FIG. 3 Daily mortality rates (predation probability per day) for nests of individuals that overlapped or did not overlap coexisting species based on nest-site characteristics (see Fig. 2). Nest-site characteristics were used to classify identity of the bird species predicted to occupy the nest site based on discriminant function analysis of nest microhabitat characteristics (see Fig. 2). By definition, nests in which the owner bird species was incorrectly classified are nests that overlapped with other species in habitat characteristics. Daily mortality rates were calculated for nest sites that were incorrectly predicted (overlapping sites) and compared to nest sites that were correctly predicted to owner species (non-overlapping sites). Differences in daily mortality rates between overlapping and non-overlapping sites were tested using the program CONTRAST. This program is appropriate for testing homogeneity of maximum-likelihood estimates, such as daily mortality rates, and uses a chi-squared approach that is analogous to ANOVA to control for experimentwise error and adjust for type I errors. Daily mortality rates were greater (P < 0.001 in all cases) for nests that overlapped with other species in nest-site characteristics than for non-overlapping nest sites in all cases except dark-eyed juncos. GTTO, green-tailed towhee; MGWA, MacGillivray's warbler; HETH, hermit thrush; VIWA, Virginia's warbler; DEJU, dark-eyed junco; RFWA, red-faced warbler; OCWA, orange-crowned warbler.

over the evolutionary histories of species. Regardless of the cause of microhabitat differences, overlap of nest sites incurs predation costs that influence the reproductive success of species in differing assemblages and so ultimately influence the patterns of coexistence.

Organisms with a body mass of more than one gram and which live at the air–water interface generally support their weight with their buoyant bodies. The maximum swimming speed these animals can attain is limited by wave-making resistance. For high-speed progression across a body of water, shore birds and basilisk lizards (Basiliscus basiliscus) support their bodies above the water surface by repeatedly striking the surface with their feet. Here we investigate the mechanism of support in moderately sized basilisk lizards (about 90 g) by combining hydrodynamic measurements of a physical model of the lizards' feet with an analysis of video records of foot movements. We find basilisks of intermediate size obtain little support for their body weight by slapping the water surface; most of the support comes from striking the foot downwards while expanding an air cavity underwater. The lizard minimizes downward forces by pulling its foot upward before the cavity collapses.

Basilisk lizards (Basiliscus basiliscus) are well known for their ability to run on water. Yet there is no fundamental mechanistic understanding of how they are able to support their weight by running. We present a hydrodynamic model of weight support which consists of three phases: (1) slap, (2) stroke, and (3) protraction. A step begins as a lizard swings its foot through the air and slaps the water surface (Fig. 1a,d). Next, as the lizard strokes downwards, an air cavity is produced when air rushes in behind the foot (Fig. 1b,c). Finally, at the end of the stroke, the lizard pulls its foot upwards (protraction) within the air cavity and prepares for the next step (Fig. 1c,f).

To determine the hydrodynamic forces produced as the lizard runs across the water surface, we made detailed measurements of the lizards' movements during water-running sequences and conducted hydrodynamic experiments with a physical model of the lizards' feet. The hydrodynamic experiments allowed us to characterize three parameters: (1) $m_{\text{slap}}$, (2) $C_r^*$, and (3) $T_{\text{slap}}$ (refs 7, 11). The virtual mass associated with the foot at the moment of impact ($m_{\text{impact}}$) was measured by dropping the foot model into the water at various impact speeds (Fig. 2a). The water-entry drag coefficient ($C_r^*$) of the foot was calculated by measuring the forces produced as the foot model descends and expands an air cavity underwater (Fig. 2b). Finally, the time between impact and...
FIG. 1 A sample step of an 87.7-g lizard, a. The lizard's foot is parallel to the water surface at the moment of water impact (0 ms). An upward impulse (slap impulse) is produced as the lizard slaps the water surface and suddenly accelerates a volume of water downwards. b. After impact, an air cavity is produced as the lizard strokes downwards and backwards while plantar-flexing its foot (44 ms). Integrated over time, the upward component of the drag force helps to support the lizard's body weight (stroke impulse). c. Finally, the lizard minimizes the downward forces associated with foot protraction by pulling its foot upwards before the cavity collapses (68 ms). Protraction drag is further minimized by the feathering of the lateral toe fringes and the reorientation of the foot such that its long axis is parallel with the direction of movement. d–f Tracings of the lizard's left foot from the images in a–c, respectively. Seven basilisk lizards (Basiliscus basiliscus; 89.3 ± 6.1 g) were captured in Golfito, Costa Rica and brought to Cambridge, MA, USA. In a series of experiments, lizards were placed in a warm enclosure (30–35°C) (10 cm) at one end of a long glass tank (3.66 m long by 0.43 m wide by 0.30 m high). A lizard was stimulated to run across the water surface by opening one side of the enclosure while startling the lizard from the opposite side. By analysing high-speed video recordings of a lizard's movements (Kodak HSIV, 500 fields/s), a plot of foot displacement with respect to time was obtained. Seventh-order polynomial fits of the displacement plots were analysed to determine foot angle (ϕ(t)), mid-foot velocity (υ(t)), and mid-foot depth (h(t)) as a function of time (LabView 2.2, National Instruments).

As the foot strokes downwards, both hydrostatic pressure and the cavity closure (T_wa) was determined over a range of speeds and compared with measurements of the time between the impacts of the lizards' steps (Fig. 2c).

With the hydrodynamic parameters of the foot characterized, the forces a foot produces can be calculated. The force impulse produced when a lizard's foot slaps the water surface (slap impulse) is the product of the virtual mass associated with the foot (m_{virtual}) and the velocity to which the virtual mass is accelerated (υ_{peak}).

\[
\text{Slap impulse} = m_{\text{virtual}} \cdot υ_{\text{peak}}
\]

(1)

As the foot strokes downwards, both hydrostatic pressure and a pressure due to the inertia of water create a drag force (Drag(t)). The component of the drag force in the vertical direction is obtained by multiplying Drag(t) by the cosine of the angle between a normal to the foot and the vertical (ϕ(t)). Finally, the stroke impulse is the integral of the upward drag force over time,

\[
\text{Stroke impulse} = \int \text{Drag}(t) \cdot \cos(ϕ(t)) \, dt
\]

(2)

We assume that as long as a lizard lifts its foot before the air cavity collapses, downward forces produced during foot protraction can

FIG. 2 Measurements obtained from two sets of hydrodynamic experiments with a model foot, a. The first set of experiments measured the slap impulse generated when the model foot strikes a water surface. The impulse increased linearly with rising impact speed. The slope of the line relating slap impulse to impact speed is a measure of the virtual mass (m_{virtual}) associated with the foot impacting the water surface (m_{virtual} = 3.30 g). b. The second set of experiments measured the drag force generated as the foot model expands an air cavity underwater. As has been found for disks, the dimensionless force (C_D*); mean ± s.d.; 39 measurements; overall mean = 0.680 ± 0.0310) that is produced as the model foot strokes downward at nearly constant velocity is invariant over a broad range in dimensionless depth (gh(t)/0.5υ^2); g is gravitational acceleration, h(t) is the depth of the model foot below the water surface, and υ is the velocity of the model foot. c. An additional measurement obtained from the cavity-experiment was the time between impact and cavity seal (T_{seal}). T_{wa} was relatively invariant over a range of speeds (crosses in shaded area). The step period (T_{gap}) that the lizards use is typically shorter than T_{seal}; thereby allowing the lizards to lift their feet before the cavity collapses (circles). The foot model, based on detailed measurements of the foot of a 95-g lizard, was made of aluminum sheet metal (thickness = 0.762 mm). In measuring the lizard's foot, each toe was lightly compressed using finger pressure from above and the lateral toe fringe extended to obtain toe width. Also, the distance from the metacarpo-phalangeal joint (MP) to the tip of the toe and the distance from the heel to the MP was recorded for each toe. Finally, the width of the plantar surface at the level of the MP of the first toe was measured. Hydrodynamic measurements were obtained by attaching the foot model to a falling-missile apparatus which measured the upward water force on the foot while the model travelled directly downwards. The surface of the model foot remained parallel to the undisturbed water surface throughout the period of force measurement. S. The area S of the model foot (0.610 × 10^-3 m^2) was measured by comparing the weight of the model foot with that of a standard of known area.
be neglected. We shall assume a lizard has only one foot in the water at a time, and the time both feet are out of the water is short or non-existent. Thus, the needed upward impulse is simply the product of a lizard’s body weight ($Mg$) and the period between foot slaps ($T_{\text{step}}$).

$$\text{Needed impulse} = MgT_{\text{step}}$$

One way to test the simple hydrodynamic model is to determine whether the sum of the slap and stroke impulses equals the overall needed impulse. We found the sum of the upward impulses, on average, amounts to 102% of the needed impulse (triangle in Fig. 3). Also, we found that basilisks of this size class (~90 g) do not exploit the full range of slap and stroke impulse combinations. Rather, they use a narrow range of slap impulse contributions (12.6–22.6%), which is then supplemented with the stroke impulse (Fig. 3). The narrow range of impulse contributions is reflected in the stereotyped movements of these lizards as they run across the water surface. In contrast, smaller lizards have much more variable limb movements which may reflect a greater ability to adjust the relative contributions of the slap and stroke impulses.

We also calculated the average mechanical power required to run on water (Fig. 3 legend). On average, the required power is approximately 29 W kg$^{-1}$. The power required is available: measurements using whole muscles from hindlimbs ($Dipsosaurus dorsalis$) indicate that lizard muscle can produce as much as 135 W kg$^{-1}$ at 35°C (ref. 8). This suggests that at least 21% of the basilisk’s body mass is involved in powering hindlimb motion.

Would humans be able to run on water? Our calculations indicate it would be impossible excluding artificial aids. An 80-kg subject who runs with a step period ($T_{\text{step}}$) similar to that of sprinters (0.26 s; ref. 9) would need to generate an upward impulse of 204 Ns. To generate the support force, suppose the subject slaps the water surface and then strokes his feet (effective radius, 0.1 m) directly downward to half his leg length (leg length, 1 m). Based on measurements of the drag forces produced by disks$^{11}$, we estimate the water-runner would need to stroke downward through the water at almost 30 m s$^{-1}$, a velocity beyond human ability. Furthermore, to stroke downward at this velocity, he would require an average power output almost 15 times greater than the maximum sustained power output for humans (20 W kg$^{-1}$ for humans running uphill)$^{12}$.

[FIG. 3 Relative contributions of slap and stroke impulses to supporting the body weight on the water surface. To support their body weight, basilisk lizards must generate an upward force impulse that is equal to the product of the body weight and the period between steps (solid line). We found that, on average, the sum of the slap and stroke impulses is 102% of the overall needed impulse (triangle; $\text{slap/needed} = 18.3 \pm 2.72$%; $\text{stroke/needed} = 83.9 \pm 12.8$%; mean $\pm$ s.d.; 32 measurements). However, in a given step the total upward force impulse can either exceed (as high as 131%) or fall short (as low as 71.8%) of the needed impulse (open circles). A force deficit in a given step can be compensated by producing a force surplus in subsequent steps (filled circles; analyses of two steps taken with the same foot during a single sequence). These force impulse fluctuations can have a relatively small effect on the motion of the centre of mass because of the short time intervals ($T_{\text{step}}$) over which the accelerations due to the force surplus (or deficit) act. The clustering of the data points over a small range in slap-impulse contributions suggests that lizards generate their support force in a stereotyped manner. Slap impulse was determined by multiplying the $m_{\text{out}}$ (Fig. 2a) by the $u_{\text{out}}$, typically occurring just after entry into the water, of the lizard’s midfoot (equation (1)). Stroke impulse was calculated by integrating the upward component of $\text{Drag}(t)$ with respect to time (equation (2)). $\text{Drag}(t)$ is the product of force area ($A$) and $C_{\text{f}}(\sqrt{\frac{\rho g t}{\nu}})$; $\rho$ is the mass density of water; $C_{\text{f}}$ is the water entry drag coefficient (Fig. 2b). Step work was calculated by summing the work done on the fluid during both the impact and stroke phases. Average step power was obtained by dividing the step work by $T_{\text{step}}$ ($28.8 \pm 5.60 \text{W kg}^{-1}$; mean $\pm$ s.d.; 32 measurements).]


ACKNOWLEDGEMENTS. We thank W. Meshaka and S. Wright for their advice and assistance. This study was supported by grants from the Office of Naval Research (N00014-87-K-0288) and the Systems Development Foundation (to T.A.M.). Support for the expedition to Costa Rica was provided by Putnam and Tinari grants as well as logistic support from the Organization for Tropical Studies.

A role for stereoscopic depth cues in the rapid visual stabilization of the eyes

C. Busetttini, G. S. Masson F. A. Miles*

Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, Maryland 20892, USA

PRIMATES have visual tracking systems that help stabilize the eyes on the surroundings by responding to retinal image motion at ultra-short latencies$^{12}$. However, as the observer moves through the environment, the image motion on the retina depends on the three-dimensional structure of the scene$^{14}$. We report here that the very earliest of these tracking responses is elicited only by objects moving in the immediate vicinity of the plane of fixation: objects nearer or farther are ignored. This selectivity is achieved by means of a stereoscopic depth mechanism which uses the fact that the two eyes have differing viewpoints, so only objects in the plane of fixation have images that occupy corresponding positions on the two retinas. Such behaviour is readily explained by the known binocular properties of some motion-selective neurons in the visual cortex$^{7}$. Some (stereonanomalous) subjects showed highly specific tracking deficits as though lacking one subtype of these neurons.

When a passenger in a moving vehicle looks out at the passing scene and fixates on the far horizon, distant objects appear

Received 18 October 1995; accepted 17 January 1996.

* To whom correspondence should be addressed.