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'Handedness' in the Pacific tree frog (*Hyla regilla*)

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The jumping directions of 24 individual Pacific tree frogs (*Hyla regilla*), in response to repeated presentations of a model predator, were recorded. The mean jump angle was 70° from the frog's initial bearing regardless of whether the jump was to the left or the right. There was a slight bias within the sample towards left jumps, and most frogs had longer right than left hindlimbs. Some individual frogs jumped preferentially to the left, indicating the existence of 'handedness' in this species.

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Vingt-quatre grenouilles arboricoles *Hyla regilla* ont été soumises à la présence répétée d'un leurre de prédateur; on a noté chaque fois la direction du saut de fuite. L'angle moyen du saut est à 70° de la position initiale, que ce saut soit vers la droite ou vers la gauche. On note une légère tendance à sauter vers la gauche et, chez la plupart des grenouilles de l'échantillon, la patte arrière droite est plus longue que la gauche. Certains individus accusent une préférence à sauter vers la gauche, ce qui signifierait pour cette espèce la possibilité d'être gaucher ou droitier.

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Introduction

A frog's jump is almost certainly an effective means of avoiding predation. It has even been suggested (Alexander 1975) that predation was the major selective pressure behind the evolutionary development of long hind limbs and concomitant leaping ability in frogs and toads. The effectiveness of escape by jumping would be enhanced if the direction of the jump were unpredictable by an approaching predator, i.e., if jumping were protean in character (Humphries and Driver 1970). Such unpredictability could come about in one of two ways: if each individual in a population chose its jump direction randomly on any particular occasion; or if the population consisted of a random mixture of directional 'specialists.' The purpose of the experiments reported here was to determine whether the jumping behaviour of the Pacific tree frog (*Hyla regilla*) is protean in character and, if so, by which of the above mechanisms this is brought about. In the course of the study it was determined that some individuals showed consistent preferences for jumping to the left, providing evidence for the existence of 'handedness' in this species.

Methods

The frogs used in the experiments were captured as tadpoles in the Chilliwack River system on August 12, 1975. After metamorphosis in late August the frogs were kept communally in a large terrarium. Testing was carried out in December, 1975 and January, 1976.

Frogs were presented with a model predator consisting of a 6-cm-diameter rubber ball, painted flat black, and suspended on a piece of nylon monofilament attached 1.95 m directly above the center of a pedestal (Fig. 1). The frog being tested was placed in the center of the pedestal facing forward, i.e., facing 0° on the ruled base. If the animal changed position before the start of the test, the pedestal was slowly rotated on its central pin until the frog once again faced forward. The 'predator' was then released from a position 50 cm in front of the frog, moving down an arc to cross the centre of the pedestal just above its surface. The Plexiglas pedestal base was marked out in divisions of 10° (Fig. 1), and the entire apparatus sat in about 5 cm of water in a large shallow aquarium constructed of white Plexiglas. White partitions on all sides provided a uniform visual environment; light was provided by fluorescent room lights overhead.
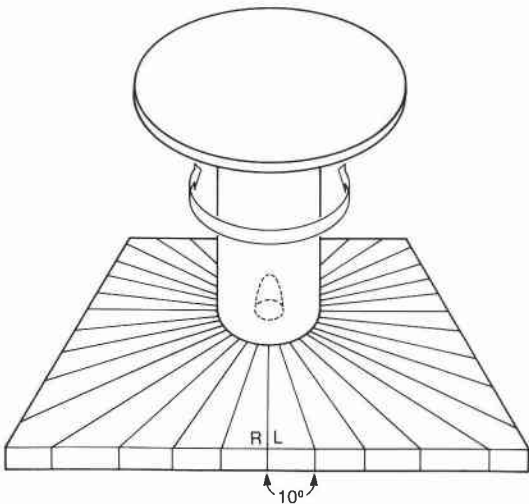
FIG. 1. Pedestal on which the frogs were placed for presentation with a model predator. The platform is 10.2 cm in diameter and stands 21.6 cm above the 50.2-cm-square base, which is marked out into 36 10° sections. All parts constructed of opaque white Plexiglas.

Frogs presented with this model predator either jumped out of its way, dodged to one side (but remained on the pedestal), ducked beneath it, or were hit and knocked off the pedestal into the water. Enough trials were conducted so that 16 distinct jumps (this number decided upon in advance) were recorded for each of 24 frogs. Only one jump per frog per day was allowed, and each frog was given a maximum of two model presentations on any given testing day. Although in theory the testing of a single frog could be completed in 16 days, in practice this required an average of 24 days.

The direction of 384 jumps was thus recorded (24 frogs × 16 jumps), the angles being measured to the nearest 10°. The observed ratios of left and right jumps for each frog were tested against the expected binomial distribution (Sokal and Rohlf 1969). Jump angle data were examined using the methods of Batschelet (1965).

After the completion of the experiments all frogs were killed and preserved in 70% ethanol. They were then cleared and stained using Taylor's (1967) method. The lengths of each frog's left and right tibiofibulae were measured, to determine if there was any skeletal asymmetry basis for the observed preference in jumping direction. Fifteen pairs of femora were also measured; the others were damaged when the left legs were removed before treatment.

Results

Of the 384 jumps recorded, 210 were to the left and 174 to the right. Although a left bias is indicated it is not quite significant ($\chi^2 = 3.375$, $p < 0.10$). When 38 observations from six other frogs which died before completing 16 jumps are included, the figures become 233 left and 189 right ($\chi^2 = 4.588$, $p < 0.05$), supporting the left bias suggestion.

The observed distribution of left:right jump ratios for individual frogs, and the expected binomial distribution for 24 frogs are shown in Fig. 2. The left bias is apparent, and the observed data do not fit the expected binomial distribution ($\chi^2 = 104.360$, $p < 0.005$). On the basis of these data, the observed jump ratios for individual frogs were tested for significant deviation from an expected 8L:8R ratio by comparing them with the one-tailed probabilities of occurrence of ratios at least that extreme. Six frogs show significant directional jumping preferences, jumping preferentially to the left in ratios of 12:4 (three frogs), 13:3 (one), and 14:2 (two). If the more conservative two-tailed test is applied, three frogs still show a significant preference, all preferring to jump left. From this it may be concluded that a proportion of the frogs sampled are 'handed' ('footed,' although awkward, is perhaps a better word); the remainder are ambidextrous.

The mean angle of left jumps was 72° (mean angular deviation 24°), that of right jumps 68° (mean angular deviation 26°). As these means were not significantly different, only the pooled data are presented in Fig. 3. The overall mean was 70° (mean angular deviation 25°). It is of interest to note that on rare occasions frogs could jump as much as 150° from their initial bearing.

In 20 of the 24 frogs, the right tibiofibula was longer than the left one (mean difference 3.6%). Two frogs had a longer left tibiofibula (mean difference 2.8%) and two were perfectly symmetrical. Of the 15 frogs whose femora could be measured, 10 had a longer right femur (mean difference 6.1%), 3 had a longer left femur (mean difference 6.5%), and 2 were perfectly sym-
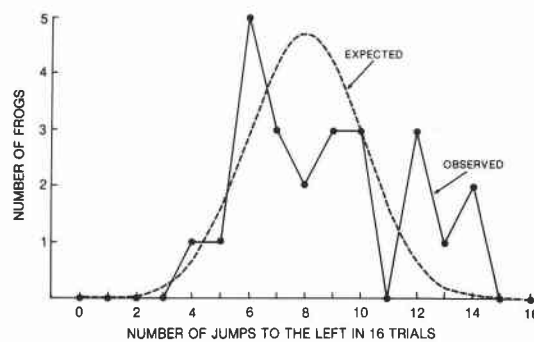

FIG. 2. The observed and expected (binomial distribution) number of frogs making various numbers of jumps to the left in 16 trials.
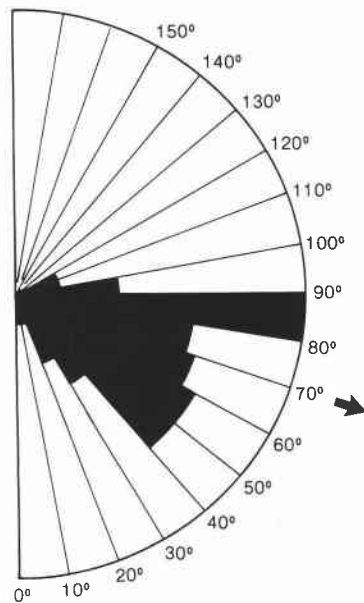
FIG. 3. Distribution of *Hyla regilla* jump angles (left and right jumps combined). The radius of the circle represents 68 jumps; lengths of other sectors proportional to this. The arrow shows the mean angle jumped (70°). The initial bearing of the frog was 0°.

metrical. The proportion of left jumps shown by individual frogs was not significantly correlated with either absolute or proportional differences in the lengths of the femur or the tibiofibula.

Discussion

Although there is a slight left bias in the jumps of the frogs examined, at the population level there is great uncertainty in the prediction of jump direction. From an attacking predator's standpoint the jump of the tree frog is protean (Humphries and Driver 1970), since the frog's position after a jump is essentially unpredictable. The predator therefore cannot aim its strike at the anticipated prey position. Not only is direction unpredictable in a bilateral sense, but there is considerable variation in jump angle as well. The protean effect would also be enhanced by the frogs' tendency, commonly observed in these experiments, to turn 180° immediately after landing, and swim off in a direction opposite to that in which the jump was launched. Several other jump characteristics (height, distance, velocity) might also vary in a protean fashion, but these were not examined in the present experiment.

While the majority of frogs had no significant

bias in jump direction, a proportion of them jumped significantly more often to the left. This may be evidence for 'handedness' at the individual level. Unpredictability is therefore generated in both of the manners noted in the introduction.

Although not previously reported in the Amphibia, handedness (defined as the preferred use of one or the other limb in a task) seems widespread in vertebrates, having been reported in various species of birds (Friedmann and Davis 1938; Allen 1939; Fisher 1957; Vince 1964; Newton 1967; McNeil *et al.* 1971; Baptista 1976) and mammals (Franz 1913; Peterson 1934; Finch 1941; Warren 1953; Cole 1955; Collins 1975).

In some cases the preferred use of a limb has been shown to be correlated with some morphological asymmetry. For example, the brown-throated parakeet (*Aratinga pertinax*) transfers food to its beak with the longer of its hindlimbs (McNeil *et al.* 1971), and in the crossbill (*Loxia curvirostra*) the foot used preferentially to hold a pine cone is on the same side to which the lower mandible is deflected (Tordoff 1954; Newton 1967). The proportion of left jumps shown by individual tree frogs was not correlated with the amount of asymmetry in the hindlimb bones of the individuals, but the left jumping bias in the population may be related to the observed tendency for the right leg to be longer (and presumably more powerful) than the left one. However, the direction of any cause-and-effect relationship is unknown.

Morphological asymmetry underlying handedness in the frog may possibly reside at the neural level as well. In several species of frogs, including one *Hyla* (species unknown), the left habenular nucleus in the diencephalon is larger and more complex than the right one (Frontera 1952; Braitenberg and Kemali 1970; Morgan *et al.* 1973). While no motor function for this structure is implied, other, perhaps more subtle, neural asymmetries may exist in amphibians.

There exists the possibility that some uncontrolled aspect of the experimental situation, such as sound or light directionality, resulted in the observed left jumping bias. One possibility in particular must be noted. The model predator was drawn back and released by a hand reached around the side of the white partition facing the frog. The hand used on various trials was neither

recorded nor randomly chosen, but since both experimenters were right handed it is likely to have usually appeared from the frog's left. However, several points argue against this as a serious source of bias: (a) frogs showed no obvious response to movements of the hand, which appeared 50 cm in front of them; (b) the observed jump angles on the two sides were not different; (c) the behavioural asymmetry was correlated with a skeletal one; and, finally, (d) the frog's observed jumping bias was towards the experimenter's arm, the opposite of what would be expected. While as many variables as possible must be carefully controlled in future experiments of this sort, the present results strongly suggest the existence of 'handedness' in Amphibia, where the phenomenon has not previously been reported.

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