Biological Journal of the Linnean Society, 2022, **XX**, 1–6. With 1 figure.

COMMENT

Where is WAIR (and other wing-assisted behaviours)? Essentially everywhere: a response to Kuznetsov and Panyutina (2022)

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Received 31 March 2022; revised 27 May 2022; accepted for publication 30 May 2022

Kuznetsov and Panyutina (2022) offer a reanalysis of the kinematic and force plate data previously published by Bundle and Dial (2003). Their intention is to describe instantaneous wing forces during wing-assisted incline running (WAIR), focusing particularly on the upstroke phase. Based on their interpretation of wing forces and muscle function, the authors conclude that 'WAIR is a very specialized mode of locomotion that is employed by a few specialized birds as an adaptation to a very specific environment and involving highly developed flying features of the locomotor apparatus', and thus not relevant to the evolution of avian flight. Herein, we respond to the authors' interpretations, offering an alternative perspective on WAIR and, more generally, on studies exploring the evolution of avian flight.

ADDITIONAL KEYWORDS: cooperative use of wings and legs – evolution of avian flight.

INTRODUCTION

We thank Kuznetsov and Panyutina (2022; hereafter, the 'authors'), and many other researchers, for their interest in wing-assisted incline running (WAIR). Here we reiterate points raised in our submitted review and respond to the main conclusions presented by the authors. A novel contribution of their analysis is to describe the instantaneous wing forces during the upstroke, and we do not question their key conclusion that forces are produced by the wings during the upstroke. However, as we describe, these forces are more likely to be inertial than aerodynamic. We also propose that musculoskeletal activity during WAIR is actually reasonably consistent with the evolutionary inferences summarized by the authors.

Based on their analyses, the authors suggest that the upstroke of an adult chukar engaged in WAIR is a unique, specialized aerodynamic event among birds, and that it should be regarded as a crown locomotor specialization not suitable as a model for the evolutionary origins of flight. The authors' rejection of WAIR as an analogue to the early evolution of avian wings is based on aerodynamic and musculoskeletal considerations, which we address, with contrary conclusions. For the purposes of discussion, we will focus on 'variant B' of the authors' reanalysis of data in Bundle & Dial (2003).

AERODYNAMIC CONSIDERATIONS

Based on a recalculation of data from Bundle & Dial (2003), the authors state that the average force acting on the wings is 113% body weight (variant B), that in the sagittal plane this force is primarily an aerodynamic force, and that the force is directed into the substrate and upward during the middle and end of the downstroke and downward during the rest of the wingbeat cycle. Averaged over the entire wingbeat

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*Corresponding author. E-mail: kpdial@gmail.com cycle, the force is directed 11° below perpendicular to the substrate surface for variant B. That the force is directed partially toward the substrate is consistent with previous work on WAIR and not a new discovery; indeed, Dial (2003) describes the wings as 'acting like the spoilers on a race car to improve traction' during WAIR (Bundle & Dial, 2003; Dial *et al.*, 2006, 2008; Tobalske & Dial, 2007). However, if the analysis is correct, and if the large force generated during the upstroke is an aerodynamic force as the authors suggest, then this finding contrasts with every previously published study on upstroke aerodynamics in bird flight, as outlined below.

To begin, it is first important to note that **the tip-reversal upstroke used by an adult chukar is not unique or particularly specialized among birds**. Light and X-ray video (Baier *et al.*, 2013; Heers *et al.*, 2016) show that chukars use relatively similar kinematics to achieve different behaviours, with joint movements becoming more exaggerated as the difficulty of the behaviour increases and culminating in an exaggerated tip-reversal upstroke. This upstroke style is widespread among avian species during movement at low advance ratios (J), where whole-body translational velocity is significantly less than wingtip velocity. For example, tip-reversal upstrokes are routinely used at low J in many birds that have relatively pointed, high-aspect ratio wings, such as parakeets and cockatiels (Tobalske *et al.*, 2003), pigeons and doves (Tobalske, 2000), and dabbling ducks (Vazquez, 1994). Species with rounded wings typically use a flexed-wing upstroke (Tobalske, 2000), but phasianids, including the chukar, use a tip-reversal upstroke in spite of having relatively rounded wings (Tobalske & Dial, 2000). The kinematics of these tip-reversal upstrokes have been recognized since (Marey, 1890). Additional kinematics are available in Lorenz (1933), Brown (1953), Tobalske & Dial (2000), Crandell & Tobalske (2015), and skeletal adaptations that facilitate hand-wing supination during tip-reversal upstrokes are in Vazquez (1992). In short, tip-reversal upstrokes are well known, widespread and fairly well studied.

Second, there is **no evidence that any bird species operating at low advance ratios can produce aerodynamic force during the upstroke that is on par with force produced during the downstroke.** Since Marey (1890), researchers have hypothesized that tip-reversal upstrokes provide substantial lift, but all available evidence instead suggests that aerodynamic force production is much less than in downstrokes. This should not be surprising given that hummingbirds, the only species to supinate almost their entire wing during the upstroke, have upstrokes that produce ~30% of downstroke lift (Warrick *et al.*, 2005, 2009). Several lines of evidence suggest that tip-reversal and flexed-wing upstrokes also contribute significantly less lift compared with downstrokes. For example, analysis of 3D kinematics and body mass distribution suggests that aerodynamic forces during tip-reversal upstrokes in turning pigeons are ~50% of those produced during downstrokes (Ros *et al.*, 2011). Dried wings mounted in a mid-upstroke tip-reversal posture and spun like a propeller produce lift that is ~36% of the body weight for both wings (Crandell & Tobalske, 2011), although this likely overestimates *in vivo* function because the wings morph dynamically during upstroke, and full supination of the hand wing occurs only during the middle of upstroke (Crandell & Tobalske, 2011). Measures of the near wake using particle image velocimetry (PIV) in diamond doves (Crandell & Tobalske, 2011) demonstrate that the primary aerodynamically active portion of tip-reversal upstroke occurs at the upstroke-downstroke transition, when the wings clap and peel. This has two effects: generating a thrusting impulse that is ~11% of the downstroke impulse, and initiating an earlier onset of circulation (hence lift) on the wing during the downstroke. Accelerometry in cockatiels shows that the tip-reversal upstroke produces ~14% of the force of the downstroke (Hedrick *et al.*, 2004), and measures of parrotlets in an aerodynamic force chamber reveal peak upstroke forces that are 10–15% of the downstroke, except during the final wingbeat of landing when the bird is using drag to decelerate (Chin & Lentink, 2017). Flexed-wing upstrokes likely produce even less aerodynamic force: zebra finches using this type of upstroke transmit minimal momentum to the upstroke wake compared to tip-reversal upstrokes (Crandell & Tobalske, 2015). Taken together, these studies suggest that the aerodynamic contribution of the downstroke far exceeds that of the upstroke.

The analysis of the authors motivated us to revisit our previous samples of PIV from chukars engaged in WAIR (Tobalske & Dial, 2007). Consistent with the data from the upstroke in diamond doves (Crandell & Tobalske, 2011), we observed induced air velocities from the late upstroke, immediately prior to the upstroke-downstroke transition. These velocities were less than those observed during the downstroke, and directed toward the substrate and not downward. In the example shown in Figure 1, the average induced velocity in the middle of the downstroke wake was 9.0 m s^{-1}, oriented at 54° relative to horizontal, meaning that it was directing force upward and toward the ramp, which was angled at 90° (i.e. vertical). The area of the wake from the beginning of the upstroke overlapped with the downstroke-upstroke transition, producing a complex flow field (Tobalske & Dial, 2007). This early phase of upstroke did direct force down and away from the substrate (with an orientation of –54° relative to horizontal); however, the average velocity

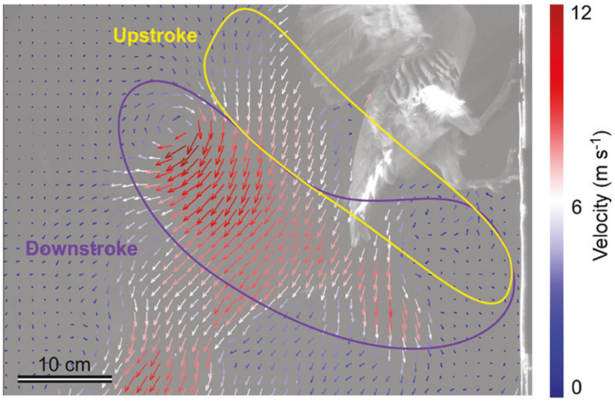

Figure 1. Induced velocities in the wake of an adult chukar using wing-assisted incline running (WAIR) to ascend a ramp set at an incline of 90°. See Tobalske & Dial (2007) for methods. The approximate boundaries are indicated as closed loops. The boundaries overlap at the downstroke-upstroke transition.

during this phase was only 0.8 m s^{-1}. Late upstroke induced velocity was 5.0 m s^{-1} oriented at 62° relative to horizontal—slightly more upward than the orientation of the downstroke. A different example from an adult chukar flap-running up an 80° incline exhibited a late upstroke induced velocity of 5.4 m s^{-1} oriented at 20° relative to horizontal, thus more directed as thrust toward the substrate and less as weight support. These patterns are consistent with previous studies showing that upstroke aerodynamic force production is less than that of downstroke, and they suggest that such forces direct the bird toward the substrate and primarily upward (rather than downward).

Previously, we measured circulation and modelled projected wake area, and spun dried wings like propellers, to estimate the average force produced during the downstroke in adult chukars (Tobalske & Dial, 2007; Heers *et al.*, 2011). These measurements indicated that aerodynamic force was approximately 60% of body weight during 65° WAIR. At a 70° incline, as in Bundle & Dial (2003), this force was likely somewhat higher. Nevertheless, even if the upstroke produced as much force as the downstroke—which seems unlikely for the reasons described above—peak aerodynamic forces are only generated for part of the wingstroke cycle, such that the aerodynamic force produced over the entire wingbeat would probably be far less than 60% body weight. This is substantially lower than the 113% calculated by the authors.

Based on these points, we instead suggest that inertia is contributing substantially to the force acting on the wings. The authors state that inertial forces 'should be mainly confined to the wingbeat plane' and that they 'cannot influence significantly the 2D accelerometer system in the sagittal-bound experimental setting'. This conclusion assumes (1) that peak magnitudes of circumferential inertial force occur at the downstroke-upstroke and upstroke-downstroke transitions, when the wing approaches the sagittal plane and circumferential inertial force would be directed transversely, and (2) that inertial forces during the rest of the wingbeat cycle are very small. However, **simulations suggest that inertial forces are quite substantial through much of the wingbeat cycle** (Heers *et al.*, 2018), **and negligible *only* during the mid-downstroke and the mid-upstroke,** indicating that inertia would contribute to forces acting on the wings during early and late downstroke and upstroke. Any upstroke with a partially extended wing requires inertial work from the wing muscles to move the wing. Indeed, direct measures of contractile behaviour of the supracoracoideus muscle in pigeons using tip-reversal upstrokes during slow flight reveal that the inertial power required for the upstroke is within one standard deviation of the power output by the muscle (Tobalske & Biewener, 2008).

In addition, **the wingstroke plane is based on the path of the wingtip through space. However, the *mass* of the wing lies posterior to the wingtip and leading edge of the wing**, because the humerus is retracted [particularly during WAIR (Heers *et al.*, 2016, 2018)] and the elbow is bent, such that the mass of the wing muscles, largest wing bones (humerus, radius, ulna) and feathers (whose mass influences inertial calculations) lies posterior to the leading edge and stroke plane. These masses thus rotate about the shoulder joint and likely exert torques that do not operate perpendicular to the sagittal plane of the bird, which should, in turn, result in inertial forces that are partially directed either anteriorly or posteriorly, depending on the portion of the wingbeat cycle. Indeed, simulations of WAIR without any aerodynamic force production result in substantial joint moments through most of the wingbeat cycle, including moments along the vertebral axis, suggesting that inertia plays an extremely important role throughout the wingbeat cycle (Heers *et al.*, 2018). The relative effects of inertia are particularly substantial when aerodynamic force production is low, as during WAIR. This is especially true for immature birds [which produce very small amounts of aerodynamic force (Tobalske & Dial, 2007; Heers *et al.*, 2011)] and presumably for extinct avian predecessors with incipient aerodynamic capacity.

Finally, it is worth noting that the calculations presented by the authors may be influenced by experimental or analytic limitations. For example, it is difficult to determine particular phases of upstroke and downstroke based solely on the figure from which the authors extracted the data used in their analysis. This is because the figure and referenced video frames were likely from different trials and/or individuals. In addition, only one wingbeat was analysed, and at a point when the bird was decelerating. Over many wingbeats, a different pattern might emerge given that the wings and legs oscillate at different frequencies, as the authors have noted. It is also possible that some forces do not act through the centre of mass and therefore produce torques; e.g. a downward-directed wing force helps to pitch the body forward (since the shoulder joints are likely anterior to the centre of mass) and balance the animal on the incline. Regardless, altering the stroke plane angle slightly helps redirect the animal during flight (Dial *et al.*, 2008). Indeed, many birds alter their stroke planes to achieve different flapping behaviours. **That WAIR may differ from flight is therefore not unexpected, and neither supports nor precludes WAIR and similar behaviours as potentially important evolutionary drivers.**

MUSCULOSKELETAL CONSIDERATIONS

In addition to the aerodynamic considerations outlined above, the authors also suggest that WAIR is inconsistent with the evolution of the supracoracoideus muscle, from a 'depressor-protractor' to a 'protractor' (Ostrom, 1976; Novas *et al.*, 2021) and then to an 'elevator and supinator' as well. They state that:

1. 'The humeral protractor muscles are not required at all during WAIR'
2. 'The morphologically necessary protractor state of the supracoracoideus muscle in a "semi-flying" ancestor, which is logically explained by the classical hypothesis of a gliding ancestor, does not fit the WAIR hypothesis of flapping flight origin'
3. 'Nowhere in the downstroke of WAIR, [are] the anterior (clavicular) fibres of the pectoralis muscle are required. Therefore, the avian-specific spreading of the pectoralis muscle origin onto the clavicle cannot be explained through the WAIR hypothesis'.

However, all of these statements are inconsistent with previously-published studies. Based on X-ray videos, which provide the most accurate method for quantifying joint movements, protraction is significant (~ 50°) during WAIR (Baier *et al.*, 2013; Heers *et al.*, 2016). Musculoskeletal modelling simulations of WAIR, which align with previously reported data on muscle activity, indicate that both the pectoralis and the supracoracoideus contribute to this protraction (Heers *et al.*, 2018). With respect to the spreading of the pectoralis muscle origin onto the clavicle, it should be noted that changes in bone orientation may have also contributed to this expansion, in addition to locomotor demands. For example, as the sternum expanded and the coracoid became more angled (i.e. producing a smaller scapulocoracoid angle), the furcula may have expanded ventrally to help maintain the cranial origins of the pectoralis (Heers *et al.*, 2021). Thus, it is not necessary to assume that the spreading of the pectoralis muscle was to enhance protraction—it also could have been a mechanism for evolving a larger and more powerful muscle.

Based on the aerodynamic and musculoskeletal considerations discussed above, the authors conclude that 'WAIR is a very specialized mode of locomotion that is employed by a few specialized birds as an adaptation to a very specific environment and involving highly developed flying features of the locomotor apparatus.' Our observations yield a very different conclusion here as well. **WAIR and behaviours like WAIR are used by *many* avian species in *many* environments** (https://youtu.be/VFUNhTdcNdk). Given that WAIR, and similar behaviours like steaming (i.e. using the feet like paddles and the wings like oars to swim) (Dial & Carrier, 2012) or wing-assisted jumping (Heers & Dial, 2015), are extremely common and employed by a diverse array of juvenile birds with very underdeveloped anatomical features compared to adults, it appears to be **one of the *least* specialized flapping behaviours observed among extant birds**. Indeed, behaviours like WAIR require less aerodynamic force production (Tobalske & Dial, 2007; Heers *et al.*, 2011) and less muscle power (Jackson *et al.*, 2011; Heers *et al.*, 2018), and can be performed by animals that have small wings with less aerodynamically effective feathers (Heers *et al.*, 2011; Dial *et al.*, 2012), smaller muscles (Heers & Dial, 2015), and less robust and specialized skeletons (Heers & Dial, 2012; Heers *et al.*, 2016).

LOOKING AHEAD

We heartily agree with Kuznetsov and Panyutina that evolutionary hypotheses should be tested and discussed. However, we believe that some conversations are more productive when they occur directly between scientists as a collaboration, rather than indirectly between articles. We would also like to reiterate that our fields can benefit from:

1. *Testing all hypotheses and behaviours similarly*—to keep conclusions in perspective and help validate methods of analysis. For example, some models describing the evolution of avian flight can be applied only to a subset of extant birds or behaviours, and limitations like these should be acknowledged.
2. *An emphasis on acquiring new data rather than reanalysing old data*—but when appropriate, *communicating with the authors whose data is being reanalysed*.
3. *Collaborating more across disciplines*. As many authors have pointed out, work with extant

organisms is necessary to validate methods of analysing extinct ones (Hutchinson & Allen, 2009; Hutchinson, 2011; Bishop *et al.*, 2021). However, eliciting behaviours and maximal performance in living animals is challenging—should one conclude that a pigeon cannot fly if it does not fly in front of a video camera? Instances like this have occurred. As biologists and palaeobiologists, we probably all agree that extinct animals can provide rich insight into extant ones, and vice versa, and our fields should reflect this belief—by encouraging new ideas, promoting rigorous and interdisciplinary collaborations, and facilitating constructive discussions in welcoming environments.

ACKNOWLEDGEMENTS

We thank Drs Kutnetzov and Panyutina for raising the issue of WAIR and for their helpful comments on the manuscript, alongside those of two other anonymous referees.

DATA AVAILABILITY

This article has not generated any new data.

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