Lill, 1974), but very little is known about how they develop their routine and how they improve their performance over time. Several studies have focused on song learning and transmission of information from tutors to juveniles (Fee & Scharff, 2010; Marler, 1997) related to courtship behaviour. To our knowledge, however, there are very few quantitative studies on the gradual development of non-vocal motor components of courtship displays (see Soma et al., 2019 for an example in java sparrows), despite abundant evidence that such gradual development occurs (Groothuis & Meeuwissen, 1992).

For example, Trainer et al. (2002) showed that coordinated duet calling performance improved in subordinate males of long-tailed manakins (Chiroxiphia linearis) with the time they spent in male-male associations. Therefore, we think that the development of motor and postural aspects of extreme courtship traits like the ones of the golden-collared manakin should be investigated in more detail. We would expect juvenile males to become more consistent and precise over time in their movements and to increase their speed with experience and practice.

Although recording might seem rather straightforward, we would like to mention that using several cameras simultaneously does come with some limitations and challenges, particularly in the field. Calibration videos with sufficient coverage of the recorded space, as well as a reliable way of synchronising cameras during recording, are essential for 3D reconstruction and can be challenging depending on environmental conditions. In addition, any data set is a trade-off between keeping file sizes realistic for fieldwork and attaining high enough spatial and temporal resolution to attain a reasonable estimate of the bird’s position in each frame of the video. This sets limits for further analysis and possibilities of automated tracking methods, particularly without marking animals beforehand. When using automated tracking and reconstruction methods, the resulting data are position estimates and always include some noise or tracking errors. Fitting a polynomial as we did here is a useful way to deal with position noise in the data, for example due to motion blur in low light conditions, or missing position estimates for frames where the individual could not be tracked, for example due to 3D reconstruction errors.

In line with the STRANGE framework, we believe the findings are generalizable across males of the same species. Future applications of the system and analysis described here could investigate juvenile courtship development in more depth in our study species. Moreover, it could be used to help unravel how females interact with males during courtship and whether they need to develop any specific behavioural traits or motor patterns. Generally, more detailed investigations of female behaviour during courtship interactions in different species could reveal important features of female choice, and we suggest female behaviour to be considered in more depth in future studies. Beyond manakins, the system could be applied in a large variety of other model systems, from other lekking species.

![Figure 9](image-url)  
**Figure 9** A comparison of different average forces during take-off of several bird species. See text for references.
where males display in a limited area, for example, ruffs (Philomachus pugnax) (Van Rhijn, 1973) or bowerbirds (Borgia, 1995), to tracking the movement of individual birds flying in a flock (Corcoran & Hendrick, 2019). Whenever scientists are interested in studying animals’ movement and at least two cameras can be placed at different angles to record a spatially delimited area, 3D reconstruction of movements is possible.

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CONFLICT OF INTERESTS
The authors declare no financial and non-financial competing interests on behalf of all authors.

DATA AVAILABILITY STATEMENT
Data and Code are available under https://github.com/fusanilab/3dManakinMethods.

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SUPPORTING INFORMATION

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