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Treecreeper climbing; mechanics, energetics, and structural adaptations

R. Åke Norberg

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The mechanics and energetics of tail-supported clinging and climbing by *Certhia familiaris* on vertical trunks were analysed from still photographs and cine films. A complete movement cycle, or stride, consists of the power stroke and a floating phase. One stride analyzed in detail was 66 mm long and took 0.1375 s. The bird moved about half the stride length in the power stroke which took about 0.0625 s. In the beginning of a stride the bird accelerates with 20 m s^{-2} ($\approx 2 g$), and the feet exert a force on the trunk about 3.2 times the bird weight Mg . Its maximum velocity is about 1 m s^{-1} vertically upwards and 0.24 m s^{-1} horizontally towards the trunk. The energy cost of one stride is 0.028 J, and 84% of this is for moving vertically upwards, while the rest goes to moving horizontally (6%), moving the legs (5.6%), and rotating the body and head (4.4%). The metabolic power due to work done in a stride is 0.2 W, which is 0.91 the basal metabolic power *BMP*. During foraging the bird climbs 0.1 m s^{-1} , and has a stride frequency of 1.5 s^{-1} , and a power output for locomotion of 0.043 W, or 0.19 BMP. The strong claw curvature, long hind-claw, and graded length of fore-toes are adaptations to climbing. Factors are considered which affect optimal tail length in tail-supported trunk-climbing birds. *Certhia* has a longer tail in relation to body size than have woodpeckers, a difference related to differences in locomotor habits.

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1. Introduction

Among boreal-forest passerine birds, the Treecreeper *Certhia familiaris* exhibits the most extreme specialization in foraging locomotion mode. Its behavioural and morphological adaptations to trunk-climbing represent a remarkable evolutionary convergence with woodpeckers *Picidae*, whereas its mode of food extraction differs from those of most woodpeckers, in that its bill is not adapted for pecking. The Treecreeper, like woodpeckers, use the tail for support during climbing, a habit associated with structural adaptations different from those involved in trunk-climbing without tail-support, as practised by nuthatches *Sitta spp.*, Darwin's Woodpecker Finch (the Galapagos Tool-using Finch) *Camarhynchus pallidus*, and others.

Structural adaptations for trunk-climbing in birds have been treated by Scharnke (1930), Richardson

(1942), Bock and Miller (1959), Spring (1965), and Rüger (1972). The mechanics of trunk-climbing with tail tail support, and structural adaptations to this climbing mode have been treated by Winkler and Bock (1967), U. M. Norberg (1979), and R. Å. Norberg (1981, 1983). I also compared the energetics of various locomotion modes of forest birds, including vertical trunk-climbing.

Owing to the Treecreeper's habit of climbing upwards while searching for food in trees, and then flying downwards to the next tree, its flight between trees becomes very cheap in energy. Most of the work done against the force of gravity during the ascending climb can be recovered during the descending flights as gravitational potential energy is used for horizontal progression between trees. This enables the bird to use gliding or partially powered flight, which is energetically much cheaper than horizontal, fully-powered, flight (R. Å. Norberg 1981, 1983). With this mode of locomotion in

forest, most work is instead done during the ascending climb in trees. And since a Treecreeper may easily climb vertically upwards several kilometers in the course of a day's foraging, there must have been strong selection for an efficient climbing gait and for structural adaptations to it.

I therefore address some questions relating to the mechanics and energetics of tail-supported climbing, as observed in *Certhia familiaris*: (1) How does the bird move to prevent falling away from the trunk when both feet leave it simultaneously at the end of the power stroke? (2) What are the magnitude and direction of the forces between bird and bark during stationary clinging to vertical as well as sloping trunks, and during acceleration at the start of a hop? (3) What is the energy cost of climbing and how is it divided between various components of movement? (4) What is the efficiency of this climbing gait, i.e. what is the ratio between useful work and total work done in vertical climbing? (5) How do the claws hold their grip to the bark? (6) What factors determine optimal tail length and distance of the bird's centre of mass from tree trunk in tail-supported tree-climbers? (7) How does tail length in Treecreeper compare with those in woodpeckers?

2. Material and methods

The following mechanical and energetic analyses are based on cine films and photographs of *Certhia familiaris* climbing on vertical trunks of spruce *Picea abies* and pine *Pinus sylvestris*. All recorded climbing occurred on the lower parts of old tree trunks, where the bark was rough and with good attachment for the Treecreeper.

I filmed and photographed Treecreepers in the wild near active nests in coniferous forest. Motion films were taken 50 km ENE of Göteborg (Stockåsen) in SW Sweden in June 1974 and still photographs from a blind at a nest 40 km E of Göteborg (Älmås) in June 1975. I used a 16 mm Pathé Reflex cine-camera, run at 80 frames s^{-1} , and equipped with a 135 mm lens, and a 35 mm Leica camera with Telyt-R 1:6.8, 400 mm, a 25 mm extension ring, and 1 ms electronic flash lighting. The use of colour film (Kodachrome) greatly facilitated tracing from the motion films since the brown bird and green background contrasted much better than different shades of grey would have done on a black-and-white film. The still photographs permitted detailed examination of claw attachment to the bark.

One stride, during which the Treecreeper passed a small twig on the trunk, serving as a convenient positional reference, was selected from the motion film for detailed analysis. The film was projected onto horizontal paper by means of a surface-laminated mirror set at 45°, and the Treecreeper was traced on the paper frame by frame. A slight unsharpness of the head identified the first frame at the onset of a hop. At 80 frames s^{-1} the time-resolution of the analysis is 0.0125 s.

The tracings of this particular stride (Fig. 1) was used in all mechanical and energetic analyses. I located the centre of mass of the Treecreeper by eye on the tracings from the film (Figs 3–5). The length scale in the figures was calibrated using length from bill tip to tail tip as measured on a dead Treecreeper (120 mm; Appendix 1). I measured it in a straightened posture, but not maximally stretched, made to resemble the attitude taken near the end of the power stroke, as traced in Fig. 1:5.

I did not catch the particular Treecreeper that I filmed and on which I based the kinematic description. Instead I use masses and measurements from other birds as set out in text and tables. I dissected one Treecreeper and weighed the body, head, and the upper, middle, and lower leg, and the foot separately. Using the percentage weights of the various parts I then estimated the weights of these elements of an average-sized 9.1 g bird for use in calculations (Tab. 1 and Appendix 1). Therefore the mechanical and energetic analyses presented may not be strictly accurate for the particular bird and stride shown in Fig. 1. But I regard the results as representative for *Certhia familiaris* in general.

Equations used appear in the illustrations. Further procedures and methods are explained where used. The S. I. system of units is used throughout, except where otherwise stated. To facilitate evaluation I also express accelerations in terms of g (acceleration due to gravity), forces in terms of weight Mg of the bird, and powers in terms of BMP (bird's basal metabolic power, or rate).

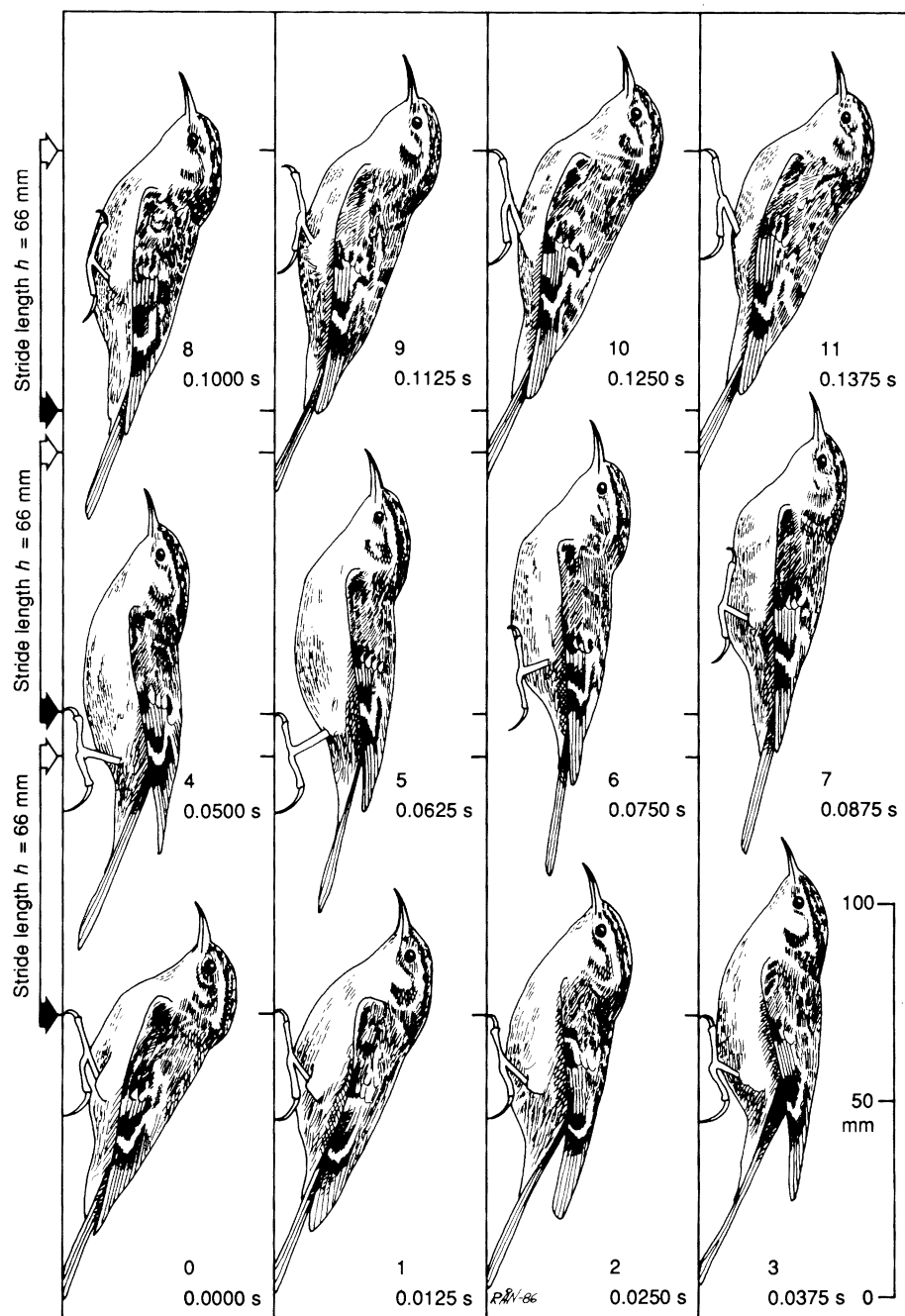
3. Climbing movement pattern, or gait

One complete movement cycle, or stride, is shown in Figs 1 and 2. Stride length is the distance travelled in a complete cycle of leg movements. This one is 66 mm long, takes 0.1375 s, and consists of two distinct phases, the power stroke (or propulsive or effective stroke) and the floating phase (or recovery stroke), each about 0.0625 s in duration.

3.1. Power stroke

The power stroke is the part of the stride during which the Treecreeper moves actively with claws still attached to the bark. At start of the power stroke the Treecreeper moves obliquely upwards and towards the trunk, and after 0.0500 s the center of mass $C.M.$ has reached its closest position to the trunk. The movement towards the trunk is not achieved by the bird simply pivoting about the tail tip, where it contacts the bark, as might be expected. Instead the bird slips closer to the trunk by rotating the body about the hip joint and at the same time possibly pulling the hip slightly towards the trunk by the legs. The distance s moved by the $C.M.$ towards the trunk during the power stroke is estimated to be only about 6 mm, whereas the head (eye) moves 12 mm (Figs 1, 2, 4 and 5). While the $C.M.$ moves distance s to its closest position to the trunk during the first

Fig. 1. A complete movement cycle, or stride, of a Treecreeper climbing upwards on a vertical trunk, drawn from a cine-film taken with 80 frames s^{-1} . The sequence is from left to right, starting from the bottom, and numbers give picture number and time from the start in resting position. Bird shown relative to positions of fore-claws on the trunk before and after the stride (black and white arrows, respectively, in left margin). These reference points on the trunk are on the same vertical level in all four pictures in each row, so the upward progression can be easily discerned. The pictures at bottom left and top right (0 and 11) show the bird at rest, as ascertained by comparison with preceding and subsequent frames.



0.0500 s, the tail tip moves very little upwards along the bark, only about 6 mm, i.e. about equal to s (Figs 1:0–3 and 5).

In the beginning of the power stroke the eye moves along a path inclines about 44° to the horizontal (Fig. 2), whereas the *C.M.*-path is inclined about 60.4° (angle β in Fig. 4; estimated in section 5). The difference stems from the forward rotation of the whole body about the hip joint. The head is stretched forwards during the ac-

celeration phase. As a result, the bill-tip to tail-tip distance increases by 9% in the first 0.0375 s, and by 11% in the first 0.0500 s, after which there is no further elongation of the body (Figs 1, 2 and 4). The orientation of the head with respect to the vertical trunk remains almost constant throughout the stride. Head orientation, measured as angle between trunk and a line through the middle of the eye and the bill tip, increases from 13° in the resting position, just before the stride, to 16° after

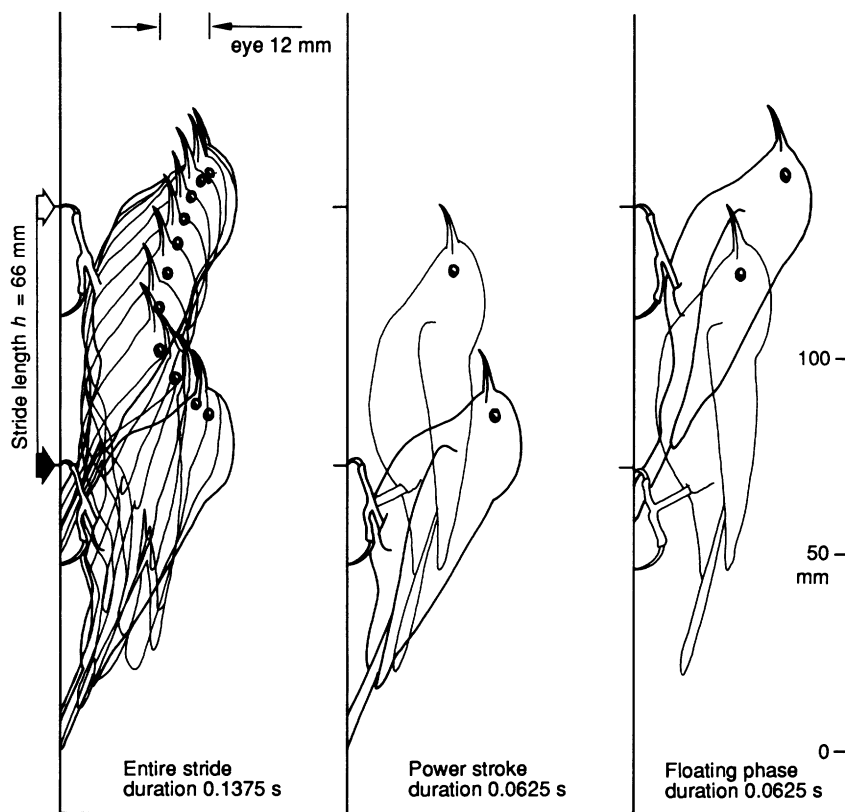


Fig. 2. Superimposed outlines of Treecreeper from Fig. 1 showing bird relative to positions of fore-claws on the trunk before and after the stride (black and white arrows, respectively, in left margin). Left: One complete stride from the 12 tracings, 1/80 s apart, in Fig. 1. Middle: From frame no. 0 in Fig. 1, with bird at rest before stride, and 5, with bird at end of power stroke after 0.0625 s. Right: From frame no 5 in Fig. 1, with bird at end of power stroke after 0.0625 s, and 10 at the end of the floating phase after 0.1250 s.

0.0375 s, reduces to a minimum of 11° in the floating phase (between 0.0750 and 0.0875 s after start), and is back at 13° at the end of the stride after 0.1375 s (Fig. 1).

At rest before the power stroke the body is inclined about 30° to the vertical, measured as angle of contour lines of belly and back, but neglecting head and tail orientations since they change with respect to the body during the stride. In the first 0.0500 s, while the *C.M.* moves to its closest position to the trunk, the body rotates through about 30° , attaining a vertical attitude, parallel with the trunk (Fig. 1:4). Throughout 0.0375 s of the 0.0500 s that this body rotation takes, the tail remains inclined about 25° to the trunk, just as at rest before the stride. This means that the tail becomes angled about 30° ventrally with respect to the body. As a result of this ventral tail flexion, the under tail-coverts become compressed, which is why the tail-base is so thin in side view in Fig. 1:3.

After 0.0375 s the tail is lifted off the bark and flicked back so that it is aligned with the body after 0.0750 s, regaining the orientation relative to the body that it had at rest before the stride. The tail then maintains this orientation throughout the remainder of the stride (Fig. 1). The tarsometatarsus rotates through 95° , from an angle of 20° with the trunk at rest, to 115° at the end of the power stroke after 0.0625 s, and then back again (Figs 1 and 2: middle and right).

Owing to the movements of head and legs relative to the body, the *C.M.* is hard to locate in the tracings of the various stride phases (Figs 1 and 2). Therefore, the distance moved by the *C.M.* during the power stroke and the floating phase cannot be estimated accurately. But the *C.M.* seems to move roughly half the stride length in each phase. This estimate is used in section 5 for calculation of accelerations and velocities.

3.2. Floating phase

The floating phase is the part of the stride during which the feet are off the stem and the bird continues moving upwards, consuming the translational kinetic energy gained during the power stroke, converting it into potential energy. Like the power stroke, the floating phase takes 0.0625 s, from about 0.0625 s to 0.1250 s after start of stride.

Throughout the floating phase the whole body rotates backward, but when the Treecreeper catches hold of the stem with its feet again at the end of the floating phase, there still remains a little backward rotation before the body is back at the 30° angle relative to the trunk, taken at rest before and after the stride. The tail tip contacts the bark slightly before the feet do (after about 0.1125 and 0.1250 s, respectively; Fig. 1). This is at the very end of the floating phase, when the upward movement has essentially ceased. During the floating phase the

legs also swing forwards, legs and feet being tucked up and feet moved very close to the body and about 5 mm off the trunk (Figs 1 and 2). The feet move 66 mm during the floating phase, which of course equals the stride length (by definition).

During the stride the head (eye) moves along a strongly curved path, reflecting the lowering of the head towards the trunk due to the forward pitching of the body about the hip joint. But the breast and belly of the Treecreeper move along a remarkably straight path parallel with the stem (Figs 1 and 2). In the beginning and end of the stride the belly is closest to the trunk, whereas the breast is closest during the floating phase when the body is oriented parallel with the trunk. So even though the *C.M.* moves towards the trunk during the power stroke, the ventral contour-line (of belly and breast) nearest to the trunk always remains 5–6 mm off the bark, throughout the entire stride (Fig. 2, left). This again demonstrates that the Treecreeper *C.M.* moves towards the trunk as a result primarily of a forward pitching rotation of the body about the hip joint (and, possibly, to a small extent also of the bird pulling its hip towards the trunk).

The claws have contacted the bark after 0.1250 s, and by the next frame, at 0.1375 s, the bird has come to rest in a clinging position, the head having moved slightly backwards as compared with the previous frame (Figs. 1:10 and 1:11). Always when the claws are in contact with the bark, at rest before and after a stride, as well as throughout the entire power stroke, the remainder of the foot is well off the trunk, neither toes nor sole of the foot being in contact with the bark. The center of the foot is always 2–4 mm off the bark (Fig. 1).

4. Mechanics of bird at rest, clinging to trunk

The mechanical analyses in Figs 3A and 3B follow Winkler and Bock (1976: Fig. 3), and were adopted also by U. M. Norberg (1979; Fig. 9). Fig. 3C shows forces acting on a bird at rest, clinging to a sloping, overhanging, surface. This situation has also been treated by Winkler and Bock (1976; Figs 2 and 6), but my analysis in Fig. 3C is simpler, since all forces acting on the bird are resolved only into components acting normal to the trunk and parallel with it, just as with the vertical trunk in Figs. 3A and B.

4.1. Vertical trunk

Fig. 3A shows the mechanics of a Treecreeper clinging with tail-support to a vertical trunk. Half the weight Mg is arbitrarily taken to be supported by the feet, the other half by the tail. The actual distribution of weight support between feet and tail in any specific situation varies with the friction between tail and bark. The significant difference between supporting weight with the feet and with the tail is that the tail may take up the load passively if the force is aligned more or less along the tail,

because then it is a compressive load, whereas any weight carried by the feet must be opposed by an equally large, vertical force exerted by the legs, and this consumes metabolic energy. Therefore, for a tail-supported climber at rest, clinging to a trunk, it should be most economical if tail-bark friction were so large that the entire weight could be supported by the tail. But the horizontal force component F_n remains, so the feet must always exert an equal but opposing horizontal force. Tail-bark friction is governed by bark and tail structure and by the force pressing tail and bark together. As shown in Fig. 3A, the force F_n on the claws, normal to the trunk, decreases with increasing length of the base-line l between feet and tail-tip and also decreases with decreasing distance of bird *C.M.* from trunk (Winkler and Bock 1976). But the force F_n on the tail tip, normal to the trunk, equals F_n so its reduction may reduce tail-bark friction, leaving more weight to be supported by the feet (all depending on the coefficient of static friction between tail and bark). This is discussed further in section 8.3. and Fig. 7.

Fig. 3B shows the mechanics of a bird at rest, clinging to a trunk without tail support and with both feet on the same vertical level. Outline of bird is from the end of the power stroke, just before the feet leave the trunk (Fig. 1:5). Since the mechanics is for a bird at rest, it is probably not applicable to the Treecreeper at the end of the power stroke; judging by the backward rotation of the Treecreeper in the subsequent floating phase (Fig. 1:6–1:10), there is no equilibrium of moments at this stage. The bird is also likely to undergo acceleration throughout the entire power stroke. Instead, Fig. 3C is intended as a general illustration of the dramatic increase of force F'_{fn} acting on the fore-claws and hind-claw alike, that results from not using the tail for support (entailing shortened base-line; from l in A to f in B). When other bird species cling to trunks without tail support, they usually place the feet on widely different vertical levels to lengthen the base-line between the two support points and reduce the penalty for not using the tail for support (see equations in Fig. 3 and Winkler and Bock 1976: Fig. 8). The only time when the Treecreeper invariably lifts the tail off the trunk while at rest (and at the same time keeping both feet at the same vertical level) is during defecation, a step of not so little practical importance.

4.2. Sloping trunk and branches

Fig. 3C shows the mechanics of a Treecreeper at rest clinging to a sloping trunk. This is a more general case than A and B. One observation from Fig. 3C is that the force F'_{fn} , normal to the trunk, becomes progressively larger the more the overhanging surface deviates from the vertical, until F'_{fn} supports the entire weight, and the tail none, when the *C.M.* falls on a vertical line through the foot support ($F'_{fr} = Mg$; but $F'_{fn} = Mg = F'_{fr}$ only when $\alpha = 0^\circ$, i.e. for horizontal, overhanging

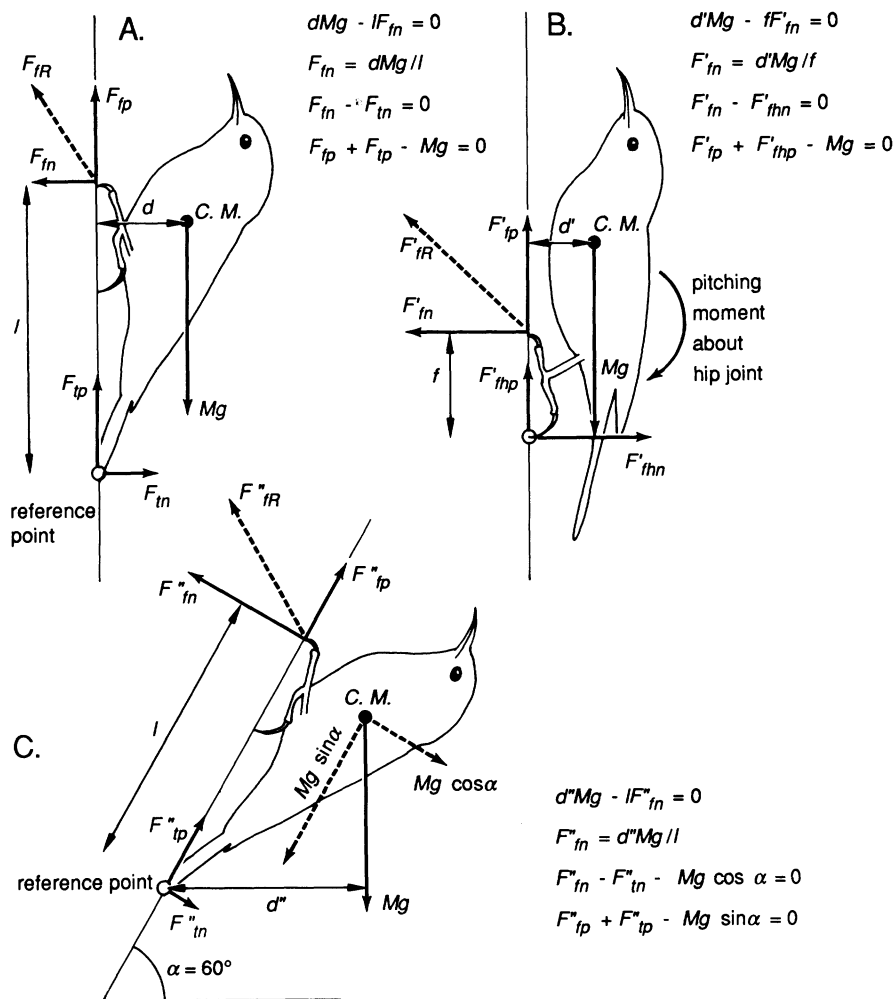


Fig. 3. Free-body diagrams showing all external forces and torques acting on a Tree-creeper at rest, clinging to a vertical trunk with tail support (A; traced from Fig. 1:0), without tail support but on a sloping trunk (C; traced from Fig. 1:0). The analyses of forces follow Winkler and Bock (1976) except that in (C) I have resolved the resultant forces only into components acting normal to and parallel with the trunk, just as with the vertical trunk in (A) and (B). The equations show how the forces normal to the trunk, acting on foot and tail, can be calculated if weight Mg , and lengths l and d (or their equivalents in B and C) are known. They express equilibrium of moments taken about the tail-tip and equilibrium of force components normal to the trunk and parallel with it. The proportion of weight Mg carried by the feet is arbitrarily chosen. It can be estimated only when the coefficient of static friction between tail and bark is known, or else has to be determined experimentally. All forces in Figs. 3, 4, 5, and 7 drawn in correct proportions. The backward pitching moment about the hip joint in Fig. 3B does not apply to the equilibrium situation shown by the forces and equations. It refers instead to the end of the power stroke with the bird moving upwards; when muscles move the legs backwards, there is an unbalanced reaction torque on the body about the hip joints.

surfaces). It can also be noted that for sloping surfaces tail-support is always superior to no tail-support in that it results in smaller forces on the claws, normal to the trunk. As an example, consider Fig. 3C, but without tail support and with the reference point at the hind-claw, as in Fig. 3B. Then the moment arm of force Mg about the hind-claw tip at the trunk would be (slightly) longer than foot span f , and therefore F''_{tn} would even exceed Mg (owing to the torque that must be applied at the feet to keep the *C.M.* off a vertical line through the foot-support). F''_{tn} would be largest for the trunk slope at which the bird *C.M.* lies on the same horizontal line as the hind-claw fulcrum at the trunk.

4.3. Overhanging surfaces – below branches

For clinging to horizontal, overhanging surfaces, tail-support is no longer superior to no tail-support since the feet have to carry the entire weight Mg anyway. And birds like *Parus* tits and *Regulus* usually hang with their *C.M.* on a vertical line through the foot-support when

foraging from the lower side of more or less horizontal branches (to contrast *Certhia* with some species that are ecologically similar to it and that are often members of the same winter foraging guilds as *Certhia*). Their lack of obvious adaptations for tail-supported clinging and climbing is related to their foraging among more or less horizontal branches where tail-support would be of little or no advantage. When they cling without tail-support to sloping, overhanging surfaces they benefit mechanically from allowing their *C.M.* to swing down to a vertical line through the foot-support, because then they need not apply any torque at all to the feet. This hanging behaviour is an alternative strategy to tail-supported clinging and climbing among branches that is used by

Parus tits, *Regulus*, *Sitta*, and others. The mechanics of hanging under branches have been worked out for some *Parus* tits and for *Regulus* by Palmgren (1932) and U. M. Norberg (1979).

5. Mechanics of acceleration phase of power stroke

5.1. Accelerations and velocities

The acceleration phase of the power stroke is interesting because this is when the forces between bird and trunk are largest and when the claws are most prone to loose their hold. I will estimate the magnitude and direction of these forces, and to this end need to know the magnitude of accelerations in different directions.

Accelerations and velocities could be calculated throughout the stride if the precise location of the bird *C.M.* were known for each stage. But the movement of the bird *C.M.* is difficult to trace, in particular because the head and legs move relative to the body so that the *C.M.* of the entire bird moves within the bird itself. And errors in the estimation of *C.M.* positions from frame to frame in Fig. 1 would easily result in large but false fluctuations of the acceleration and velocity estimates. Therefore a different approach is taken. It relies on an averaging process. Based on measurements and estimates of distances moved in Fig. 1 I assume accelerations to be uniform throughout discrete time intervals which are also read off Fig. 1. This may result in a slightly idealized locomotor pattern (more regular than in reality), but the mechanical calculations based on it are probably more accurate than those obtainable with the alternative method, namely a strict frame-by-frame analysis.

The power stroke and the floating phase each take about 0.0625 s. From this observation from the film (Fig. 1) I assume that the bird *C.M.* moves half the stride length, or 33 mm, in each phase. This also seems to fit with what can be judged approximately from Fig. 1. Next I assume that the acceleration vertically upwards a_v is uniform over the 0.0625 s that the power stroke lasts, corresponding to $a_v = 16.9 \text{ m s}^{-2}$, or $1.72 g$ (from $a_v = 2 \cdot \text{distance} \cdot t^{-2}$).

The forward pitching rotation of body and head through 30° , and the concomitant movement of the *C.M.* 6 mm towards the trunk, both take place in the first 0.0500 s, after which both movements cease (Fig. 1). I assume that the angular acceleration of the forward pitching rotation of body and head, and the linear acceleration of the *C.M.* towards the trunk, are both uniform over the first 0.0250 s of the stride, which is half the time taken by each movement. I further assume that during this time the body and head rotate 15° (half the entire rotation) and the *C.M.* moves 3 mm towards the trunk (half the entire distance s moved towards the trunk). This corresponds to an angular acceleration a_r of $48000^\circ \cdot \text{s}^{-2} = 838 \text{ rad s}^{-2}$ [from $a_r = 2 \cdot (\text{angular displacement}) \cdot t^{-2}$], and a linear, horizontal acceleration a_h of 9.6 m s^{-2}

$= 0.98 g$. After this, decelerations of equal magnitudes to the accelerations are assumed to bring the movements to a halt in the following 0.0250 s, during which body and head rotate the remaining 15° and the *C.M.* moves the remaining 3 mm.

From the vertical and horizontal components of acceleration (a_v and a_h), the resultant acceleration a_r is calculated to be $19.4 \text{ m s}^{-2} = 1.98 g$ and has an inclination angle β of 60.4° relative to the horizontal (Fig. 4).

With a vertical acceleration of 16.9 m s^{-2} the velocity of the bird vertically upwards at the end of the power stroke after 0.0625 s is 1.06 m s^{-1} ($a_v \cdot t$). This seems to be a slight overestimation as judged from Fig. 1 and after calculating also the amount of kinetic energy of head and body that is required at the end of the power stroke to lift the whole bird the distance actually moved in the floating phase. This value on vertical acceleration is used only for estimating the forces between bird and trunk during the acceleration phase of the power stroke (section 5.3.). It is not used for calculating energy costs of climbing (section 6.2.).

The maximum speed estimate from Figs 1 and 2 is 0.88 m s^{-1} as measured for the eye between 0.0500 and 0.0625 s after start of stride (eye moved 11 mm in 0.0125 s). The head was not stretched forwards after 0.0500 s so this speed applies to the body also, but not to the legs, so the *C.M.* was travelling slower. If the final velocity is lower than 1.06 m s^{-1} , but the power stroke still lasts 0.0625 s, then acceleration must be higher early in the stride. Therefore this acceleration estimate will lead to a slight underestimation of the vertical force between bird and trunk during acceleration (section 5.3.).

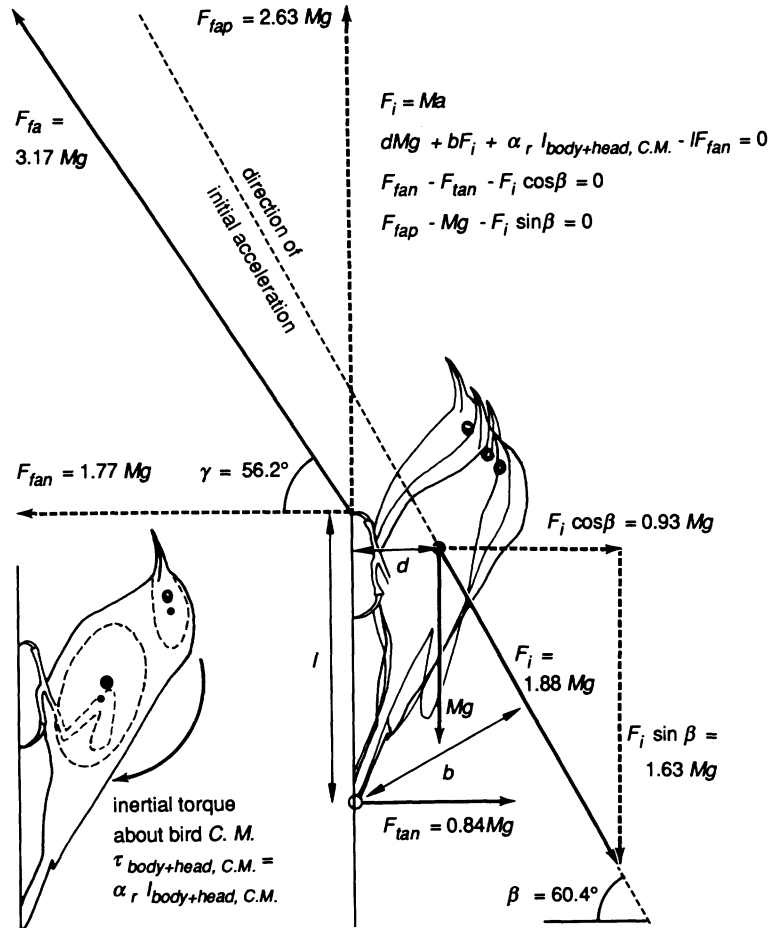
The horizontal acceleration 9.6 m s^{-2} acting during 0.025 s results in a maximum horizontal velocity of 0.24 m s^{-1} towards the trunk.

5.2. Inertial torque of body and head

Except for accelerating its *C.M.* in the beginning of the power stroke, the Treecreeper also pitches its body and head, which necessitates an extra force to be exerted by the feet, over and above that required for bringing about the linear accelerations. I will estimate the size of the imaginary, inertial torque relative to the bird's *C.M.* caused by angular acceleration of body and head.

I treat the bird's body as a homogeneous ellipsoid. Based on measurements of the body of a dead Treecreeper, and restricted by the requirement that the ellipsoid mass must equal that of the bird's body and also assuming bird density is 1000 kg m^{-3} , I set the ellipsoid axes to $2i = 29.5 \text{ mm}$ and $2j = 15.8 \text{ mm}$, corresponding to a mass of 7 g for the bird's body. The moment of inertia $I_{e.CM.}$ of a homogeneous ellipsoid of mass m and diameters $2i$ and $2j$ about its short diameter is $0.2 m (i^2 + j^2)$ (Alexander and Vernon 1975, p. 269). But I need to know the moment of inertia $I_{body.C.M.}$ of the ellipsoid relative to the *C.M.* of the entire bird, which is esti-

Fig. 4. Forces acting on Tree-creeper during the acceleration phase in the first 0.0250 s of the power stroke. Out-lines from Fig. 1:0-1:2. Acceleration is assumed to be uniform and the resultant vector acting on the feet is calculated as shown. The inertial torque, due to forward pitching angular acceleration, is indicated at bottom left. Approximate positions of the C.M. of body ellipsoid and of the head are marked out with small filled circles, and the C.M. of the entire bird with a large filled circle. The inertia force F_i , its two component vectors, the torque bF_i due to linear acceleration, and the inertial torque due to angular acceleration of body and head are all imaginary.



mated to lie 3.7 mm ahead of the ellipsoid C.M. According to the parallel axis theorem, $I_{body, C.M.} = I_{e, C.M.} + k^2 m$, where k is the distance between the axis through the ellipsoid C.M. and, here, a parallel axis through the C.M. of the entire bird. $I_{body, C.M.}$ is thus estimated to $0.49 \cdot 10^{-6} \text{ kg m}^2$.

The head is treated as a point mass ($m = 1.0 \text{ g}$) located 24 mm (r) ahead of the C.M. of the entire bird, so its moment of inertia $I_{head, C.M.}$ relative to the C.M. of the entire bird is estimated to $0.58 \cdot 10^{-6} \text{ kg m}^2$ ($I = mr^2$). The head does not rotate about its own C.M. but maintains the same orientation relative to the trunk throughout the entire stride, so no other moment of inertia of the head need be considered.

The combined inertial torque of body and head relative to the C.M. of the entire bird is given by $\tau_{body+head, C.M.} = \alpha_r I_{body+head, C.M.}$, and is estimated to $0.000897 \text{ kg m}^2 \text{ s}^{-2}$.

5.3. Forces acting on bird during acceleration

The forces acting on the Treecreeper during acceleration in the beginning of the power stroke are estimated as shown in Fig. 4. The analysis is analogous to that in

Fig. 3 but complicated by forces and moments that give the bird linear and angular accelerations.

To be able to equalize moments about the point of tail support in order to estimate the forces acting between fore-claws and trunk, and tail and trunk, I first estimate the imaginary inertial force F_i , acting through the C.M., and set up as a result of acceleration (first equation in Fig. 4). F_i is estimated to 0.167 N ($= 1.88 Mg$) and is directed opposite to the direction of the resultant linear acceleration a_R , which forms angle 60.4° (β) with the horizontal. The backward pitching moment caused by the gravitational force Mg , acting on moment arm d ($= 23 \text{ mm}$) about the point of tail support, and the moment caused by the inertia force F_i (set up as a result of linear acceleration, opposing it) acting on moment arm b ($= 51 \text{ mm}$) about the point of tail support, as well as the combined inertial torque of body and head $\tau_{body+head, C.M.}$ (set up as a result of angular acceleration, opposing it), are all cancelled by the opposing moment caused by force F_{tan} acting on the fore-claws, normal to the trunk, and acting on moment arm l ($= 73 \text{ mm}$) (second equation in Fig. 4). The horizontal force F_{tan} on the fore-claws is thus estimated to 0.157 N ($= 1.77 Mg$).

By equalizing the horizontal forces (third equation in Fig. 4), the horizontal force F_{tan} between tail and trunk is estimated to 0.075 N ($= 0.84 Mg$), which is considerably smaller than the horizontal force F_{fan} ($= 1.77 Mg$) at the feet. This contrasts with a bird at rest, clinging to a trunk, for which these forces are equal (Fig. 3A).

Since the tail-tip drags upwards along the trunk at this stage, it can support no weight. The feet therefore have to carry the gravitational force Mg as well as the vertical component $F_i \sin \beta$ of the inertia force F_i (fourth equation in Fig. 4). The vertical force F_{fap} on the fore-claws is thus estimated to 0.234 N ($= 2.63 Mg$).

From F_{fan} and F_{fap} the resultant force F_{fa} between fore-claws and trunk is estimated to 0.282 N ($= 3.17 Mg$) and its inclination relative to the horizontal to 56.2° (γ).

To illustrate the effect that the inertial torque of body and head (elusive in Fig. 4) has on the analysis, the forces between fore-claws and trunk are estimated again, but with this torque ignored. It gives $F_{fan} = 0.145$ N ($= 1.63 Mg$), which is 0.92 the previous value, $F_{fa} = 0.275$ N ($= 3.09 Mg$), which is 0.98 the previous value, and the same value for F_{fap} .

The resultant force F_{fa} ($= 3.17 Mg$) at the feet during acceleration (Fig. 4) is considerably larger than the maximum value $1.05 Mg$ for a bird at rest, clinging to a vertical trunk and using tail-support, but with the tail supporting no weight (F_{fr} in Fig. 5). The angle between the horizontal and the resultant force at the feet is 56° during acceleration and 73° at rest (Figs 4 and 5). The more vertical the resultant force at the feet can be kept throughout acceleration, the easier it should be for the claws to remain attached to the trunk. A long base-line l between the points of attachment to the bark obviously tends to rotate the resultant force closer to vertical by reducing the force (F_{fan}) at the claws, normal to the trunk (second equation in Fig. 4). So a long tail is advantageous in this respect.

6. Energetics and efficiency of climbing and energy content of food

6.1. Definition of external and internal work and mechanical efficiency of muscular work

In mechanical analyses of animal locomotion a distinction is usually made between external and internal components of mechanical work (or energy) and power. The external mechanical work is the part of the total mechanical work associated with movement of the *C.M.* of the whole body. The internal mechanical work is the part associated with movements of parts of the body relative to the *C.M.* of the whole body. It includes backward and forward translational movements of the legs, rotation of leg segments, and pitching rotation of head and trunk. The internal mechanical work is usually relatively small in terrestrial animal locomotion when speed is low (Clark and Alexander 1975, p. 95, on running quail; Alexander and Vernon 1975, p. 281, on hopping

kangaroos; Fedak et al. 1982 on four birds and three mammals).

To convert mechanical work and power into metabolic equivalents, the former have to be divided by a coefficient η , the mechanical efficiency of muscular work, which is the proportion of the metabolic energy consumed that is converted into mechanical work by the muscles. Muscles that are active, generate force, and consume metabolic energy may operate in any of three modes; (1) they shorten and perform mechanical work (positive work done by the muscles), (2) their length is unchanged as they exert force and stabilize joints (zero work), and (3) they are stretched, forcibly extended, while exerting tension, thus dissipating mechanical energy (negative work done on active muscles).

The mechanical efficiency of muscular work is sometimes remarkably similar for different kinds of muscular activity in different animals. In human locomotion it is about 0.25 for positive work and -1.2 for negative work (Margaria 1968), and for powered flight (positive work) it is 0.23 in *Larus atricilla* (Tucker 1972) and *Corvus ossifragus* (Bernstein et al. 1973). But there may also be large differences between differently sized animals (Heglund et al. 1982, pp. 63–64) and between different working rates (Taylor et al. 1972). I follow Clark and Alexander (1975, p. 110) and Alexander and Vernon (1975, p. 297) and use $\eta_+ = 0.25$ and $\eta_- = -1.2$ here (the metabolic energy cost of 1 J positive mechanical work taken to be 4 J and that of 1 J negative work 0.8 J).

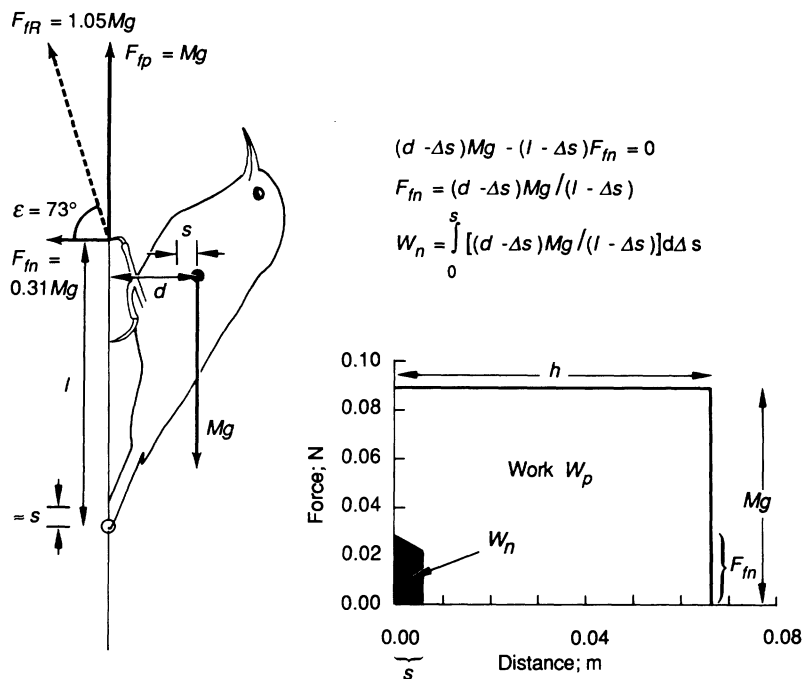
Based on the previous kinematic description I estimate the mechanical energy cost separately for each of the various components of motion in a stride. I also convert the mechanical work into equivalent metabolic energy costs, using the efficiency coefficients for positive and negative muscular work.

6.2. Energy cost of moving upwards and towards the trunk, and back

I estimate the external work separately for movements in two mutually perpendicular directions; for the vertical stride length h , parallel with the trunk, and for the entire horizontal movement s towards the trunk, and then back again. The sum of these work components is identical to what could be calculated by tracking the curved path actually moved. I estimate these components separately, partly because it is simpler, but also because I want to know the energy cost of each movement, since the vertical component represents useful work, while the horizontal one is wasted energy, even though it is mechanically favourable (see section 7).

The mechanical work W_p done parallel with the trunk is simply total weight Mg times vertical distance h moved against the force of gravity, amounting to 0.00589 J and a metabolic energy cost of 0.02357 J for positive muscular work (Fig. 5; force-vs-distance diagram).

Regarding the horizontal component of movement, I



first estimate the work that must be done against the horizontal force between feet and trunk when acceleration is ignored, and then the energy required to accelerate and decelerate the bird horizontally. A bird at rest, clinging to a trunk, exerts a horizontal force by the feet, away from the trunk, equal to F_{fn} (Figs 2 and 5). But F_{fn} decreases when the C.M. moves closer to the trunk and increases when the tail-brace moves upwards while claw attachment remains the same. Now the upward movement of the tail-tip along the trunk in the first 0.0500 s is approximately equal to the maximal distance s moved by the C.M. towards the trunk in the same time, so these two movements are taken to vary in parallel in the first 0.0500 s. The magnitude of F_{fn} as a function of horizontal distance Δs moved from the start, is given by the second equation in Fig. 5, and the mechanical work W_n done normal to the trunk is given by the integral in Fig. 5 and shown shaded in the diagram. The mechanical work done moving the bird C.M. horizontal distance s is 0.000 152 J, corresponding to 0.000 608 J metabolic energy for positive muscular work.

The maximum horizontal velocity of the bird is 0.24 m s⁻¹ (section 5.1.), so the maximum translational kinetic energy in the horizontal direction is 0.000 262 J. This is when the C.M. has moved half the distance s and 0.0250 s has elapsed. From then on it takes 0.000 068 J for the C.M. to move the remaining 0.5 s against the horizontal force F_{fn} (from third equation in Fig. 5). This energy component is supplied by conversion of some of the horizontal kinetic energy of the body, but it has already been included in the estimate of the work done against the horizontal force F_{fn} and so must be ignored

Fig. 5. Calculation of external work associated with horizontal and vertical translational movements of the bird's C.M. in a stride. Drawing on the left shows distance s moved by the C.M. normal to trunk in a stride, and the same approximate distance s moved upward by the tail-tip during the first 0.0375 s of the power stroke with tail braced against the trunk (from Fig. 1:0). The tail drags upwards along the trunk in the beginning of the stride, and so carries no part of the weight, which is instead supported entirely by the feet. The first equation shows equilibrium of moments about the tail-tip, the second shows how the force F_{fn} normal to trunk, acting on the feet, is calculated for various horizontal distances Δs moved by the bird's C.M. from its resting position, and the third shows how the translational work W_n , done normal to trunk during a stride, is estimated. The diagram at bottom right shows work W_n done normal to vertical trunk, and work W_p done parallel with trunk, against the force of gravity, during a stride of length h . Work W_n is over and above W_p , albeit superimposed in the diagram.

here, leaving 0.000 194 J of excess kinetic energy. It is supplied by positive muscular work during acceleration and removed by negative muscular work during deceleration at the metabolic energy costs of 0.000 776 J and 0.000 162 J, respectively, or taken together 0.000 938 J.

In the floating phase the bird C.M. moves backwards with 0.08 m s⁻¹ (unaccelerated, about 5 mm in 0.0625 s; Fig. 1:5–9) corresponding to 0.000 029 J kinetic energy. This must be supplied by positive muscular work at a metabolic cost of 0.000 116 J at the very end of the power stroke. The metabolic cost of the negative muscular work required to halt the backward movement after the feet have attached to the stem after the floating phase is about 0.000 024 J.

Summarizing, the energy cost of the vertical movement has been estimated in terms of gain of potential energy (so the vertical velocity which might be overestimated in section 5.1. was not used), while the cost of the horizontal movements has been estimated as work done against the horizontal resting-force F_{fn} , and also as gain and loss of horizontal translational kinetic energy. The metabolic energy cost for the external work done in a stride is 0.023 568 J for the vertical movement and 0.001

686 J for the horizontal movement ($0.000\ 608 + 0.000\ 776 + 0.000\ 162 + 0.000\ 116 + 0.000\ 024$).

Locomotion on level ground with a standstill between each stride would be extremely uneconomical, because all the horizontal translational kinetic energy would then have to be supplied by positive muscular work and entirely dissipated again (possibly by negative muscular work) in each stride. This mode of progression occurs in, for instance, leaping frogs, even though they may not use muscles to halt their forward motion at touch-down. But in vertical climbing upwards the halt between each stride is no disadvantage since the kinetic energy of the body's vertical translational movement has all been converted into potential energy by the end of the floating phase, i.e. it has all been used for progression upwards along the trunk.

6.3. Energy cost of moving the legs

6.3.1. Movement of legs

The backward and forward movements of the feet and tarsi do not proceed along a circular path relative to the hip joint. In the power stroke the hip instead moves upwards along a rather straight path, parallel with the trunk, while the feet remain attached to the trunk. In the recovery stroke the feet first move away from the trunk and then follow a rather straight path vertically upwards while attaining their maximum speed. I treat the translational movements and the rotational movements separately when calculating the energy cost of moving the lower and middle leg. First I estimate the gain and loss of translational kinetic energy of the feet, and of the lower and middle leg (the upper leg moves with about the same speed as the body so its translational kinetic energy has been included in the work done moving the entire bird upwards). Then I estimate the gain and loss of rotational kinetic energy of the lower and middle leg about their respective *C.M.* and of the upper leg about its proximal end (the feet do not rotate).

6.3.2. Translational kinetic energy of legs

If the maximum upward speed that the legs attain were just enough to lift them the remaining part of the stride, i.e. from the height where they are no longer accelerated (the maximum speed point) to their destination height on the trunk, then their maximum kinetic energy would all be converted into potential energy. The work associated with the vertical translational movement of the legs then would not need to be considered separately, because it has already been included in the work done moving the entire bird the whole stride length against the force of gravity. But during the power stroke the feet do not move at all and the leg segments move less than the body, so during the floating phase they obviously have to move faster than the body to reach the destination height at the same time. Consequently, they are given more kinetic energy than required to lift them to their new position, and this excess will be calculated, since it adds to the energy costs considered so far.

The translational velocity of the feet vertically upwards relative to the trunk is 1.68 m s^{-1} in the time period between 0.0625 and 0.0750 s after start of stride and then declines rapidly (average from 21 mm moved by center of foot in 0.0125 s between Fig. 1:5 and 1:6). The vertical velocity of the Treecreeper *C.M.* is estimated to be 1.06 m s^{-1} after 0.0625 s and so should be 0.94 m s^{-1} after 0.0750 s. Using Fig. 11a: iii, in U. M. Norberg (1979) (showing Treecreeper in floating phase, based on my Fig. 1:7 in this paper, but with approximate positions of leg elements drawn in) I estimate the distance from the hip joint to the centre of mass of the lower leg to 0.7 times the distance from the hip joint to the centre of the foot, and the distance from the hip joint to the centre of mass of the middle leg to 0.25 times the hip-to-foot distance. This applies also when the feet move fastest during the floating phase (my Fig. 1:6). Using this and the respective velocities of bird *C.M.* and feet I estimate the translational velocities of leg elements (Tab. 1).

The combined translational kinetic energy (relative

Tab. 1. Leg elements of *Certhia familiaris*. All data are for the two legs combined. Masses are from own dissection of one bird, lengths from U. M. Norberg (1979, Table 3), translational velocities and heights still to move by the various leg segments when they have reached their maximum translational velocity are from this paper, and angular velocities are from estimates in this paper on times taken for leg movements, combined with information from U. M. Norberg (1979, Fig. 11) on angles swept by the various leg segments. The moment of inertia and kinetic energy of rotation are calculated relative to the proximal end for the upper leg but relative to the mid-point along their respective lengths for the middle and lower legs. Further explanations in the text.

Element	Mass kg	Length m	Transl. veloc. m s^{-1}	Kinetic energy of trans- lation J	Height to move after 0.075 s m	Potential energy to achieve J	Excess kinetic energy J	Moment of inertia <i>I</i> kg m ²	Angular velocity ω rad s ⁻¹	Kinetic energy of rota- tion J
Upper leg	0.000484	0.0108	—	—	—	—	—	$18.8 \cdot 10^{-9}$	14.5	$1.98 \cdot 10^{-6}$
Middle leg	0.000429	0.0190	1.13	0.000274	0.029	0.000122	0.000152	$12.9 \cdot 10^{-9}$	13.4	$1.16 \cdot 10^{-6}$
Lower leg	0.000062	0.0153	1.46	0.000066	0.034	0.000021	0.000045	$1.2 \cdot 10^{-9}$	27.0	$0.44 \cdot 10^{-6}$
Foot	0.000125	—	1.68	0.000176	0.045	0.000055	0.000121	—	0	—
Totals	0.001100	—	—	0.000516	—	0.000198	0.000318	—	—	$3.58 \cdot 10^{-6}$

to the trunk) of the middle and lower leg and the foot of the two legs is 0.000 516 J when 0.0750 s has elapsed (Tab. 1). From then on it takes 0.000 198 J to lift these leg elements the distances remaining to their destination heights at the end of the stride. This energy component is supplied by conversion of some of the kinetic energy of the legs, but it has already been included in the estimate of the work done lifting the entire bird the entire stride length, and so must be ignored here, leaving 0.000 318 J of excess kinetic energy (Tab. 1). This is supplied by positive muscular work during acceleration, and removed by negative work during deceleration for setting down onto the trunk. The associated metabolic energy costs thus are 0.001 272 and 0.000 265 J, together 0.001 537 J.

It is possible that interconversion occurs so that some of this energy is transferred to the body and used for vertical progression, but I treat it as wasted energy here because when the legs decelerate at the end of the floating phase, their angular momentum is likely to be transferred mainly into a backward rotation of the body. These energy components are therefore added to the previous costs.

6.3.3. Rotational kinetic energy of legs

While the legs swing backwards in the power stroke relative to the bird *C.M.* and forwards in the recovery stroke, each segment also performs a rotational movement, except for the feet which do not rotate. The kinetic energy of rotation equals the muscular work done setting up the rotation. Therefore I will estimate the kinetic energy of rotation of the lower and middle leg about their respective centre of mass (their translational kinetic energy was estimated above) and of the upper leg about its proximal end. The moments of inertia I of the lower and middle leg relative to their respective *C.M.* are estimated as for a thin rod with mass m and length l as $ml^2/12$. The moment of inertia of the upper leg about its proximal end is estimated as for a thin rod as $ml^2/3$. In all three cases the *C.M.* is taken to be half-way along the length of the respective segment. The kinetic energy of rotation is $0.5I\omega^2$, where ω is angular velocity.

The various leg segments are taken to have their maximum kinetic energy of rotation at the same time so that no interconversion occurs between segments and so that the energies are additive. The maximum kinetic energy of rotation as summed across the leg segments is $3.58 \cdot 10^{-6}$ J (Tab. 1). For simplicity, this rotational kinetic energy is assumed to be the same in the power stroke and in the recovery stroke. This amount of energy is supplied for angular acceleration by positive muscular work and subsequently removed for angular deceleration by negative muscular work once in the power stroke and once in the floating phase. The mechanical work done thus is 0.000 014 J and the metabolic energy cost 0.000 035 J (Tab. 2). The work done rotating the leg segments (as opposed to giving them

translational motion) is thus totally negligible in calculating the total work done in a stride.

6.4. Energy cost rotating body and head

The bird must use energy rocking itself during the stride. The work required to give body and head their angular velocity equals their kinetic energy of rotation with respect to the *C.M.* of the bird. The angular velocity is higher in the forward rotation in the power stroke than in the subsequent return rotation in the floating phase, so different amounts of work are required for the two rotations.

The body and head are assumed to undergo uniform angular acceleration during the first 0.0250 s, while rotating through 15° , corresponding to an angular acceleration of 838 rad s^{-2} , and a maximal angular velocity of 21 rad s^{-1} after 0.0250 s. The horizontal translational velocity of the *C.M.* and the angular velocity relative to the *C.M.* reach their maximum at the same time, after 0.0250 s, since they are two manifestations of the body rotation about the hip joint. Therefore the kinetic energy of these movements can be added together.

The body and head have the same angular velocity ω , so their combined kinetic energy of rotation is $0.5 (I_{\text{body}} + I_{\text{head}}) \omega^2 = 0.000 236 \text{ J}$ (body approximated by an ellipsoid and head by a point mass 24 mm ahead of bird *C.M.* as explained in section 5.2. and Fig. 4). This kinetic energy is supplied to the body positive muscular work for angular acceleration in the beginning of the power stroke. And it is removed again during angular deceleration later in the power stroke, probably by negative muscular work between 0.0250 and 0.0500 s after start of stride, before the return acceleration occurs. The metabolic energy cost so far is 0.001 141 J.

The return rotation is initiated at the very end of the power stroke while the feet still attach to the trunk. It is caused by a reaction torque on the body set up by muscles swinging the legs backwards, and also by the moment set up about the hind-claws by the inertia force through the bird *C.M.*, due to acceleration. These torques are not balanced by the tail, which is off the trunk at this stage, and obviously not by the feet either (Fig. 3B). The backward rotation then continues throughout the floating phase, is unaffected by external forces, and therefore proceeds with constant angular velocity. (This is for the bird as a whole; acceleration and deceleration of the legs give slight reaction rotations of the body, but the net effect of these successive, opposite reaction rotations should be zero at the end of the floating phase.) Between 0.0625 and 0.1125 s after start of stride, the body thus performs an unaccelerated rotation backwards through 17° , corresponding to an average angular velocity of 340° s^{-1} or 6 rads s^{-1} . The kinetic energy of rotation is 0.000 019 J. It is supplied by positive muscular work at the very end of the power stroke and removed by negative muscular work after the claws have attached to the trunk after the floating phase. The meta-

Tab. 2. Energy costs of various components of movement during the stride shown in Fig. 1. The mechanical work has been converted into metabolic energy costs with the aid of coefficients for mechanical efficiencies of positive and negative muscular work as required and as explained in the text. The numbers of digits given here and in the text are in no way justified by the accuracy with which they were estimated, but are given only to facilitate comparison of the minor energy costs with the important ones.

Movement	Mechanical work done by bird J	Metabolic energy cost J	% of total metabolic energy cost
Translational movement of entire bird vertically upwards entire stride length.....	0.005892	0.023568	84
Translational movement of body and head horizontally.....	0.000608	0.001686	6.0
Translational movement of legs and feet; excess energy.....	0.000318	0.001537	5.5
Rotational movement of legs.....	0.000014	0.000035	0.12
Rotational movement of body and head.....	0.000510	0.001234	4.4
<i>Sum of energy costs of all movements in stride.....</i>	<i>0.007342</i>	<i>0.028060</i>	<i>100</i>

bolic energy cost therefore is 0.000 093 J. The combined metabolic energy cost of the forward and backward body rotations in a stride thus is 0.001 234 J.

6.5. Total energy cost of of climbing in relation to energy content of food

Energy costs for various components of movement during a stride are listed in Tab. 2. The estimates of energy costs of rocking the body and moving it towards the stem, and of moving the legs, are subject to some error due to uncertainties about distances moved and linear and angular accelerations. But the calculations show that these costs are small compared with the work done moving upwards against the force of gravity, which accounts for about 84% of the total metabolic energy cost of the stride examined.

The metabolic energy cost of the 66 mm long stride examined is 0.028 J. A Treecreeper making 66 mm long strides would need 15.2 strides to move 1 m, so its metabolic energy cost for climbing vertically 1 m is 0.43 J (over and above the cost for basal metabolism and for clinging to the trunk between strides). This estimate is not very informative in itself but will be set in perspective by comparison with energy contents of prey.

Among food brought to nestling Treecreepers in southern Finland (Kuitunen and Törmälä 1983), spiders made up 90% by number, the rest being mostly insects. The commonest prey by number were 2–3 mm long, the commonest by weight 5–6 mm, and the average prey size was 3.7 mm. The energy content of one spider of each of these sizes is about 11 J, 100 J, and 33 J (R. Å. Norberg 1978, table 5 on spiders; approximately valid also for insects). If only the metabolic energy cost for climbing is considered (over and above the cost for basal metabolism), and assuming an assimilation efficiency of 75%, one spider of each of these sizes enables the Treecreeper to climb vertically upwards about 19 m, 174 m, and 58 m, respectively.

6.6. Efficiency of climbing

The energy cost of the movement component parallel with the trunk may be regarded as useful energy, because this movement is the objective of the locomotor activity. Climbing is normally used for foraging, and each stride enables the bird to search a previously unexploited area of bark surface for food. A climbing efficiency may therefore be defined as the ratio between useful and total metabolic energy cost of a stride, here amounting to 84% (Tab. 2).

6.7. Climbing power

Power is work done per unit time. I will estimate climbing power as averaged over a single stride and also over a climbing sequence. The power estimates are not very informative in themselves, so I compare them with the Treecreeper's basal metabolic power, *BMP*, estimated with a power function fitted to empirical data for passeriform birds (Calder 1974, p. 93; my Appendix 1). The two climbing powers are over and above *BMP* and expressed in terms of it.

As averaged over an entire stride of 0.1375 s duration the metabolic power becomes 0.204 W, or 0.91 *BMP* (Tab 2 and Appendix 1).

To estimate power production over a sequence of strides and inter-stride pauses, the stride frequency or climbing rate must be known. I recorded climbing rates of Treecreepers foraging in coniferous forest in SW Sweden in October 1972. For each tree that Treecreepers visited, I recorded total climbing height and total time spent there. Average climbing rates were about 0.10 m s⁻¹. This was for undisturbed Treecreepers engaged in normal foraging activities on tree trunks, with pauses to search for and to glean prey off the bark.

With a climbing rate of 0.10 m s⁻¹ and with stride length taken to be 66 mm as for the stride examined here, the stride frequency becomes 1.52 s⁻¹ and the average metabolic power 0.043 W, or 0.19 *BMP*, a very low working rate for locomotion. (The *BMP* and the power for clinging to the trunk between strides are not included.)

7. Function of pitching rotation of body throughout stride

In the power stroke the body pitches forwards about 30° . This rotation is assisted by the tail, acting as a lever against the trunk (Fig. 4). But an additional torque might also be applied by the feet, even though this would be disadvantageous since it requires a much larger horizontal force F_{fn} on the fore-claws. Owing to rotational inertia, the body continues rotating slightly after the tail is lifted off the stem after 0.0375 s (Fig. 1:3-4). From 0.0500 s through 0.1250 s there is a return rotation, back to the inter-stride body orientation.

It might be thought that the body rotates forward during the power stroke in order for the resulting angular momentum to prevent the bird from rotating backwards away from the trunk in the absence of the horizontal force F_{fn} on the feet while they are off the bark in the ensuing floating phase (Figs 1 and 3). But in the floating phase, with tail off the trunk, there is no horizontal force to be opposed, only the vertical gravitational force Mg . Any horizontal movement or rotation of the whole bird in the floating phase must be initiated while the claws still attach to the bark. So it would actually be possible for the Treecreeper to hitch upwards without any pitching body rotation.

Instead I will now examine some real effects of the pitching body rotations, deleterious as well as beneficial. Throughout the power stroke there is a backward pitching torque about the hip joint, acting on the body as a reaction to the muscle torque swinging the legs backwards relative to the body while the feet remain attached to the trunk (Fig. 3B). If the body did not pitch forward at start of the power stroke, but maintained its resting inclination away from the trunk, then this backward torque on the body would have to be constantly balanced by an opposing torque provided by the tail, braced against the trunk, throughout the power stroke.

The forward pitching rotation at the start of the stride thus provides a forward angular momentum, later to be cancelled by the unbalanced backward torque on the body at the end of the power stroke (about the hip joint, from muscles swinging the legs backwards), also starting the return body rotation that continues in the floating phase. Because leg mass is small relative to that of the body, and since the legs move very close to the body, the reaction torques from angular acceleration of the legs are very small and have little effect on body pitching.

The forward body pitching reduces the muscular force that has to be applied to the legs during the power stroke. Because the *C.M.* moves towards the trunk, the resultant force F_{fa} at the feet becomes inclined so that its line of action passes much closer to the hip joint than if there had been no body pitching (Fig. 4). This shortening of the external force lever arm about the hip joint allows a corresponding reduction of the muscular force exerted in the beginning of the power stroke (with the same stride length).

Another favourable consequence of the forward body rotation in the power stroke is that the tail need only drag along the trunk for a very short distance before it can be lifted off the bark (Figs 1 and 5). This should radically reduce tail wear as well as the work the bird has to do against tail-bark frictional drag, because without body pitching the tail would drag along the trunk throughout the entire power stroke.

When the claws contact the bark again after the floating phase, they are likely to push slightly against the bark before attaching to it. But owing to the forward body rotation in the power stroke, the bird *C.M.* is closer to the bark than in the resting posture, even at this late stage. This allows a margin for the body to be pushed away a little from the trunk by the claws before they catch hold of bark irregularities.

A reason why the bird moves its *C.M.* closer to the trunk by rotating the body about the hip joint rather than pivoting the whole body about the tail tip is that the bird could not move closer to the trunk since it must leave space for the feet to move to their new position during the floating phase.

To summarize, body pitching reduces muscle forces and torques, and so facilitates climbing. Tail wear, and work done against tail-bark friction, are radically reduced by body pitching. But body pitching also adds the extra work required to move the *C.M.* towards the trunk against force F_{fn} and to rotate the body and head (Fig. 5 and Tab. 2). It is not possible to assess quantitatively the net result of these diverse effects of body pitching.

8. Structural adaptations to tail-supported climbing

8.1. Claws

When clinging to a trunk, the Treecreeper probably does not grasp the bark with its feet, as the long hind-claw seems to be merely propped against it (Figs 1 and 6). Because of the weak foot, and the toe and claw disposition during clinging, the claws cannot penetrate into the bark. Instead, the fore-claws simply hook on to bark irregularities, as evidenced by still photographs (Fig. 6). Therefore it is essential that the fore-claws be strongly curved (U. M. Norberg 1979, p. 161); claw curvature and orientation need be such that the extreme claw tip forms an angle $\leq 90^\circ$ with the resultant force between claw and bark (Figs 3, 4, 5, and 7).

The Treecreeper also has extremely curved claws, much more so than the non-climbing *Regulus regulus* and three *Parus* species which belong to the same foraging guild as *Certhia* (U. M. Norberg 1979, pp. 139 and 145). The fore-claws are also needle-sharp, facilitating attachment to tiny bark irregularities.

The hind-claw is extremely long in *Certhia* (U. M. Norberg 1979: Tab. 1). An effect of this is to lengthen the span between the support points of the foot, reducing the forces between foot and trunk when the tail is not used for support (Fig. 3B). The long length of the

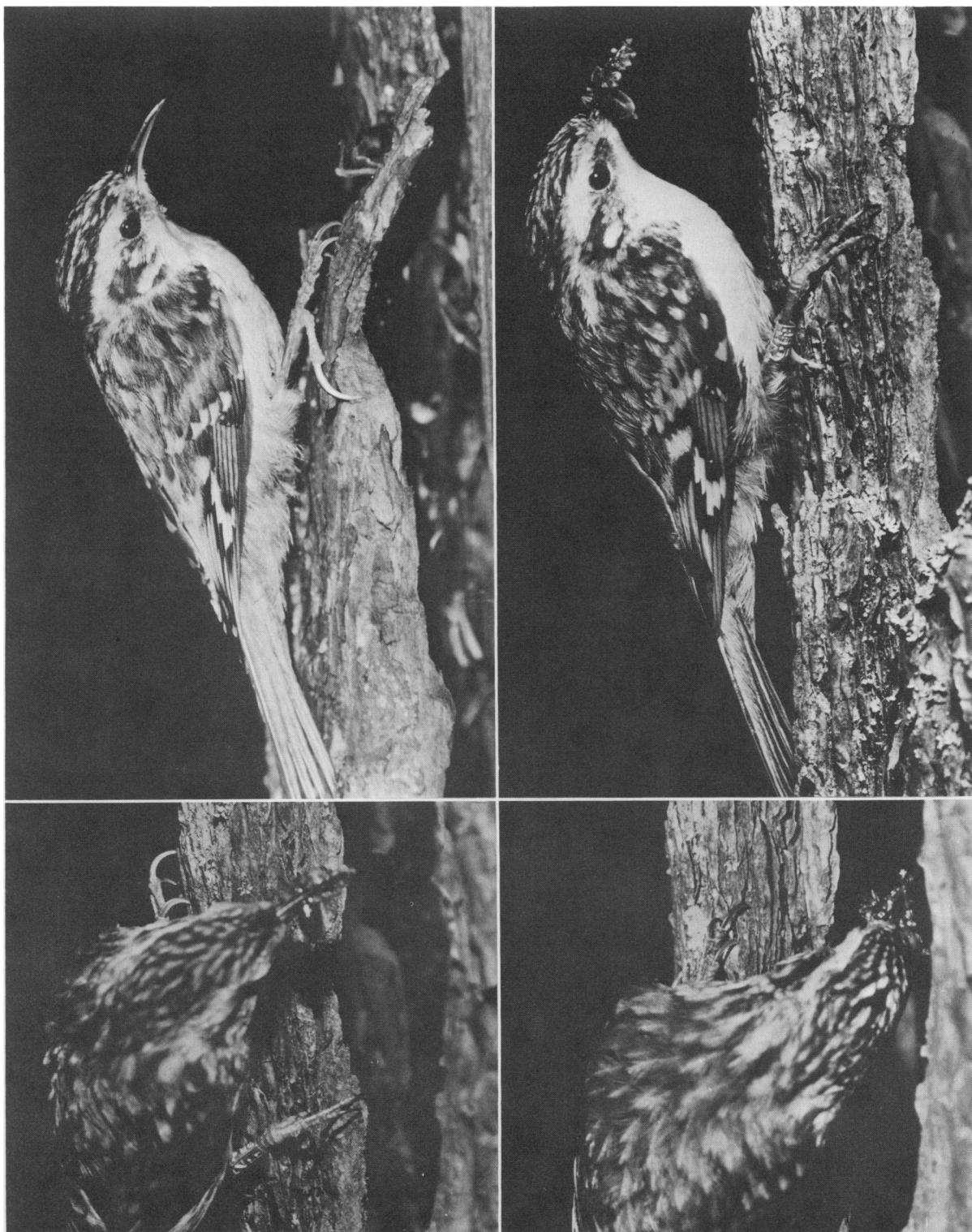


Fig. 6. Treecreeper clinging to old bark of *Pinus sylvestris*. The graded lengths of the front toes and the disposition of the toes and claws are discussed in the text. In the photograph at top left the tip of the hind-claw is not propped against the bark (the medial side only is resting against it), demonstrating that the fore-claws just hook on to bark irregularities, and do not penetrate the bark since the foot does not grasp it. Photo: R. Å. Norberg.

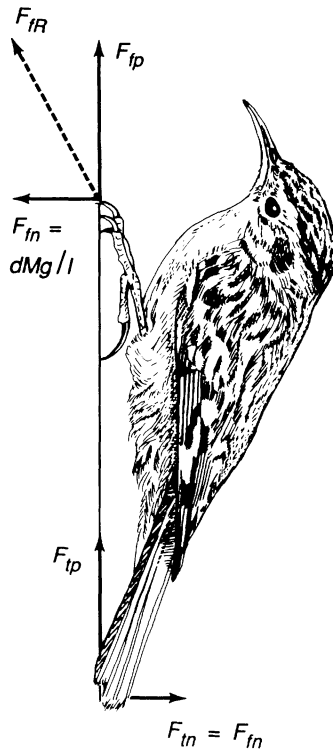


Fig. 7. Summary of selective forces likely to affect tail and leg length and clinging posture of tail-supported, trunk-climbing birds.

hind-claw also makes it more likely for the claw tip to contact irregular bark, where otherwise the toe might form the hind contact, with less vertical support as a result.

8.2. Toes

The three front toes are of unequal length, the middle toe being longest, the lateral next, and the medial one shortest. The gradient is even, the lateral claw attaching to the bark 3 mm, the medial 6 mm, behind the middle claw (Fig. 6). The three front toes are held very closely together. Their graded lengths should reduce distance slipped before at least one claw hooks on to some bark irregularity at the end of a stride.

8.3. Optimal ratio between length from fore-claw to tail-tip and distance of *C.M.* from trunk; comparison with woodpeckers

Fig. 7 summarizes how tail length affects the magnitude and direction of forces between bird and bark and also

LENGTHENING OF BASE-LINE / BETWEEN SUPPORT POINTS OF FEET AND TAIL AND SHORTENING OF DISTANCE *d* OF BODY *C.M.* FROM TRUNK

1. Reduces angle between long body axis and trunk and, hence, distance of head from trunk; reduces acceleration distance of head and, hence, bill impact momentum during pecking.
2. Reduces resultant force F_{fR} at the feet so long as tail-bark friction remains large enough to enable tail still to carry the entire weight Mg (i.e., $F_{fR} = F_{tn}$). But reduction of F_{tn} ($= F_{fn}$) also reduces tail-bark friction, at least on smooth bark, and when the tail can no longer support entire weight Mg , the resultant force F_{fR} eventually increases again with further lengthening of tail (the feet having to support an increasing proportion of Mg). Therefore, F_{fR} will be smallest at an optimal tail length that varies with the coefficient of static friction between tail and bark. While clinging to a trunk the bird expends metabolic energy in maintaining the muscle tension required to oppose force F_{fR} at the feet.
3. Reduces the horizontal force F_{fn} between feet and trunk and hence the muscular work done against it in a stride. In the power stroke the bird must work also against the whole weight Mg regardless of tail length.
4. During acceleration at start of a stride rotates resultant force at feet closer to vertical, facilitating claw attachment to bark while the force reaches its maximum.

the energy costs of climbing. For a bird at rest, clinging to a vertical trunk, there is an important distinction to be made between supporting the weight by the feet and by the tail. Loads supported by the feet, as shown in Figs 3, 5, and 7, require metabolic energy, whereas loads supported by the tail, and aligned more or less along its long axis, do not. Leg loads should therefore be minimized. The optimal tail length according to the criterion in Fig. 7, point 2, can be determined only if coefficients of static friction between tail and bark are known (see section 4.1.). The optimal compromise between the various considerations in Fig. 7 depends on what the birds mostly do.

I will now compare tail lengths in the Treecreeper and woodpeckers. Although it is the ratio d/l that matters functionally (ratio between distance d of body *C.M.* from the trunk and distance l between support points of feet and tail; Figs 3, 4, 5, and 7), only tail lengths are available in the literature. The comparison is therefore restricted to the tail.

Data on tail length vs body mass from Appendix 2 are

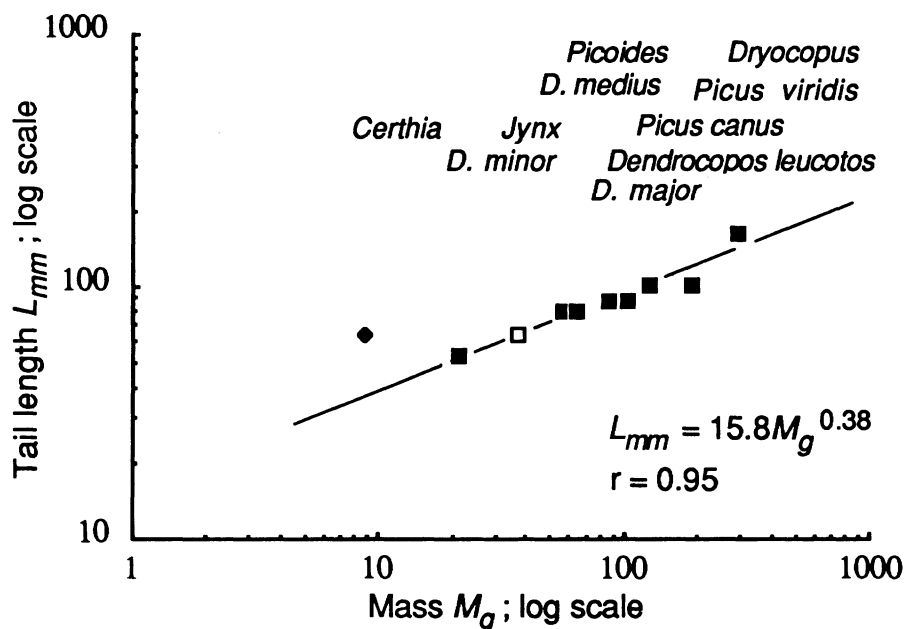


Fig. 8. Tail length (in mm) vs body mass (in g) in woodpeckers (filled squares), the Wryneck (open square), and the Treecreeper (filled diamond). Power function fitted by least squares regression to data for woodpeckers only. Data points for *Jynx torquilla* and *Certhia familiaris* plotted for comparison. The equation for the reduced major axis is $L_{mm} = 15.9 M_g^{0.38}$, which is almost identical with that for the least squares regression line.

plotted in Fig. 8. The regression line is fitted to data on woodpeckers only. When geometric similarity (isometry) applies to birds of different size, tail length increases with mass^{1/3}. Elastic similarity is an alternative scaling principle, based on a constant safety factor of differently sized structures against buckling under their own weight. It dictates the power 1/4 for longitudinal (as opposed to transverse) length vs mass (McMahon and Bonner 1983). The obtained exponent 0.38 (slope in log-log plot in Fig. 8) thus indicates that differently sized woodpecker species are nearly geometrically similar with respect to tail length, but do not fit the elastic similarity model. Tail length of *Jynx torquilla* is as for woodpeckers. But the Treecreeper has much longer relative tail length than woodpeckers. The woodpecker regression model predicts a tail length of 37 mm for *Certhia*, whereas the actual length is 63 mm, 1.7 times longer.

This difference in tail length is probably related to differences in foraging behaviour. In contrast to woodpeckers, *Certhia* mostly gleans prey and very seldom uses pecking, its thin curved beak not being adapted for it. A long tail in *Certhia* therefore is no disadvantage in this respect (Fig. 7, point 1). Even though woodpeckers forage almost exclusively on tree-trunks, like *Certhia*, they do not climb by far as much as *Certhia*, which is almost constantly climbing upwards while foraging. And it is only during climbing that work is done against the forces between feet and trunk. It takes far less metabolic energy simply to maintain the static force required to cling at rest to a trunk (zero work; Fig. 7, point 2) than to move against it (by positive muscular work). The work done normal to the trunk during climbing is inversely related to tail length, so the difference in

climbing activity is probably the main reason for the different tail lengths in woodpeckers and *Certhia* (Figs 3, 5, and 7, point 3). An additional aspect is that in contrast to woodpeckers, *Certhia* has weak feet, and so is more favoured than woodpeckers by a long tail that reduces the forces between feet and trunk (Fig. 7, point 4).

It should also be noted that the distance of the C.M. from the trunk depends largely on the degree to which the legs are flexed, so the *d/l* ratio can be adjusted behaviourally. *Certhia* has shorter legs (both absolute and relative length) than three *Parus* species and *Regulus regulus* in the same foraging guild (U. M. Norberg 1979: Fig. 5 and Tab. 3). It is because the legs are short, but also because of their flexing, that *Certhia* moves about almost sitting on its belly.

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Appendix 1. Symbols, variables, and various morphological, kinematical, and mechanical data for a Treecreeper. Mass, weight, and tail length from living or dead birds (from own dissection and from U. M. Norberg, 1979). Other measurements, postures, and kinematics from cine film as traced in Figs 1 and 2.

<i>M</i>	Total mass	0.0091 kg
<i>Mg</i>	Total weight	0.089 N
	Mass of body	0.0070 kg (77%)
	Mass of head	0.0010 kg (11%)
	Mass of both legs and feet	0.0011 kg (12%)
	Body length, from bill tip to tail tip in a straightened posture like the one near the end of the power stroke, as traced in Fig. 1:4	0.120 m
<i>l</i>	Base-line on bark; distance between anteriormost claw and tail support on bark; Fig. 1:0	0.073 m
<i>f</i>	Span of claw grip; distance between tips of anteriormost and hind-claws on bark; Fig. 1:0–3	0.027 m
<i>d</i>	Lever arm of force of gravity about support point of tail against bark on vertical trunk in Figs 3A, 4, and 5	0.023 m
<i>s</i>	Horizontal distance moved by bird <i>C.M.</i> , normal to trunk, during a stride; Figs 1, 2, 4 and 5	0.006 m
<i>h</i>	Stride length. Distance between attachment of fore-claws to trunk before and after stride	0.066 m
<i>t_i</i>	Duration of stride	0.1375 s
<i>t_p</i>	Duration of power stroke; Fig. 1:0–5	0.0625 s
<i>t_r</i>	Duration of floating phase; Fig. 1:6–10	0.0625 s

<i>a_v</i>	Acceleration (assumed to be uniform) of bird <i>C.M.</i> vertically upwards in power stroke. Accelerates over half the stride length, i.e. over 0.033 m, in 0.0625 s; $a = 2 \cdot \text{distance} \cdot t^{-2}$	16.9 m s ⁻² = 1.72 <i>g</i>
<i>a_h</i>	Acceleration (assumed to be uniform) of bird <i>C.M.</i> horizontally, towards the trunk, in power stroke. Accelerates over half the distance <i>s</i> , i.e. over 0.003 m, in 0.025 s	9.6 m s ⁻² = 0.98 <i>g</i>
<i>a_R</i>	Resultant acceleration	19.4 m s ⁻² = 1.98 <i>g</i>
<i>V_p</i>	Vertical speed of <i>C.M.</i> at end of power stroke; $v = a \cdot t$	1.06 m s ⁻¹
<i>F_{fn}</i>	Force on fore-claws normal to bark during motionless clinging to vertical trunk with tail support; Figs 1:0, 3A, and 7; dMg/l	0.028 N = 0.31 <i>Mg</i>
<i>F_{fR}</i>	Resultant force on fore-claws during motionless clinging to trunk with tail support but with tail supporting no weight; Fig. 5	0.093 N = 1.05 <i>Mg</i>
<i>F_{fnn}</i>	Force on fore-claws normal to bark during uniform acceleration at start of stride on vertical trunk; Fig. 4; $F_{fnn} = (dMg + bF_i)/l$	0.157 N = 1.77 <i>Mg</i>
<i>F_{fnp}</i>	Vertical force on fore-claws parallel to bark during uniform acceleration at start of hop on vertical trunk; Fig. 4; $Mg + F_i \sin \beta$	0.234 N = 2.63 <i>Mg</i>
<i>F_{fn}</i>	Resultant force on fore-claws during uniform acceleration at start of stride on vertical trunk; Fig. 4	0.282 N = 3.17 <i>Mg</i>
β	Direction of initial acceleration of <i>C.M.</i> relative to horizontal; Figs 2 and 4	60.4°

γ	Direction, relative to horizontal, of resultant force F_{res} on fore-claws during acceleration at start of stride; Fig. 4	56.2°	f_s	Average stride frequency; V_c/h = 0.10/0.066	1.52 s ⁻¹
ε	Direction of resultant force on fore-claws during motionless clinging to vertical trunk with tail support, but with tail supporting no weight; Fig. 5	73°		Average metabolic power output during one stride (the one examined here; over and above <i>BMP</i>)	0.204 W = 0.91 <i>BMP</i>
η_+	Mechanical efficiency of positive muscular work	0.25		Average metabolic power output during climbing at 0.10 ms ⁻¹ with 66 mm long strides (over and above <i>BMP</i>)	0.043 W = 0.19 <i>BMP</i>
η_-	Mechanical efficiency of negative muscular work	-1.2	<i>BMP</i>	Basal metabolic power (resting, postabsorptive, and in thermoneutral zone); <i>BMP</i> = 6.605 $M^{0.72}$ (Calder 1974, p. 93)	0.224 W
V_c	Average climbing rate	0.10 m s ⁻¹			

Appendix 2. Mass and tail length of European woodpeckers (data from Central and North Europe from compilation in Cramp 1985) and the Treecreeper (from U. M. Norberg 1979, and pers. comm.). Where only the range of measurements is available, the mid-value is used. A local average is calculated for each sex, then a species average from the two local sex values, and, finally, a species average across the local species-values. Mass in gram and length in millimeter [given in the form of single measurements or \bar{x} (n)].

Jynx t. torquilla. Mass: Netherlands, late April and early May, ♂ 38.8 (6), ♀ 35.9 (1). West Germany, May–June 40.3 (11); during nesting 36.5 (13). \bar{x} = 37.9.
Tail: Migrants, Netherlands and West Germany, late August to early October and mid-April to early May. ♂ 64.6 (37), ♀ 63.8 (20). \bar{x} = 64.2.
Picus c. canus. Mass: West Germany, ♂ 122, ♀ 127, 138. Switzerland, ♂ 137 (18), ♀ 136 (10). Norway, ♂ 125, 131, ♀ 123. \bar{x} = 129.8.
Tail: ♀ 98.9 (16), ♂ 98.6 (8). \bar{x} = 98.8.
Picus v. viridis. Mass: Britain, mainly June–August, ♂ 189 (12), ♀ 198 (6). Netherlands, May–October, ♂ 196 (7), ♀ 186 (4). \bar{x} = 192.3.
Tail: Netherlands, all year. ♂ 98.9 (21), ♀ 100 (19). \bar{x} = 99.5.
Dryocopus m. martius. Mass: Netherlands, ♂ 272, 287, 315 (June), 294 (December), ♀ 255 (April). Norway, autumn, 318 (4). \bar{x} = 295.8.

Tail: Netherlands, France, West Germany, and Switzerland, all year, ♂ 162 (10), ♀ 164 (15). \bar{x} = 163.
Dendrocopos m. major. Mass: Netherlands, during eruptions, September–December, juv., ♂ 89.0 (3), ♀ 87.8 (5). Norway, Utsira, during eruptions, ad. 87.5. Helgoland, during eruptions, ad. 89.4. Norway, ♂ 91, ♀ 80, 84, 93. \bar{x} = 88.4.
Tail: Northern Europe, all year, ♂ 87.7 (17), ♀ 85.7 (9). \bar{x} = 86.7.
Dendrocopos m. medius. Mass: Central Europe, all year, ♂ 59.2 (17), ♀ 58.8 (14). West Germany, ♂ 63 (January), 56, 58 (March), ♀ 57 (April). \bar{x} = 58.5.
Tail: ♂ 79.0 (6), ♀ 78.7 (12). \bar{x} = 78.9.
Dendrodopos l. leucotos. Mass: USSR, ♂ 105–112, ♀ 105, 106. \bar{x} = 107.
Tail: northern Europe, all year, ♂ 88.6 (9), ♀ 86.5 (6). \bar{x} = 87.6.
Dendrocopos minor hortorum. Mass: Central Europe, ♂ 17–25 (11), ♀ 20–25 (10). \bar{x} = 21.8.
Tail: Netherlands, West Germany, and East Germany, all year, ♂ 51.6 (23), ♀ 52.4 (13). \bar{x} = 52.0.
Picoides t. tridactylus. Mass: Norway, ♂ 70.1 (10), ♀ 61.2 (5). \bar{x} = 65.7.
Tail: Northern Europe, all year, ♂ 80.2 (8), ♀ 77.8 (6). \bar{x} = 79.0.
Certhia f. familiaris. Mass: SW Sweden, 9.1 (8).
Tail: SW Sweden, 63 (5).