

SHORT COMMUNICATION

**THE FLAPPET LARK *MIRAFRA RUFOCINNAMOMEA*  
DOUBLES ITS WINGBEAT RATE TO 24 Hz IN WING-CLAP  
DISPLAY FLIGHT: A SEXUALLY SELECTED FEAT**

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The flappet lark *Mirafra rufocinnamomea* (Salvadori) is widespread in open bush country across central Africa in an equatorial belt between 20° S and 20° N. It has a display flight during which it produces sounds by a series of bursts of rattling wingbeats. The basic sound unit is a wing 'clap' or 'flappet' as Mackworth-Pread and Grant (1970, p. 624) and Bertram (1977) termed it. Based on a large number of sonograms, Bertram (1977, p. 166) stated: 'Each flappet is a single clear click...'. Each of these transient sound units contains frequencies from a few hundred hertz up to about 8 kHz, with most energy at 0.5–2.5 kHz (Wickler, 1967; Payne, 1973; Bertram, 1977). The claps are typically produced in three bursts in rapid succession, but lower and higher numbers occur (Seibt, 1975). A typical three-burst wing-song contains 6, 4 and 19 claps, produced at a rate of 24 claps s<sup>-1</sup>. The number of claps in a burst and the number of bursts in a series are consistent for the individual bird but differ among individuals. Geographical variation, or local dialects, of the wing clapping have been described (Payne, 1973, 1978, 1981; Seibt, 1975; Bertram, 1977).

The mechanism of production of the wing sound is not clear. Niethammer and Wolters (1966, p. 162) suggested that the sound is produced by the wings clapping together below the body. But the high clap frequency of 24 Hz in a burst (Wickler, 1967; Payne, 1973, 1978; Seibt, 1975, from Fig. 1; Bertram, 1977) causes doubts as to whether the lark actually beats its wings so fast; only 11 wingbeats s<sup>-1</sup> are expected (see below). Mackworth-Pread and Grant (1970, p. 624) wrote: 'It is not certain if the noise is produced by the wings meeting below as well as above the body'. Wickler (1967, p. 163) suggested that the wings do not clap together but that sound is produced as the primary feathers within each wing strike together, and later Bertram (1977, p. 165) wrote: 'the noise is caused either by the striking together of adjacent feathers or by sudden interruption of the air flow between them'. Wickler based his view on a double structure in his sound spectrograms, each sound unit being split in two parts, separated by 7 ms. But 7 ms corresponds

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to a sound travel distance of 2.4 m, so the sounds could not be from simultaneous closure of the feathers in each of the two wings. And such sounds would have to be simultaneous since the wings must beat in synchrony, and with bilaterally symmetrical motions, so as not to give any net rolling moment to the body. Niethammer and Wolters (1966, p. 162) found no structural characteristics of the wing feathers that could be related to sound production.

Based on a high-speed motion-picture film, I here describe the wing kinematics during normal flight and during the rattling wing claps. After documenting wingbeat frequencies in normal flight and in display flight, I estimate the corresponding flight powers and consider sexual selection as a driving force behind the evolution of the wing-clap display.

I filmed the lark at the Serengeti Research Institute, east of Seronera in the Serengeti National Park, Tanzania, in January 1971. I used a Pathé Reflex 16 mm motion-picture camera, a 135 mm lens and a filming rate of 80 frames  $s^{-1}$ , accurate to within 1.5% as found by filming a stopwatch. One film sequence included ordinary pre-clap flight, continuing into a three-burst, wing-clap display. I analysed this film frame-by-frame by projecting it horizontally *via* a 45° inclined, mirror silvered on the front surface, and drawing the lark's outline from 481 film frames, covering 6 s, and then plotting the relative positions of the wings against time (Figs 1, 2 and 3). I also examined the film in a microscope at 50 times magnification and adjusted details of the tracings in Figs 2 and 3.

On the film, the lark is seen from in front and obliquely below, silhouetted against the sky, and with no details discernible in the dark parts. The purpose of Fig. 1 is to track the wing movements throughout the entire flight sequence. Because of the oblique view, exact digitization of wing positions were not attempted. Instead I marked the vertical position of the wing-tip from each frame on a relative scale between its bottom and top positions. Because of a temporal resolution of only 80 Hz (1/80 s between consecutive frames), as compared with wingbeat frequencies of 11 and 24 Hz, there are several wingbeat cycles with no frame showing the wings at their turning positions. When drawing the connecting line between the data points in Fig. 1, I therefore took the wingbeat amplitude to be the same throughout, and for some stroke cycles extrapolated the wing-tip path according to the turning points observed elsewhere on the film. The horizontal lines at an intermediate height refer to non-flapping periods with the wings more or less folded against the body or fully spread near the horizontal plane in gliding

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Fig. 1. Continuous record of a flappet lark in normal flight, continuing into wing-clap display. The tracing covers 6 s and 481 film frames, numbered 0–480, from a ciné film taken at 80 frames  $s^{-1}$ . The dots are thus separated by 1/80 s, 12.5 ms, and show the relative positions of the wing-tip between its bottom and top positions. The dots are connected by a curved line, which is extrapolated in amplitude for some stroke cycles according to turning positions observed elsewhere on the film. Frames 0–269 show intermittent, pre-clap flight with wingbeats at about 11 Hz, continuing into a three-burst wing-clap display in frames 328–448. The sound-producing wingbeats, underlined by horizontal arrows, occurred at about 24 Hz. Two eight-frame sequences marked with an 8 are shown in silhouette tracings in Fig. 3.

flight. Since I could only mark out the wing positions approximately, on a relative scale, I did not vary the vertical spread of the wing curves in Fig. 1, even though the wings moved deeper and probably struck together below the body in the wing-clap phases. Despite these shortcomings in the analysis, there should be good accuracy in the determination of wingbeat frequencies and wingbeat temporal patterns. The sound-producing phase was easily identified on the film by its

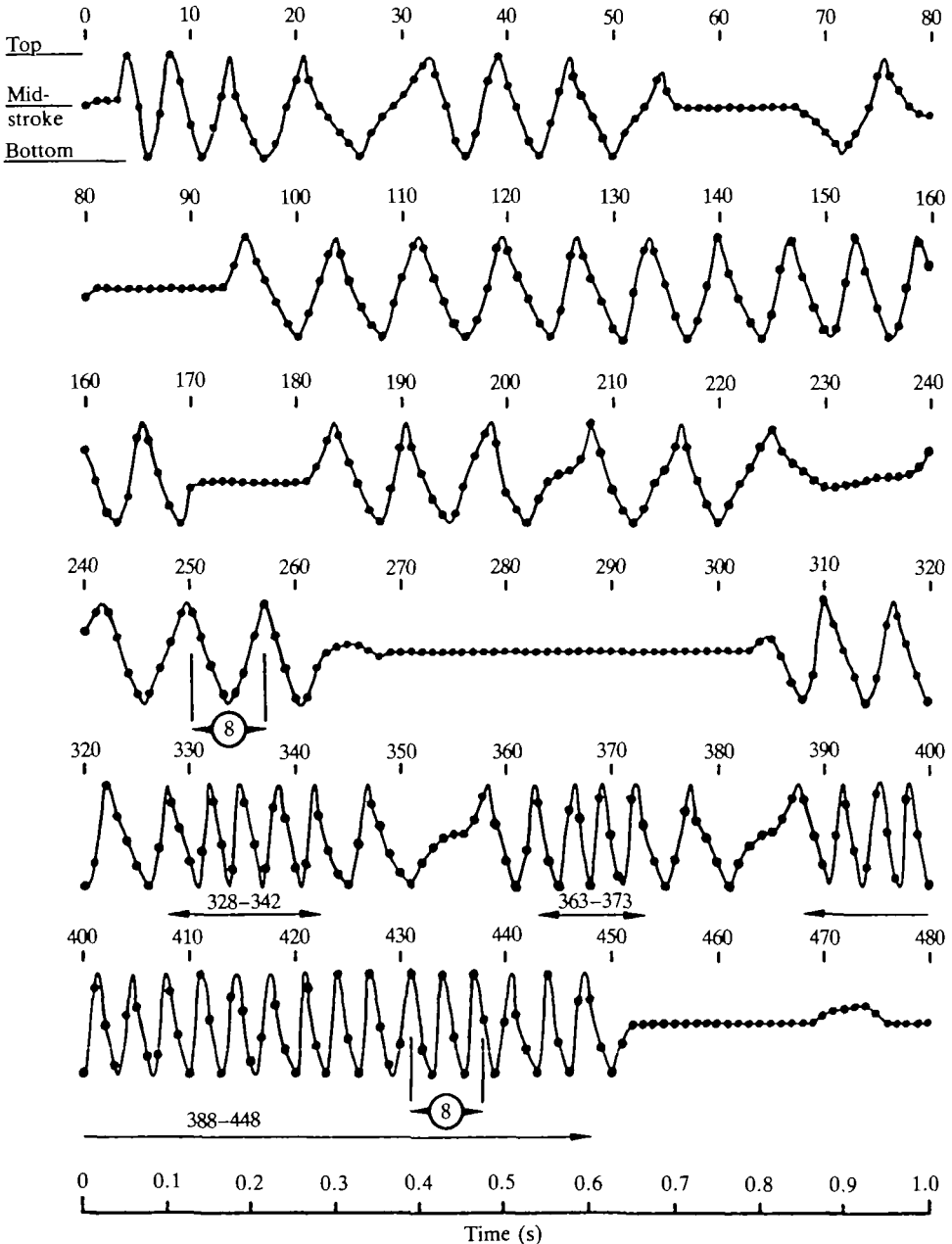


Fig. 1

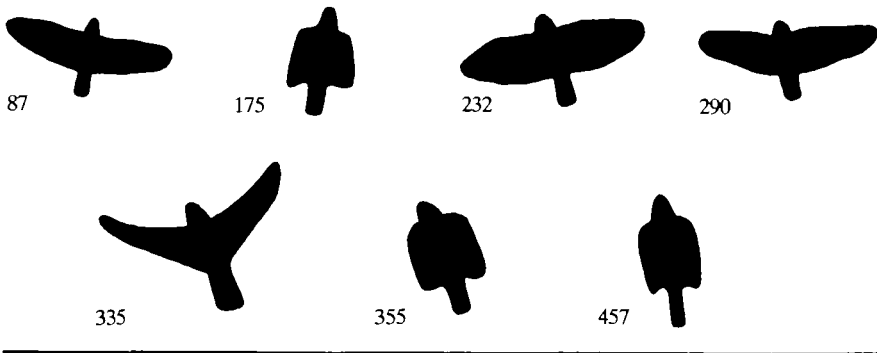


Fig. 2. Silhouette tracings from various stages of the flight shown in Fig. 1, identified by their frame number, and described in the text. See also legend to Fig. 3.

increased wingbeat rate with three easily recognizable bursts of wing claps at about twice the rate observed in normal, pre-clap flight.

Before the sound-producing phase, the lark flew with intermittent flight, beating its wings between about  $30^\circ$  above the horizontal plane and about  $40^\circ$  below it. In the 3.8 s pre-clap flight sequence shown in Fig. 1 (frames 0–269) there are five bouts of wingbeats with 1–11 beats in each (8, 1, 11, 6 and 3), interspersed with four short resting periods 0.14, 0.15, 0.13 and 0.09 s long. In three of the four resting periods the lark glided on fully extended wings (Fig. 2, frames 87 and 232), whereas in the third resting period (0.13 s long, frames 171–181) the wings were folded against the body and kept only partly open (Fig. 2, frame 175). The wings beat at about  $11 \text{ strokes s}^{-1}$ ; there were 11 wingbeats at an average of  $11.4 \text{ Hz}$  in frames 93–170, 5 wingbeats at  $9.8 \text{ Hz}$  in frames 184–225 and 3 wingbeats at  $10.4 \text{ Hz}$  in frames 239–262.

Immediately before the sound-producing wing-claps there was a 0.43 s glide on fully extended wings (frames 269–303 in Fig. 1; frame 290 shown in Fig. 2). Each one of the subsequent three bursts of sound-producing wing-claps was preceded by 1–4 wingbeats at about the normal rate. It is uncertain from the film exactly which wingbeats produced sound, but 4, 3 and 18 beats in the respective three bursts in Fig. 1 were faster than the others and occurred at about  $24 \text{ Hz}$ . In the three bursts there were 4 wingbeats at an average of  $22.9 \text{ Hz}$  lasting 0.175 s (frames 328–342), 3 wingbeats at  $24.0 \text{ Hz}$  lasting 0.125 s (frames 363–373) and 18 wingbeats at  $24.0 \text{ Hz}$  lasting 0.750 s (frames 388–448). The brief pause between the first and second sound bursts and that between the second and third bursts were caused by one or two slow, and probably silent, wingbeats at about the normal frequency and one slow upstroke in which the partly folded wings were nearly arrested in the middle of the upstroke (Fig. 2, frame 355 from the pause between the first and second bursts). So delimited, the entire wing-clap sequence lasted 1.5 s (frames 328–448), the first sound pause was 0.26 s (frames 342–363) and the second pause 0.19 s (frames 373–388).

Sound was obviously produced during these fast wingbeats whose temporal pattern agrees closely with published sonograms of the wing-clap sound: (1) the wingbeat frequency of about 24 Hz equals the rate of production of sound units in sonograms, (2) the numbers of fast wingbeats in each of the three bursts agree with the numbers of sound units in sonograms, and (3) the interburst pauses are of similar lengths to those in sonograms. The following data from sonograms are given for comparison with my film data above. The rate of production of sound units in Bertram's (1977, p. 166) sound recordings varied between 22 and 29 Hz (calculated from the 0.035–0.045 s gaps between sound units), and Payne (1978, p. 204) reported a rate of 24–25 notes  $s^{-1}$  in a burst. Furthermore, Bertram (1977, p. 167) reported 4–8 sound units in the first burst, 3–4 in the second and 16–21 in the third. His sonograms show a 0.16–0.26 s pause between the first and second bursts and a 0.14–0.27 s pause between the second and third bursts.

From an across-species regression for various birds, including passerine species (Rayner, 1979, p. 45; U. M. Norberg, 1990, p. 169), the wingbeat frequency  $f$  has been shown to vary with body mass  $M$  as:

$$f = 3.03M^{-0.36}. \quad (1)$$

Niethammer and Wolters (1966, p. 161) reported the mass of two male flappet larks to be 26 and 27 g. For 27 g, equation 1 predicts a wingbeat frequency of 11.1 Hz, which agrees well with the 9.8–11.4 Hz from the film for pre-clap flight. Inserting instead a wingbeat frequency of 24 Hz into equation 1, and solving for mass, gives 3.2 g. This shows how exceptionally high the 24 Hz wingbeat frequency is for a 27 g lark.

The kinematics of the sound-producing wingbeats is similar to that of the pre-clap wingbeats, except that the former are deeper, with the wings probably clapping together ventrally. Because of the angle of view, and because there are no discernible details in the dark silhouette, the wings cannot be seen actually to clap together below the bird, although it seems likely from Fig. 3, frames 433 and 436, that they did. The wings were not raised higher at the top of the upstroke than in pre-clap flight; in none of the frames covering the 25 wingbeats in the whole wing-clap sequence were the wings in a higher position than in Fig. 2, frame 335. Therefore, the film shows conclusively that the wings do not clap together above the back and that there is only one sound unit per wing stroke.

Apart from the basal metabolic rate (BMR), there are four power drains in flapping flight; *induced power* (for creating lift), *parasite power* (for overcoming body drag), *wing profile power* (for overcoming wing profile drag) and *inertial power* (for accelerating the wings). To reduce aerodynamic power output during the inertially strenuous wing-clap display, the lark could feather its wings, i.e. reduce the effective angle of attack to 0°, thereby bringing induced power to zero. Apparently this does not occur, however, since Wickler (1967, p. 162) observed that larks climb fairly steeply in three stages during the three bursts of wing claps, and Bertram (1977, p. 165) also noted a steep ascending flight over 1–2 m during the wing claps. This indicates that the wings work under fully effective angles of

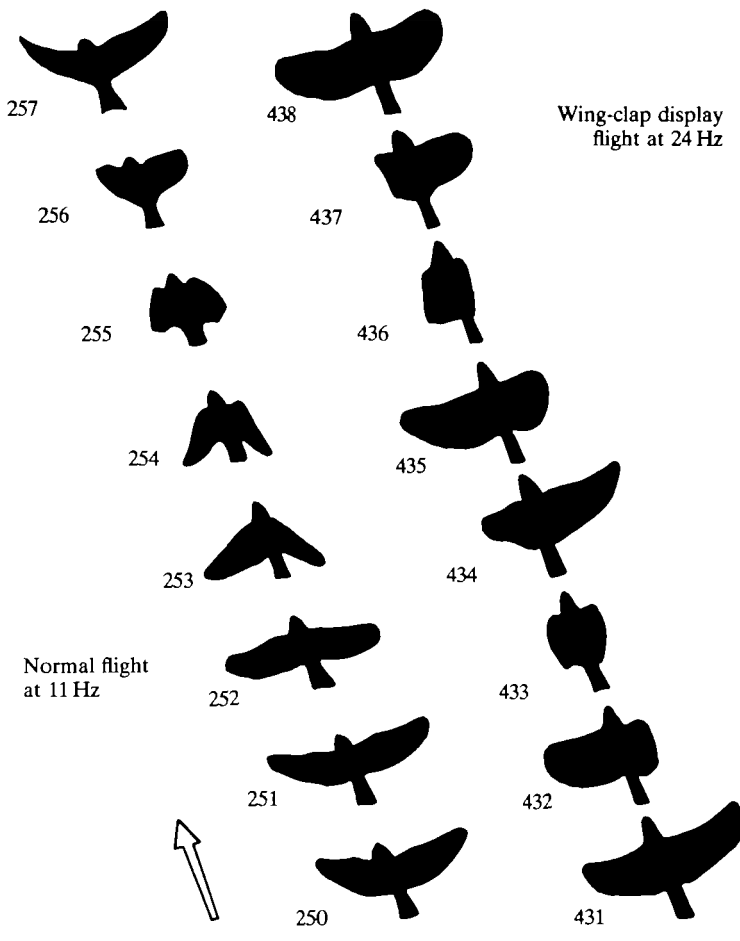


Fig. 3. Silhouette tracings of a flappet lark seen from in front and obliquely below, flying overhead and obliquely towards the camera. The images should be viewed from the bottom upwards. The bird's ventral side is facing downwards and somewhat to the left. The images show one wingbeat in normal, pre-clap flight with  $11 \text{ wingbeats s}^{-1}$  (left; frames 250–257) and two sound-producing wingbeats in wing-clap display with  $24 \text{ wingbeats s}^{-1}$  (right; frames 431–438). Consecutive tracings are separated by  $1/80 \text{ s}$  (12.5 ms). The spatial distances between consecutive tracings do not accurately show distances flown. The lark is larger in the right-hand series because it was closer to the camera than in the earlier sequence to the left.

attack and that induced power is therefore expended. Actually, the amount of induced power needed for weight support during the wing-clap display is almost the same as that in normal flight; in addition, extra induced power is required for vertical acceleration. Additional power is also expended on the climb itself (gain in potential energy), amounting to about  $1 \text{ W}$  of metabolic power for a  $27 \text{ g}$  bird climbing at  $1 \text{ m s}^{-1}$  (average climbing speed from  $1.5 \text{ m}$  in  $1.5 \text{ s}$ ; see above and

Fig. 1) and with a mechanical efficiency of 0.25 for flight muscles [mass (kg)  $\times$  9.81 ( $\text{m s}^{-2}$ )  $\times$  climbing speed ( $\text{m s}^{-1}$ )  $\times$  1/0.25]. This addition is twice the basal metabolic rate, BMR, estimated to be 0.46 W from:

$$\text{BMR} = 6.25M^{0.724} \quad (2)$$

in U. M. Norberg (1990, p. 42, based on Lasiewski and Dawson, 1967).

Because of the doubled wingbeat rate, the wing claps must demand a considerable increase in wing profile power (which increases with the third power of the wings' relative air speed, i.e. an eightfold increase for a doubling of air speed) and in inertial power (which increases with the third power of the wingbeat frequency, i.e. an eightfold increase for a doubling of frequency). But the flapping velocity adds vectorially to the forward and induced speeds, so the resultant relative air speed over the wings does not double upon a doubling of the wingbeat rate. Moreover, the wing profile power makes up only about half of the total flight power in normal flight (U. M. Norberg, 1990, p. 144). Without a detailed knowledge of the aerodynamic characteristics of the wings, the wingbeat plane inclination and the flight speed of the displaying lark, I can make no precise calculations. A rough estimate, however, based on the above aerodynamic considerations, gives a doubled power consumption for the wing-clap bursts compared with that in normal flight.

Using a regression across data for seven bird species flying in wind tunnels at their minimum power speed, oxygen consumption  $\dot{V}_{\text{O}_2}$  can be estimated and converted into metabolic power consumption  $P$  from the relationship  $1 \text{ ml O}_2 \text{ min}^{-1} = 0.335 \text{ W}$ :

$$\begin{aligned} P &= \dot{V}_{\text{O}_2} \times 0.335 \\ &= 0.335 \times 150M^{0.73} \end{aligned} \quad (3)$$

(U. M. Norberg, 1990, equation 3.26 and p. 55). This gives 3.6 W for a 27 g bird in normal flight, which is 7.8 times BMR (from equation 2). For the wing-clap display, the estimated metabolic power consumption is thus about 16 times BMR.

Because of the high power consumption of the wing-clap bursts, the display flight may be constrained in two ways: (1) by the lark's ability to work at a high rate and (2) by its ability to cover the enhanced metabolic energy expenses over a period of time with a high frequency of display bouts. Therefore, the wing-clap display could be an excellent marker of male quality. The capacities for producing (1) claps at a high rate, (2) long bursts of wing claps and (3) high burst rates should all depend on the male's phenotypic quality, which in turn is at least partly dictated by his overall genetic quality.

The phenotypic quality of the male might be a reliable indicator to females of the material benefits he may provide, such as a high-quality territory or his likely future parental care (for example, food provisioning for the young). This would affect the prospects for the production of young, and his genetic qualities will, of course, be transmitted to the young. A male of lower phenotypic quality would

have to pay a relatively higher cost to produce a power-demanding display than would a male of higher quality, so a low-quality male could hardly afford dishonest high-quality signalling [by analogy with Andersson's (1986) arguments about condition-dependent sex ornaments, the expression of which may increase with the phenotypic condition of the possessor]. The wing-clap display is therefore presumably a reliable indicator of male quality. As such, it would be an ideal target for sexual selection – intrasexual selection *via* male–male deterrence and intersexual selection *via* female choice of mates.

The evolution of the wing-clap display to its present exaggerated frequency and length obviously occurred as a result of sexual selection. There is now considerable individual variation in the length and structure of the clap-bursts (Bertram, 1977; Payne 1978, 1981), providing ample cues for sexual selection. To find out the extent of sexual selection acting today, it should be rewarding to study possible associations between breeding performance and male phenotypic attributes such as the morphology and condition of individual birds, the length and structure of their clap-bursts, and the number of display flights per unit time.

In conclusion, during wingbeat bursts in normal, intermittent flight the wings beat at about 11 Hz. This is exactly as expected for a 27 g passerine bird, like the flappet lark. In the wing-clap display, however, the wings beat at about 24 strokes  $s^{-1}$ , and the wingbeat amplitude is even larger than in normal flight. This observation of a bird doubling its normal wingbeat frequency without reducing the wingbeat amplitude is striking. To my knowledge it has not previously been observed in any flying animal. There is only one sound unit for each wingbeat, and the wings do not clap together above the back. Tracings from the film suggest that sound is produced by the clapping together of the two wings at the bottom of the downstroke (Fig. 3, frames 433 and 436).

Because of the doubled wingbeat rate and large wingbeat amplitude, the wing-clap display must require bursts of high power output, estimated to be twice that of normal flight, about 16 times BMR *versus* 8 times BMR. The length of wing-clap bursts and the number of display flights per unit time may advertise heritable male viability. Such an honest quality signal would be an ideal cue for female choice of mate, and it seems likely that the wing-clap display has evolved to its present power-demanding nature as a result of sexual selection.

In biomechanical studies it is usually assumed that natural selection has led to animals adopting locomotor patterns with low energy costs. But sexual selection theory predicts that quality-signalling displays should be costly, something that seems to be borne out by the kinematics of display flights in insects and birds. I see various types of display flights as rewarding targets for mechanical, aerodynamic and energetic analyses, interpreted in terms of sexual selection theory.

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