



SYMPOSIUM

Aerial Righting Reflexes in Flightless Animals

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Synopsis Animals that fall upside down typically engage in an aerial righting response so as to reorient dorsoventrally. This behavior can be preparatory to gliding or other controlled aerial behaviors and is ultimately necessary for a successful landing. Aerial righting reflexes have been described historically in various mammals such as cats, guinea pigs, rabbits, rats, and primates. The mechanisms whereby such righting can be accomplished depend on the size of the animal and on anatomical features associated with motion of the limbs and body. Here we apply a comparative approach to the study of aerial righting to explore the diverse strategies used for reorientation in midair. We discuss data for two species of lizards, the gecko *Hemidactylus platyurus* and the anole *Anolis carolinensis*, as well as for the first instar of the stick insect *Extatosoma tiaratum*, to illustrate size-dependence of this phenomenon and its relevance to subsequent aerial performance in parachuting and gliding animals. Geckos can use rotation of their large tails to reorient their bodies via conservation of angular momentum. Lizards with tails well exceeding snout-vent length, and correspondingly large tail inertia to body inertia ratios, are more effective at creating midair reorientation maneuvers. Moreover, experiments with stick insects, weighing an order of magnitude less than the lizards, suggest that aerodynamic torques acting on the limbs and body may play a dominant role in the righting process for small invertebrates. Both inertial and aerodynamic effects, therefore, can play a role in the control of aerial righting. We propose that aerial righting reflexes are widespread among arboreal vertebrates and arthropods and that they represent an important initial adaptation in the evolution of controlled aerial behavior.

Introduction

Numerous behavioral scenarios can be identified in which animals become dislodged and fall from vegetation or an otherwise elevated substrate. Relevant inter- and conspecific encounters include territoriality and fighting, acquisition of food, and mating (Sinervo and Losos 1991; Schlesinger et al. 1993; Jurmain 1997; Nakai 2003). Injuries such as major limb–bone fractures deriving from accidental falls have been characterized in arboreal mammals (Jurmain 1997; Nakai 2003). Arboreal lizards of the genus *Sceloporus* are also known to either intentionally or inadvertently fall from heights under experimental conditions (Sinervo and Losos 1991) as well as in the field (Schlesinger et al. 1993). To avoid damage to tissues from collision with objects during free-fall, animals must turn themselves

around to a desired gliding or parachuting posture, and ultimately land safely.

The aerial righting reflex has traditionally been seen as recovering from an upside-down to a dorsoventrally upwards posture during a linearly downwards free-fall. However, aerial righting potentially characterizes many more behavioral situations, such as leaping and jumping at variable angles relative to the substrate from which launching occurred. The capacity for recovery from an inverted body orientation while in midair is thought to be well-developed in classical animal gliders (e.g., flying squirrels), although this phenomenon has not been well studied. The onset of gliding from initial postures other than the preferred dorsoventral body orientation may in fact be common in natural habitats. Whether or not an animal is in a preferred posture

at take-off can also determine the outcome of gliding (Young et al. 2002). A first step in traditional gliding as well as in directed aerial descent (*sensu* Yanoviak et al. 2005) must be to reorient in midair. Transitions from a given initial orientation to the desired dorsoventral posture must necessarily precede more sophisticated aerial behaviors, including maneuvers.

How animals achieve a rapid inversion of body orientation from a supine to a prone posture during free-fall has long fascinated humans. High-speed photography was first used at the end of the 19th century to address the controversy of whether falling cats reorient themselves in midair without pushing off the substrate (Marey 1894). It was found that free-falling cats do indeed possess an aerial righting reflex. Aerial righting maneuvers have since been mainly described for various mammalian taxa such as cats, dogs, guinea pigs, rabbits, and primates (e.g. Magnus 1924). Aerial righting behaviors have remained largely unexplored in other non-volant vertebrates, including arboreal reptiles and amphibians. Animals with diverse body morphologies and overall mass may well utilize different mechanisms to achieve aerial righting. The effects of external aerodynamic forces during aerial righting, particularly given the high angular velocities of limbs and body during this behavior, are also under-explored. Here we compare the various forms of self-righting described for diverse animals, illustrate in detail this procedure for two reptilian species and for wingless larvae of stick insects, and discuss new directions for the study of aerial righting.

Aerial righting by way of inertia

Widely known reorientations in midair are the graceful maneuvers of human springboard divers, whereby body segments are moved relative to each other such as to change the instantaneous orientation of the body (Edwards 1986). If no external forces are acting on the system, then angular momentum is conserved. When animals place segments of the body in certain configurations they change shape and the instantaneous moment of inertia (Marsden and Ostrowski 1998).

Torso-induced righting

The first aerial-righting studies on the falling cat noted flexions in the spine (Marey 1894; Magnus 1922). The salient features of this phenomenon were later explained using analytical models in which righting behavior was attributed to bending

and rotation of both anterior and posterior segments of the torso (e.g., Kane and Scher 1969; Edwards 1986; Fernandes et al. 1994; Marsden and Ostrowski 1998). Rodents, in contrast, appear to rely on twisting of the body. Kinematic analysis shows that midair righting is induced by rotations between the head–shoulder and the shoulder–pelvis junctions (Schönfelder 1984; Laouris et al. 1990a). Rotations of the cervical vertebrae underlying the head–shoulder connection were also found to be important in initiating the aerial righting responses of mammals such as rabbits (e.g., Schönfelder 1984). The torso-induced righting has been investigated via systematic mechanical modifications, such as adding mass to the head, thorax, and pelvis (Laouris et al. 1990b). Modulation of aerial righting by visual and vestibular systems has also been explored during free-fall in some mammalian species (e.g. Magnus 1924; Lacour and Xerri 1980; Pellis et al. 1989, 1996).

Leg-induced aerial righting

The extent to which legs contribute to mammalian self-righting in the air is not known (Arabyan and Tsai 1998). Multiple scenarios pertain in which animals could use systematic rotations of the legs to achieve reorientation of the body. For example, cats could theoretically modify the moment of inertia of the anterior segment of the torso by either projecting their forelegs outwards, or by tucking them in. The animal could rotate its shoulders while the rear legs are extended in the posterior segment of the torso. Next, it could extend the forelegs while tucking in the hind legs and reorient the pelvis in conjunction with torsion of the spine. Theoretical considerations from studies of attitude control in human athletes (e.g. Kane and Scher 1970) are also relevant to the means whereby tetrapods may reorient through systematic displacement of appendages. Moreover, astronauts maneuvering in the absence of gravity illustrate the effectiveness of appendicular inertia for reorientation (Passerello and Huston 1971). Motion of appendages has also been noted in several species of reptiles and amphibians exposed to weightlessness on parabolic flights of aircraft (Wassersug et al. 2005), although it is not known whether these animals would employ the same behaviors in free-fall under gravity.

Tail-induced aerial righting

Whereas most mammals rely on bending and twisting between the anterior and posterior regions of

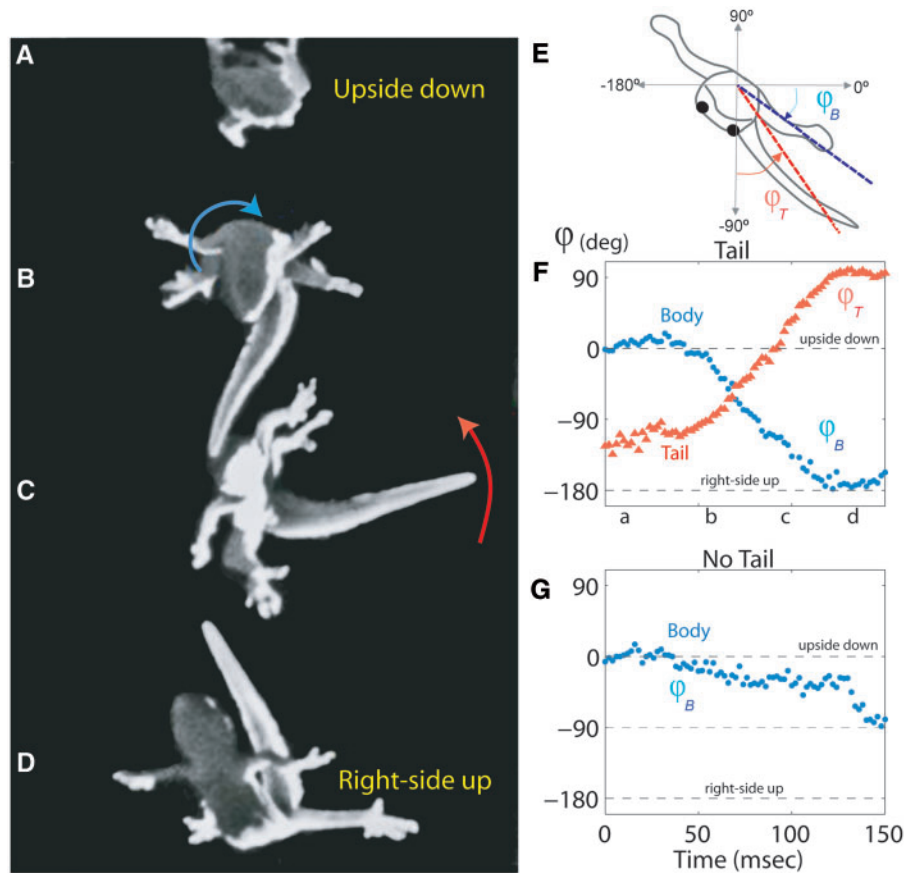


Fig. 1 Aerial righting maneuvers in a gecko with intact tails and post caudal autotomy. Flat-tailed house gecko *H. platyurus* in free-fall. (A) Geckos in supine posture on the underside of a loosely mounted, lightweight platform. (B) Animals free-fall in upside-down posture for ca. $45\text{ ms} \pm 5$. (C) Onset of rotation of the tail and of the body occurs simultaneously. The tail rotates clockwise, and the body rotates anti-clockwise. (D) The tail ceases to rotate when the body reaches near horizontal posture sufficient for landing. (E) Schematic illustrates axes of rotation. (F) Rotation of the body (symbol \bullet and ϕ_B) and of the tail (symbol \blacktriangle and ϕ_T) during aerial righting maneuver as a function of time. (G) Rotation as a function of time in tailless animals during an attempted aerial righting maneuver as a function of time. From Jusufi et al. (2008).

their body to effect aerial righting (Arabyan and Tsai 1998), recent work with lizards (*Hemidactylus platyurus*) has demonstrated that they rotate their large tails and induce body roll to reorient their bodies dorsoventrally (Jusufi et al. 2008). A dorsoventrally upward posture was attained in all drop trials ($n = 16$, see Fig. 1A–D) in which geckos rotated their tails. There was no apparent bending of the back in the majority of trials (Fig. 1E and F). The righting performance of tailless geckos was markedly reduced as none of them was able to attain a 180° rightside-up posture ($n = 19$, Fig. 1G) over the same vertical transit. Experiments with *H. platyurus* also suggested that they rely predominantly on inertia of the tail as the major strategy for righting. There is a tremendous diversity of body morphology evident across lizard taxa, especially when it comes to relative tail length. Given such morphological variation, we investigated how lizards with different body plans might solve the problem of aerial righting.

To investigate mechanical effects, righting experiments were carried out with two lizard species that have approximately the same body size but differ in relative length of the tail. Specifically, the righting performance of the Green Anole, *Anolis carolinensis*, was compared with that of the flat-tailed house gecko, *H. platyurus*, and a three-dimensional computational model was developed to better understand the effects of variation in length and orientation of the tail (Jusufi et al. 2010). Tail length in *H. platyurus* approximately equals the snout-vent length, but geckos in general have relatively shorter tails. In *A. carolinensis* the tail is about twice as long as the torso. Preliminary observations with *A. carolinensis* suggest that they rotate their tails in a direction opposite to the direction of rotation of the body and that they do not exhibit major twisting or flexion of the spine. There were, however, differences in the placement and orientation of the tail relative to the body, when compared to the gecko.

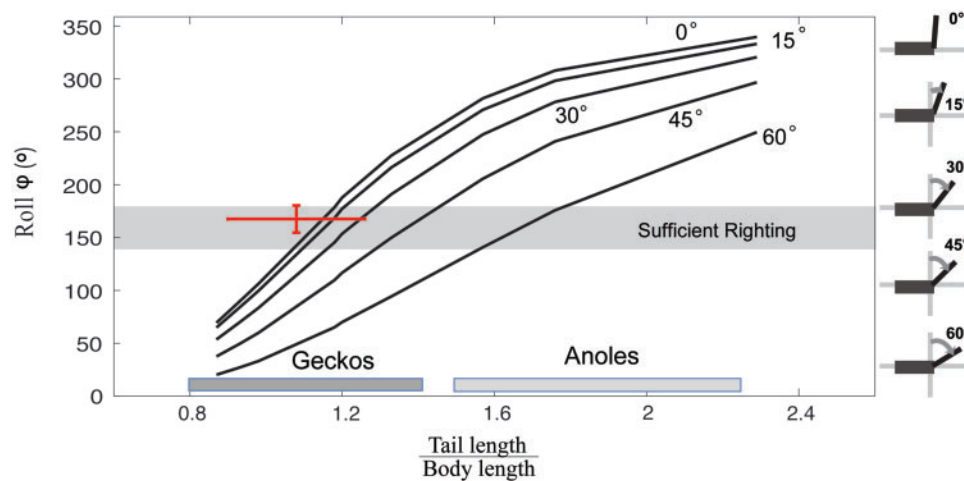


Fig. 2 Aerial righting performance in two lizard species as a function of tail movement. The amount of body roll yielded by one revolution of the tail with respect to the body is illustrated for geckos (*H. platyurus*) and anoles (*A. carolinensis*). The graphs represent the body roll as predicted by a dynamic model for relative tail length (ratio of tail length to body length) and angle of inclination of the tail. The corresponding icons on the right show righting with the tail held at angles of 0°, 15°, 30°, 45°, and 60° from vertical, from top to bottom, respectively. The gray bars show the range of tail length relative to body length for house geckos and green anoles. Tail lengths used for calculation span the range of those measured for house geckos extrapolated to hypothetical tail lengths approaching those in lizards such as anoles. The tail length and the radius of the tail base are scaled isometrically to keep density constant. All other body parameters were held fixed. Sufficient aerial-righting to rightside-up posture falls within the shaded region indicating the performance range for near-prone posture. The cross represents measurements from the experiments on aerial righting by *H. platyurus*. The final position of the body relative to the horizontal during aerial righting (mean \pm 1 SD) is indicated by the vertical line. From Jusufi et al. (2010).

Orientation of the tail relative to the body is of critical importance for lizards such as *H. platyurus*, and can ultimately determine success in righting.

The dynamic model allowed a direct comparison of aerial righting situations in which the tail is held orthogonally to the body (whereby the tip of the tail sweeps out a circle with respect to the tail's base) with other situations in which the tail is held at shallower angles, thereby sweeping out a conical trajectory (Fig. 2). *H. platyurus* could reorient its body dorsoventrally if it rotated its tail (of length 5.4 cm and a tail:body length ratio of 1.18) in a plane perpendicular to the body (see Supplemental Movie S1 for simulation of this motion). However, the model also predicted that the output in body roll would decrease as the tails were held at an incline. Righting performance dropped significantly when geckos' tails were inclined at 45° angles. In this configuration, geckos could only reach 110° of body roll (Fig. 2) per one revolution of the tail with respect to the body, and would land more on their side. At tail angles of 60°, even those geckos with the longest tails could only reorient halfway, to 95° of necessary body roll. These predictions were consistent with direct measurements of the aerial righting response in *H. platyurus*, during which animals held their tails nearly perpendicular to the longitudinal axis of the body (Fig. 2). In so doing, the

lizard distributed mass so as to maximize the moment of inertia of the tail for rotations about the cranial–caudal body axis, thereby making it most effective for generating body roll. At shallow angles of the tail, geckos with relatively short tails (i.e., a tail length to body length ratio of 0.8) can only generate 70° of body roll if the tail makes one revolution with respect to the body (Fig. 2). Conversely, lizards with tails that are double the snout-vent length (8.1 cm is the average value for *A. carolinensis*) can hold the tail at near horizontal angles and still produce a full reorientation of the body to 176° (Supplemental Movie S2), a value consistent with behavioral observations of green anoles. Such tail movements could also be used by the arboreal lizards when traversing foliage and other vegetation.

Flexion and twisting of the torso appear not to be the dominant feature in the air-righting responses of lizards. The neural control required to orchestrate activation of the skeletal musculature of the torso during aerial righting is likely greater than that required for a rotation of the tail. Therefore, one possible explanation is that these lizards refrain from torso-induced reorientation to simplify control (Jusufi et al. 2010). Rotation of the tail has also been observed in free-falling cats, although no difference was found between aerial righting in tailed versus

tailless cats (McDonald 1960). However, some species of mammals with longer tails have been studied as well. For example, many rodent species (e.g. mice) have very long tails that result in a large moment of inertia even if tail mass is modest. Through a series of experiments in which degrees of freedom for rotation along the torso were restrained with cuffs, it was found that albino rats could not execute air-righting responses when only their tail was left free to rotate (Laouris et al. 1990a). In contrast, Kangaroo rats (*Dipodomys merriami* and *D. panamintinus*) have been reported to use their long tails for righting and turning in midair (Bartholomew and Caswell 1951). If they also use body torsion similar to that used by righting rats (Pellis et al. 1989; Laouris et al. 1990a), then this strategy would combine the behaviors observed in mammals and reptiles. Prosimians can use tail rotations to assist maneuvers associated with jumping and leaping (Peters and Preuschoft 1984; Dunbar 1988; Günther et al. 1991; Demes et al. 1996). Animals with tails that are functionally less effective (due to a relatively small moment of inertia) must rely on movement in other parts of the body, such as arm rotations in humans, to a greater degree (Günther et al. 1991).

Although animals can rotate their appendages at high angular velocities during reorientation in midair, calculations of the resulting drag forces, based on wind tunnel measurements, suggest that the aerodynamic effects are small and do not account for the observed changes in body posture in *Tarsuis* (e.g. Peters and Preuschoft 1984). Righting by way of inertial responses can be effective across a range of body sizes, but large regions of this spectrum remain unexplored. The mechanism of righting in midair is also essentially unstudied in arthropods, which comprise the majority of arboreal fauna. Use of inertia of limbs and body in the righting reflex of arboreal invertebrates cannot be excluded, but equally relevant for this much smaller size range is the possibility of external fluid forces and their control in effecting reorientation.

Aerial righting by way of aerodynamic torque

Animals capable of flapping flight exhibit extensive behavioral repertoires for midair reorientation. For example, when released from an inverted upside-down body position pigeons *Columba livia* (Warrick and Dial 1998) could perform self-righting by using asymmetric motion between their left and right wings in excursion and velocity. Moreover,

winged insects, such as fruit flies, can accurately recover their flight direction after perturbation (Ristroph et al. 2010), and orchid bees can increase their moment of inertia in roll by projecting legs outwards to enhance flight stability in turbulent flow (Combes and Dudley 2009). In contrast, aerial locomotion in wingless insects, and of larval instars of winged insects, are underexplored. Recent studies, however, have demonstrated the capacity for controlled aerial behaviors in ant workers and in the ancestrally wingless bristletails (Yanoviak et al. 2005, 2009). Compared to vertebrates, most insects are much smaller (with an average adult body length of 4–5 mm) and are exposed to more viscous aerodynamics. Aerial displacement of falling insects therefore can be strongly influenced by the ambient flow, and aerodynamic interactions may dominate relative to inertial effects. Aerial righting in insects may thus be partially or completely passive, contrasting with the inertial responses discussed previously for vertebrates.

In flying insects generally, a tarsal reflex is triggered by the loss of leg contact with the substrate, eliciting immediate leg retraction and the flight response (Pringle 1940; Dingle 1961; Binns 1977; Cruse 1979). Various environmental stimuli, such as optic flow in the visual environment, instantaneous airspeed, and acceleration, also may be used to assess and complete aerial righting. For a relatively small insect falling upside-down, the generation of bilaterally asymmetric forces off the center of mass may generate torque sufficient to induce rotation of the body. The magnitude of the associated aerodynamic forces will depend on the initial body posture and on the features of leg and body morphology. Active appendicular control also can be used to alter the distribution of aerodynamic forces as well as the distribution of the mass of the whole animal; different behavioral reflexes may be involved in successive stages of righting.

Preliminary experiments on righting in larval stick insects (*E. tiaratum*, mean body length of 1.7 cm) revealed a phasic pattern of leg activities (Fig. 3). Ventral retraction of all legs due to the tarsal reflex was completed 47 ms (\pm 3.5 SE) after the loss of leg contact. Immediately afterwards all legs were dorsally projected simultaneously. From an initially upside-down orientation of the body (i.e., body roll angle $\geq 140^\circ$, see Fig. 3C), righting is completed within 143 ms over a 20 cm loss of elevation ($n=8$). Notably, all legs are maintained relatively still during righting (Fig. 3), suggesting that aerodynamic torque instead of inertial twisting may be responsible for rotation of the body. Recovery of

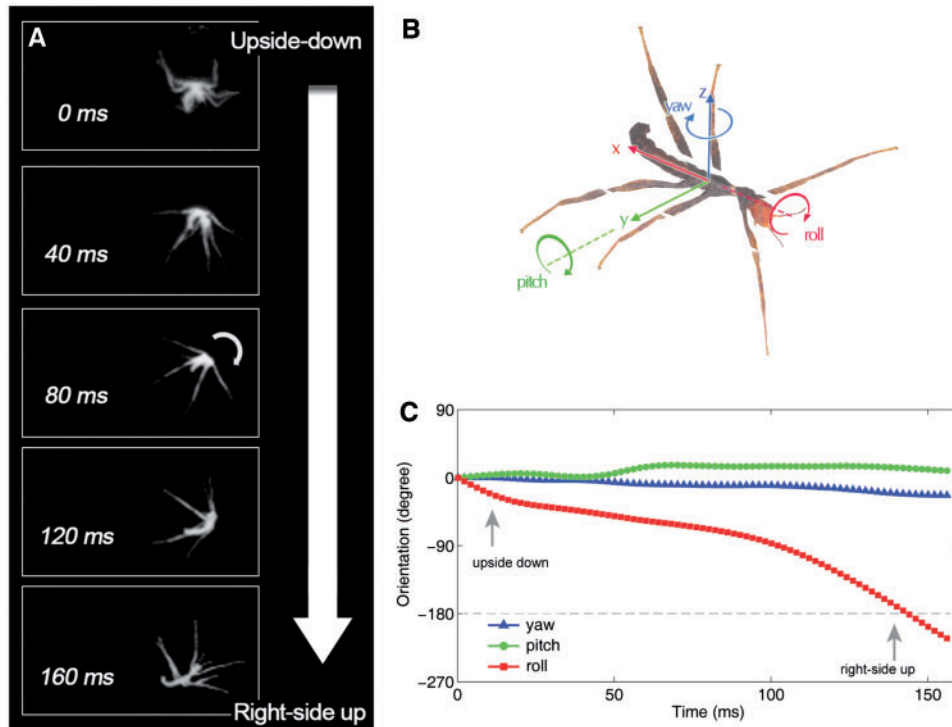


Fig. 3 Aerial-righting sequence for a larval stick insect (*E. tiaratum*, first instar). The insect was dropped freely from a Teflon-coated surface upside-down. **(A)** Consecutive moments of righting. Note that the legs were maintained in a relatively stationary posture during righting. **(B)** Body coordinate system frame used in analysis of the righting behavior. **(C)** Body rotation during righting as a function of time.

leg posture occurs toward the end of the righting behavior. Although the detailed mechanics of this behavior in stick insects await description, aerial righting characterizes all wingless taxa described to date that can carry out directed aerial descent, and represents an essential first step in a sequence of progressively enhanced capacity for flight (Dudley and Yanoviak 2011).

Conclusions and future directions

How animals are able to recover rapidly when falling upside-down is not immediately obvious. The salient features of aerial righting in mammals are bending and twisting of segments that comprise the torso. In contrast, lizards appear to rely more on inertia of their appendages to reorient their bodies. Aerodynamic effects may predominate in smaller animals, as illustrated by our preliminary findings with stick insects. Both inertial and aerodynamic torques may pertain at intermediate body sizes. We propose that aerial righting responses are widespread among arboreal arthropods and vertebrates, and more generally among taxa that may fall, jump, or be chased from elevated substrates. Understanding the mechanisms of this reflex also advances our

understanding of incipient flight behaviors and control of attitude in complex three-dimensional environments. To this end, experimental manipulations to understand the relative roles of inertial and aerodynamic effects (e.g., alteration of distribution of mass or change in surface area of the body) are now required in a broad comparative context.

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Supplementary material

Supplementary data are available at *ICB* online.

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