

MEASURING LEG THRUST FORCES IN THE COMMON STARLING

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Summary

We describe the design of a force-transducing perch which measures the reaction forces of small birds taking off and landing. In common starlings, landing forces are lower than take-off forces, because the bird may decelerate prior to landing by using its wings. Both landing and take-off forces are significantly correlated with body mass; however, the angles of these reaction forces show no

significant mass-dependence and are not repeatable within individuals. Diversity in take-off or landing strategy could be advantageous in confusing predators.

Key words: force perch, leg, thrust, take-off, landing, scaling, repeatability, predation, birds, common starling, flight.

Introduction

One method of determining the forces acting on skeletons and the muscular power output during terrestrial locomotion is to measure the magnitude and direction of the ground reaction force. Force plates have a long history of use in the study of terrestrial locomotion (see Cavagna, 1985). Although this technique is superficially more applicable to running and walking than to flight, in passerine and other small birds, the initial acceleration during take-off may be almost entirely due to leaping from a perch: the wings may remain folded during this initial phase of take-off, so that all initial acceleration is due to leg thrust. Witter *et al.* (1994) have discussed the importance to predator escape of this initial leaping phase of take-off. Fisher (1956*a,b*) measured the forces produced during take-off and landing in pigeons with a mechanical force plate. Heppner and Anderson (1985) constructed a simple force perch to determine the leg thrust during take-off in pigeons but, owing to the design of their apparatus, they did not determine the forces during landing and their analysis did not resolve the direction of the reaction force.

Semiconductor or metal foil strain gauges that detect strains in the material to which they are bonded have been used to construct force transducers in force plates to examine terrestrial locomotion (see Heglund, 1981; Full and Tu, 1990; Biewener and Full, 1992). A well-designed force platform should fulfil several criteria. The load/displacement behaviour of the mechanical system and the electrical transduction should be linear. The horizontal and vertical (x- and y-) force components should be separately resolvable, and there should be minimal cross-talk between the two components. Finally, the components of the device, and especially the force blades, should not be subject to forces that exceed the material elastic limit, i.e. yield. This paper demonstrates the application of

these principles to the design of an instrumented perch which we have used to determine the landing and take-off forces in the common starling (*Sturnus vulgaris* L.). For the purpose of this paper, we define leg thrust as the peak reaction force during landing and take-off.

Materials and methods

Mechanical and electronic design

The instrumented perch consists of three components: a narrow cylindrical wooden perch (diameter 12 mm, length 240 mm) and two brass supports (Fig. 1), similar in form to the ends of the force beam of Heglund (1981). Each support was machined from a length of solid, square-section brass (19 mm × 19 mm). The brass supports have two perpendicular flat blades. The blade thickness h (m) was determined by applying beam theory to predict the highest forces that would be present; if the blade is too thin, the yield stress of the brass may be exceeded and the perch would no longer deflect linearly with increasing loads. The stress σ (N m⁻²) on the surface of the blade is $Mh/2I$, where I is the second moment of area of the section (m⁴) and M is the applied moment (N m). I for the blade is $bh^3/12$, where b is the blade width (m). From these equations:

$$h = \sqrt{6M/b\sigma}. \quad (1)$$

The applied moments at the blades at either end of the perch were calculated using beam theory equations (Young, 1989). Heglund (1981) suggests that a safety factor of 14 times body mass in the beam blade is appropriate with small (approximately 100 g) animals. The beam was designed to withstand forces of birds up to 300 g in mass (peak force is

41 N). b will be constrained by the width of the metal from which the ends are constructed and, in any case, is considerably less important in determining I than is h . σ is best taken as the yield stress of the metal, since this will constrain the upper limit of the linear force/deflection behaviour of the blade.

For birds of mass up to and including 300 g, and with a safety factor of 14, the appropriate blade thickness is 3 mm (yield stress of brass taken as 70 MPa). Each blade was 15 mm in length, and both were separated by a 20 mm unmachined section to minimise cross-talk. The wooden perch, length 0.24 m, was glued, using epoxy adhesive, into holes drilled at the end of each support (see Fig. 1).

The use of a single blade has certain advantages over the two-blade design suggested by Full and Tu (1990) and Biewener and Full (1992). A two-bladed design is inherently stiffer than a single-bladed design of similar cross-sectional area. To produce reasonably large deflections, the twin-bladed design must have very thin blades.

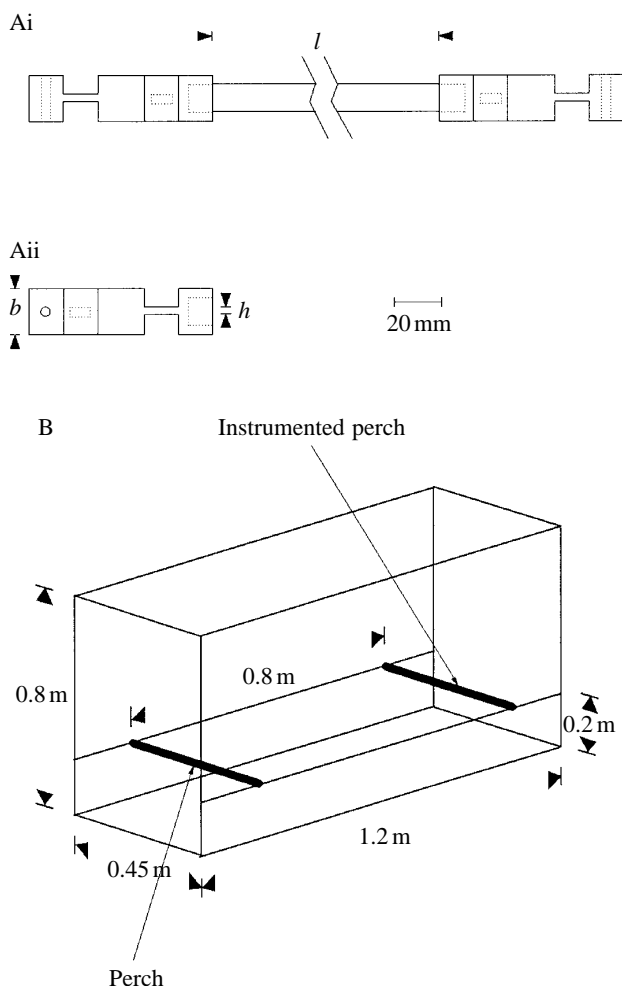


Fig. 1. (A) Scale drawings of the brass supports; (i) side elevation, including section of perch, (ii) plan view. Dimensions indicated on drawing are as follows: l , 240 mm; b , 19 mm; h , 3 mm. Positions of the strain gauges are indicated by the dotted rectangles on the transducer blades. (B) Diagram showing flight cage and position of the instrumented perch.

Gauges were applied to the middle of each face of the blades, four to each one, to detect horizontal and vertical strains. Each group of four gauges was wired as an independent Wheatstone bridge, supplied and amplified by a commercial strain gauge amplifier (RS Components Ltd, Corby, Northants, UK). The configuration of the gauges to form the Wheatstone bridge is important; lateral variation in force transduction was minimised (at 3.6%) when gauges from each end were connected to the same polarity of bridge supply (i.e. left end to negative, right end to positive).

Calibrations were performed by static loading of the perch using a spring balance. Cross-talk was determined by measuring the horizontal output while loading only in the vertical plane; the measured cross-talk was approximately 4.6%. A torsional moment of 0.1 N m applied to the mid-point of the perch did not produce a measurable output from either the x or y amplifier outputs. The natural frequency of the output, with the perch unloaded, was approximately 250 Hz, determined using an Iso-Tech 103 digital multimeter. Linearity of force transduction exceeded 99.5% at the midpoint of the perch.

Output from the x and y strain gauge amplifiers was passed to a Kompensograph X-T, C1012 (Siemens Ltd, Bracknell, Berkshire, UK) two-channel chart recorder. Reaction forces were calculated from these traces as the root of the sum of the squares of the x and y force components. The angle of the force was calculated as the inverse tangent of the y -component divided by the x -component. Time-expanded traces were produced by recording the amplifier outputs using an instrumentation cassette recorder (DA 1442, Data Acquisition Ltd, Stockport, UK). Take-off and landing events were sampled using a PC-based A/D converter (DAS 50, Keithly Instruments Inc., Cleve, OH, USA) with a sampling rate of 1 kHz.

Experiments were conducted in a flight cage (0.45 m \times 0.8 m \times 1.2 m) constructed from steel angle and wire mesh, with a spacing of 0.8 m between the force perch and an uninstrumented wooden perch. The instrumented perch was bolted to horizontal metal frames on either side of the cage. Equal illumination on either side of the cage ensured that the birds always landed on the mid-length of the force perch (confirmed by observations).

The 14 birds used in this experiment were all from a colony of wild-caught individuals maintained in large outdoor aviaries. Mass range of the birds was 62–80 g.

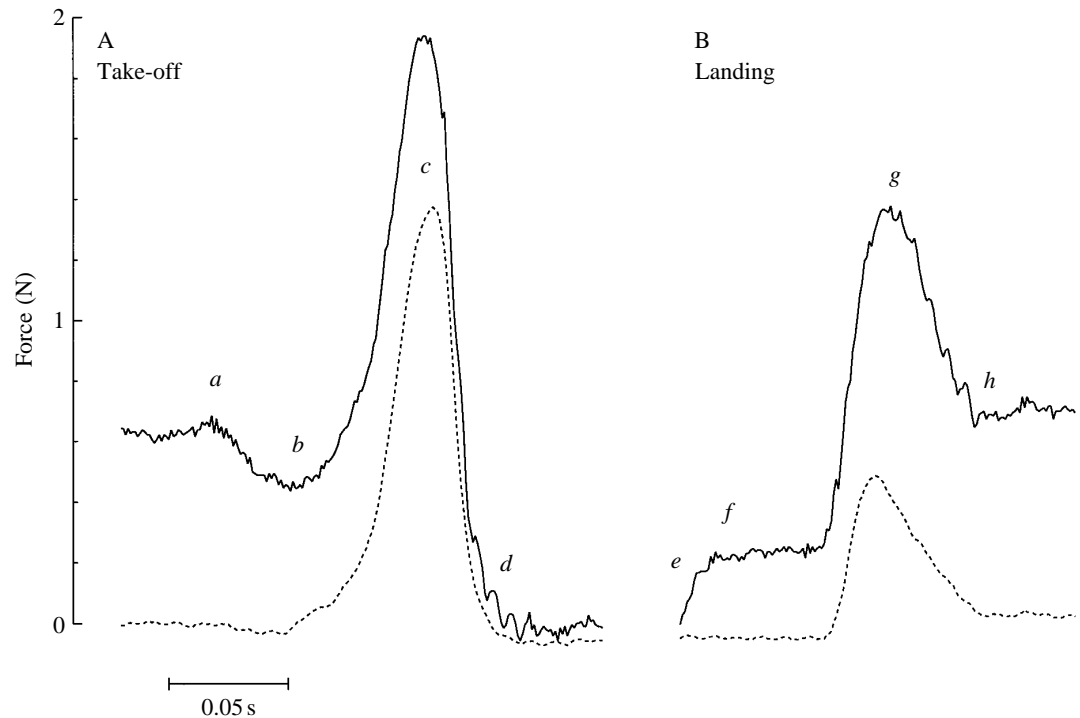
Results

Landing and take-off forces in common starlings

A total of 202 take-offs and 213 landings were recorded from the 14 birds.

Fig. 2 shows a typical time-expanded chart output of x and y force components during a take-off and landing. Peak reaction forces during take-off were significantly higher than those during landing [repeated-measures general linear model

Fig. 2. Typical traces of the y- (dashed line) and x- (solid line) force components of a take-off (A) and landing (B) event. Four distinct phases can be observed in each event. During take-off, region *a* is the bird at rest on the perch. *b* shows a decrease in vertical force probably due to rapid leg flexure prior to leap. Both the x- and y-forces reach their peak at *c*, and then rapidly decrease to *d*, when contact with the perch is released. On landing, after the initial foot-to-perch contact, *e*, the vertical force initially rises to a plateau, *f*, while there is no change in horizontal force. After approximately 0.05 s, x- and y-forces both increase rapidly to peak at *g*, then decrease until the bird is at rest at *h*.



(GLM), $F_{1,414}=811.97$, $P<0.001$]. Take-off forces were approximately 45 % higher than landing forces (Fig. 3A). Forces during landing and take-off increased linearly with body mass, m (Fig. 4A,B):

Landing force =

$$59.54m - 2.993, r^2=0.365, N=213, P<0.001, \quad (2)$$

Take-off force =

$$58.83m - 2.388, r^2=0.387, N=202, P<0.001. \quad (3)$$

No significant difference was found between the angles of the reaction force during landing and take-off (repeated-measures GLM, $F_{1,414}=0.08$, $P=0.774$) (Fig. 3B). In neither case was mass significantly correlated with the angle of the reaction force ($r^2=0.001$) (Fig. 4C,D).

Repeatability R (Harper, 1994) of ground reaction forces, within birds, was high during landing ($R=0.72$) and take-off ($R=0.60$). However, the angle of the force vector had a low repeatability during landing ($R=0.22$) and take-off ($R=0.53$).

This reflects the absence of a significant relationship between the mass of the bird and take-off and landing force angles.

Discussion

Reaction forces and angles during take-off and landing

The forces experienced by the legs during take-off are much greater than those during landing. The wings are folded during the initial phase of leaping (R. H. C. Bonser, personal observation) and cannot contribute to initial acceleration, so this phase of take-off is due entirely to the leg thrust force. On landing, the wings can be used to slow down the rate of descent; this may have adaptive significance, as lower impact velocities on perches may minimise the risk of perch failure or injury to the bird. Peak forces are mass-dependent; however, the angle of the reaction force shows no such mass-dependence. Witter *et al.* (1994) established that, within individuals, increases in mass lead to decreases in the initial

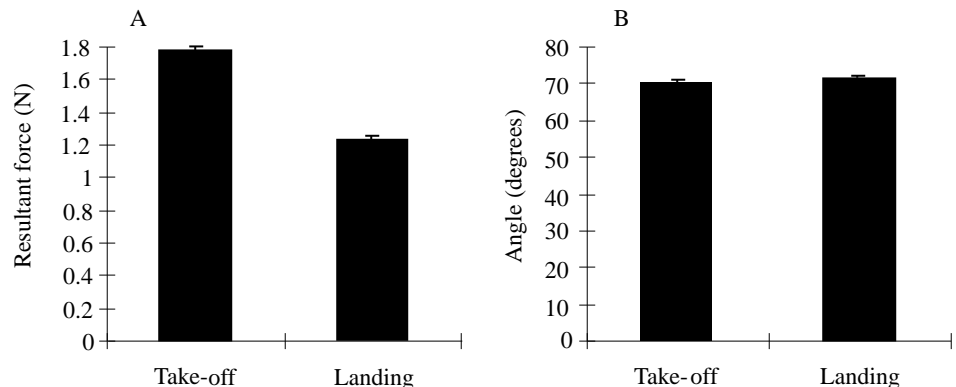


Fig. 3. Comparison of take-off ($N=202$) and landing ($N=213$) forces (A) and angles (B). Values are mean + S.E.M.

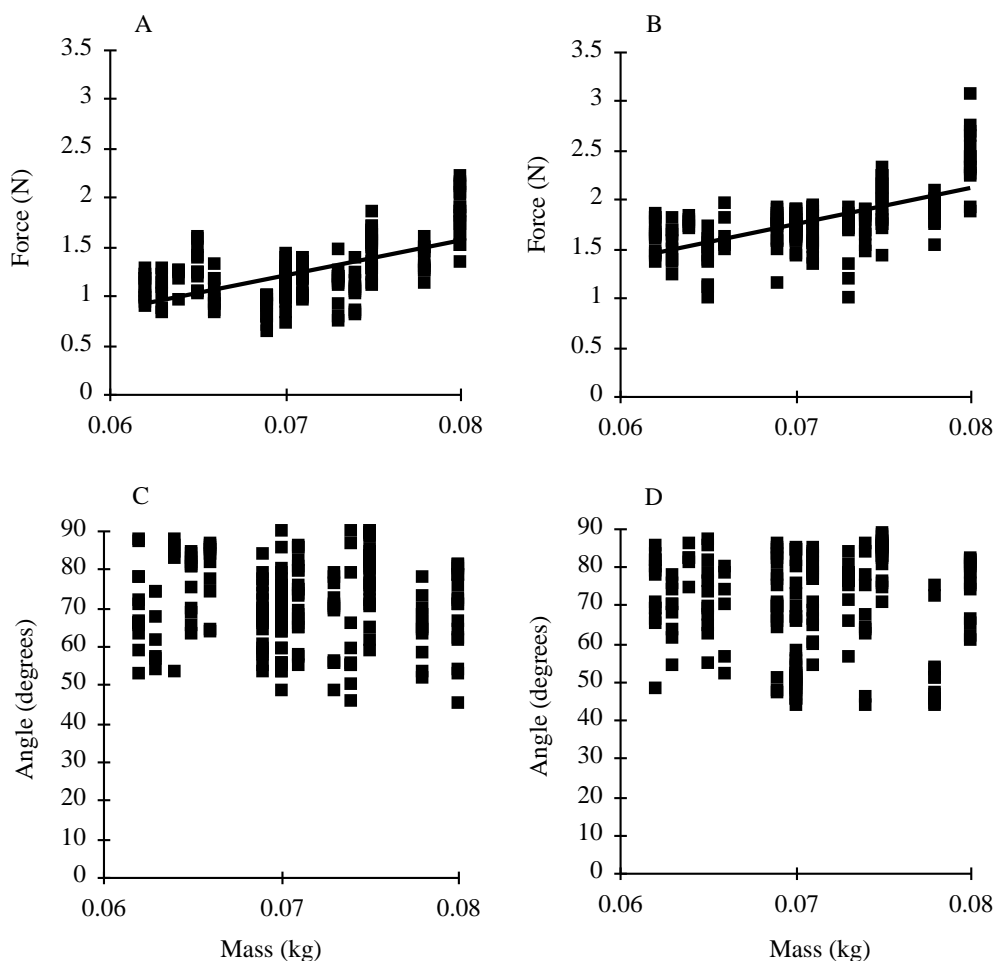


Fig. 4. Plots of reaction force *versus* bird mass during landing (A) and take-off (B), and reaction force angles *versus* bird mass during landing (C) and take-off (D). Details of the regression lines are given in the text.

angle of leaping; with apparatus such as we have described in this paper, it should be possible to determine the extent to which the initial angles during take-off are dependent upon the angle of the resultant leg thrust force. From the results we present here, however, it seems that, when birds are offered a free choice of trajectory and no pressure for a rapid or escape take-off, they may have highly variable angles of force production.

Scaling of forces within and between species

Clark and Alexander (1975) found that during running and jumping in quail the highest resultant force was approximately 3.9 times the bird's weight. Studies of pigeons landing and taking off (Fisher, 1956*a,b*; Heppner and Anderson, 1985) demonstrated similarly large weight-specific forces. Heppner and Anderson (1985) reported that the leap force of a pigeon taking off was 1.3–2.3 times body weight and instantaneous acceleration was 15.63 m s^{-2} . The results presented here for starlings show a mean force of 2.6 times body weight (range 1.4–3.9) and mean acceleration of 25.10 m s^{-2} (range $13.60\text{--}38.41 \text{ m s}^{-2}$). There is a large size difference between starlings (mass approximately 70 g) and pigeons (mass approximately 400 g); our own unpublished data suggest that in 12 g zebra finches acceleration may be even higher. We are

currently investigating the scaling of leap forces in a range of birds.

Repeatability

Whilst the forces generated during landing and take-off depend significantly on mass, the angle of the perch reaction force shows no such relationship. The results of the repeatability analysis demonstrate that the within-individual consistency of the angles is very low; birds are clearly applying forces at different angles to the perch with consecutive landings and take-offs. It may be the case that lack of predictability is an adaptation to predator avoidance. Suppose that the steepness of ascent of a bird was highly dependent upon mass; this would give a good indication of the 'quality' of the bird as a prey item and, hence, might enable predators to choose the most profitable bird to follow on the basis of its take-off trajectory. Presumably it might be better to attempt to escape from a predator by maximising escape velocity rather than by changes in angle, particularly if the nature of the predator (i.e. cursorial rather than volant) was unknown.

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