two largest islands, Hawaii and Maui, is scant, and there is as yet no way to assess changes in the avifaunas of these islands caused by prehistoric man, although three species of birds are known to have become extinct prehistorically on each. There is no fossil record from the islands of Lanai, Kahoolawe, or Niihau. No endemic species of land birds were ever recorded from the last two, although the absence of endemic birds cannot be a reflection of natural conditions. It is probable that the historically known avifauna represents only a third, or less, of the total number of endemic species of birds that were present in the Hawaiian Islands when man first arrived there.

These findings have implications for studies of island biogeography. The equilibrium theory of island biogeography (*12*), for example, was applied to the historically known avifauna of the Hawaiian Islands, with the results being congruent with the theory (*13*); the fossil record shows these results to be spurious, however (*1*). The assumption that the historically known biota of a prehistorically inhabited island contains an intact complement of species in a natural state of equilibrium is invalid for the Hawaiian Islands, and is most likely invalid for other islands as well.

Note added in proof: Much more extensive deposits of bird bones have very recently been found in lava tubes on Maui. Two or three species of geese, including flightless forms, are represented, along with other birds.

STORRS L. OLSON
HELEN F. JAMES
National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560

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2. We use the term "fossil" to refer both to fossil and "subfossil" bones, including those from archeological midden sites.
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6. On Molokai and Kauai the major collecting localities are in calcareous dune sand. Those on Oahu are from a raised coral-algal reef replete with sinkholes and caverns containing abundant fossil birds.
7. We exclude taxa that are not endemic at the species level from the calculations; that is, five freshwater birds that are only subspecifically distinct from mainland species, as well as the short-eared owl *Asio flammeus*, which appears to have colonized the archipelago subsequent to the arrival of man (*1*).
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Androgens Alter the Tuning of Electroreceptors

Abstract. *Weakly electric fish possess electroreceptors that are tuned to their individual electric organ discharge frequencies. One genus,* Sternopygus, *displays both ontogenetic and seasonal shifts in these frequencies, possibly because of endocrine influences. Systemic treatment with androgens lowers the discharge frequencies in these animals. Concomitant with these changes in electric organ discharge frequencies are decreases in electroreceptor best frequencies; hence the close match between discharge frequency and receptor tuning is maintained. These findings indicate that the tuning of electroreceptors is dynamic and that it parallels natural shifts in electric organ discharge frequency.*

In communicatory and active sensory systems, motor outputs and sensory inputs are often matched so that sensory receptors are most sensitive to the frequency components that predominate in the output. For example, in different species of weakly electric fish, tuberous electroreceptors, which are modified hair cells, are most sensitive to the peak power of the species-specific electric organ discharge (EOD) used in electrolocation and communication (*1, 2*). Among the "wave" species, so called because their EOD is nearly sinusoidal, each animal discharges within a species-specific frequency band, with each individual typically discharging at its own characteristic frequency within that band. These individual differences in discharge frequency are reflected in individual variations in electroreceptor tuning: the receptors of a given fish are closely tuned to its EOD frequency (*1*).

Despite the high stability of discharge frequencies in these fish (*3*), there may be changes over the lifetime of an individual. In the South American gymnotoid *Sternopygus* there is a sexual dimorphism in discharge frequencies whereby mature males discharge at lower frequencies than mature females (*4*). This difference apparently results from (i) the gradual divergence of male and female discharge frequencies from the intermediate discharge frequencies found in juveniles (*4, 5*) and (ii) a seasonal enhancement of the difference between male and female discharge frequencies (*5*). These shifts in EOD frequency may be under hormonal control, since treatment of fish

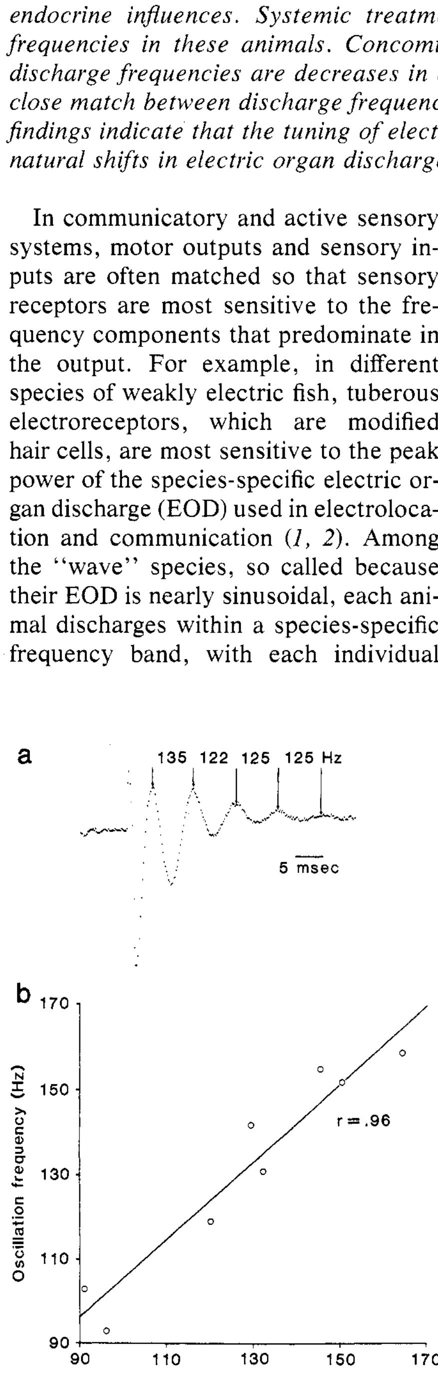


Fig. 1. Receptor oscillation characteristics in *Sternopygus*. (a) Average oscillation from a fish whose EOD frequency was 122 Hz, showing the initial stimulus artifact followed by five peaks. The signal was analog-to-digital converted at a sampling rate of 5 kHz: each point represents a bin width of 200 μsec. We used 512 stimulus presentations in obtaining this response. The number of bins between each peak was used to calculate the period between peaks and then to calculate the frequency of the oscillation. The frequencies, as calculated from the four interpeak periods, are shown above the oscillation. (b) Illustration of the close correspondence between individual EOD frequencies and oscillation frequencies for the eight animals used in the study (day 0).

with gonadal steroids influences their discharge frequencies. In particular, androgens cause long-lasting decreases in EOD frequencies (*5*). In the work reported here we found that, rather than maintaining original frequency sensitivities, electroreceptors alter tuning characteristics to correspond with these hormone-induced changes in discharge frequency.

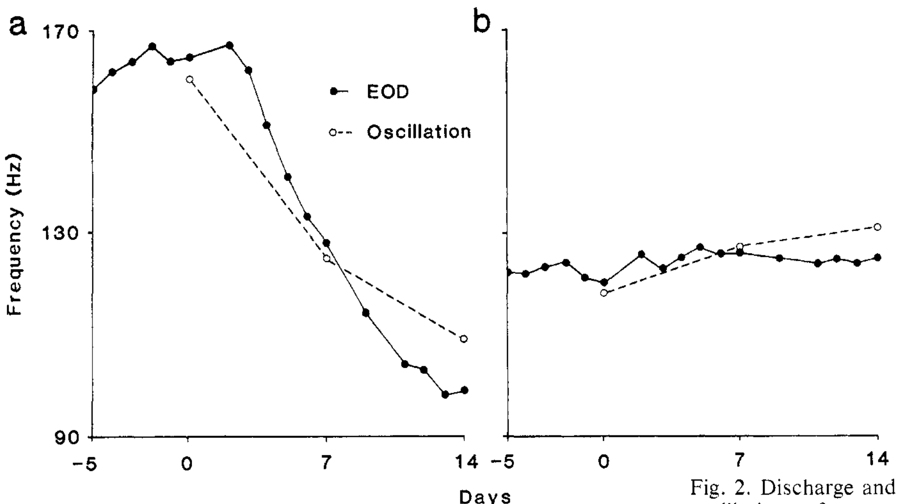
To monitor the tuning characteristics of electroreceptors, we studied their impulse responses by presenting them with brief square-wave electrical pulses, which cause the receptors to "ring" with damped oscillations (*6, 7*). Previous studies indicated that the frequencies of such oscillations, calculated as the mean of the inverse period of the oscillation cycle, agree with the best frequencies of primary afferent electroreceptive fibers (*7*); best frequency is defined as that frequency to which the afferent fiber is most sensitive. Because these oscillations can be recorded from the body surface, this method provides a convenient and noninvasive means for assaying the tuning characteristics of electroreceptors in the same individual over the course of weeks.

Eight adult *Sternopygus* were separated into two groups of four and placed in a divided, temperature-controlled aquarium (*8*). After several days, baseline recordings of EOD and oscillation frequencies were made for each individual. Electric organ discharge frequencies were determined by amplifying each fish's discharge and then passing the amplified signal to a frequency counter. To determine receptor oscillation frequencies, individual fish were removed from the aquarium and placed in a Plexiglas tank. The fish was held in a foam-lined holder and lightly anesthetized by placing in its mouth a glass tube through which ran a weak solution of MS-222. The anesthetic caused the fish to silence its EOD so that throughout the recording session the only stimulus to the receptors was our imposed field. Square-wave pulses from a function generator were presented through two carbon rods placed parallel with the fish on opposite sides of the tank (*9*). The resultant extracellular receptor oscillations were recorded with a fire-polished micropipette (tip diameter, 200 μm) filled with aquarium water and placed on the skin near the head, where the highest concentrations of electroreceptors are found (*10*). The signal was amplified by a high-impedance preamplifier and passed to a digital signal averager. Multiple stimulus presentations, typically from 256 to 1024, were used in obtaining an averaged response.

After the baseline determinations of EOD frequency and receptor oscillation frequency were completed, each fish was given ten injections of saline or 5α-dihydrotestosterone (DHT) over a 2-week period (*11*). During this time, EOD frequencies of each individual were monitored at intervals of 1 to 2 days while oscillation frequencies were determined at 1-week intervals.

A typical oscillation recording from *Sternopygus* is illustrated in Fig. 1a. The periods between adjacent peaks in the oscillations were all similar, with the occasional exception of the period between the first and second peaks. This was due to the interaction of the first peak with the stimulus artifact, and it resulted in artifactually decreased interpeak intervals. Because of the occasional slight dissimilarity between the first period and the other periods, and the fact that fourth and fifth peaks were not always obtained, whenever possible the frequency of the oscillation was calculated on the basis of the inverse period between the second and third peaks. In agreement with previous findings, stimulus duration and polarity influenced the latencies of the peaks with respect to stimulus onset, but had no effect on the period between peaks. Stimulus amplitude also had no effect on the period, but did influence the number of cycles in an oscillation: large stimulus amplitudes caused an increased number of cycles (*6*).

The relation between baseline oscillation frequencies and baseline discharge frequencies of the eight animals was linear, with the oscillation frequency being slightly greater than the EOD frequency (Fig. 1b). The close correspondence between oscillation frequency and EOD



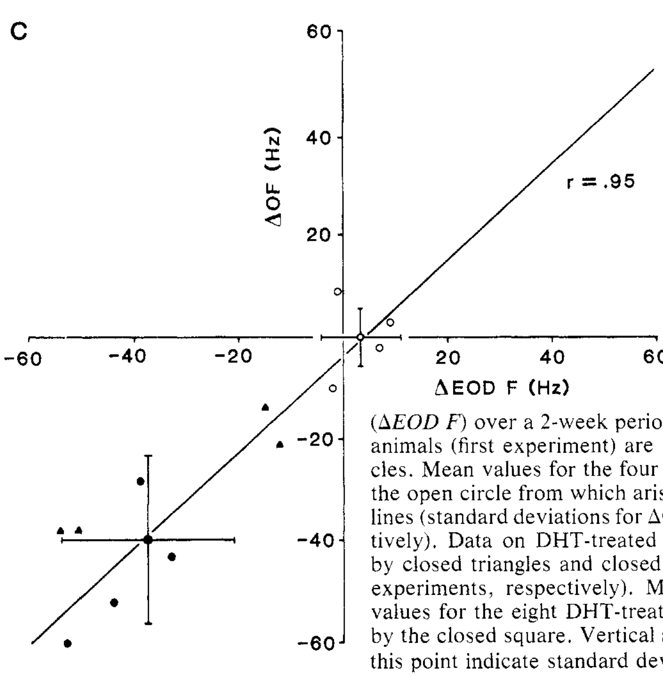


Fig. 2. Discharge and oscillation frequencies over the duration of the 2-week experimental period for a DHT-treated animal (a) and a saline-treated animal (b). EOD recordings were initiated several days before baseline recordings of EOD and oscillation frequencies (day 0). Injections began on day 2. (c) Change in oscillation frequency (ΔOF) as a function of change in discharge frequency ($\Delta EOD\ F$) over a 2-week period. Data on saline-treated animals (first experiment) are represented by open circles. Mean values for the four animals are indicated by the open circle from which arise vertical and horizontal lines (standard deviations for ΔOF and ΔEOD F, respectively). Data on DHT-treated animals are represented by closed triangles and closed circles (first and second experiments, respectively). Mean ΔOF and ΔEOD F values for the eight DHT-treated animals are indicated by the closed square. Vertical and horizontal lines from this point indicate standard deviations.

frequency is in agreement with results for other species (*6*), and would be expected from the previous findings that the oscillation frequencies provide an indication of unit best frequencies and that unit best frequencies are closely related to an animal's discharge frequency (*1*, *2*).

Starting 1 day after the initial DHT injection, all four experimental animals, both males and females, showed decreases in discharge frequency. The time course of the response in one of these animals, a female, is illustrated in Fig. 2a. To quantify the changes in discharge frequencies, we determined the difference between each individual's discharge frequency at the start and at the completion of the 2-week injection period (ΔEOD). Females had higher discharge frequencies and showed larger ΔEOD values than males. Also, females showed larger fractional changes (calculated by dividing ΔEOD by the fish's initial discharge frequency). Control animals did not show such pronounced changes in discharge frequency (Fig. 2b).

The DHT treatment not only affected discharge frequency but also elicited changes in receptor oscillations. All four experimental fish exhibited declines in oscillation frequency which paralleled the declines in EOD frequency (Fig. 2a). Again, no such changes were apparent in the oscillations of the control animals. As a further test of DHT's influence, control animals from the first experiment were given DHT injections over a subsequent 2-week period. As in the first experiment, DHT caused decreases in discharge frequency and closely matched decreases in the frequency of oscillations.

Figure 2c summarizes the changes in EOD and oscillation frequencies for the experimental and control groups. The effect of DHT on discharge and oscillation frequencies was significantly different from that of saline ($P < .01$, Student's t-test). To determine the overall relation between the changes in EOD frequency and the changes in oscillation frequency we combined the results for the saline-treated and DHT-treated groups and performed a linear regression. The results of this analysis demonstrate a one-to-one correspondence between the changes.

The reduction in oscillation frequencies in *Sternopygus* by DHT indicates that the tuning characteristics of electroreceptors in these animals are dynamic and that electroreceptors are likely to show ontogenetic and seasonal changes corresponding to such changes in discharge frequency. By means of this shift in receptor sensitivity, an individual can maintain maximum sensitivity to its changed motor output. This conclusion has since been confirmed by single-unit recordings from electroreceptive primary afferent fibers (*10*).

The mechanism underlying DHT's effect on receptor tuning remains to be determined. It is possible that electroreceptors are not directly affected by the steroid, but rather that their tuning characteristics are determined by the frequency of the electric field of the ongoing EOD. That is, steroids might affect only the EOD-generating circuitry; the changed electric field would then directly alter tuning. This hypothesis is compatible with the results of a study of pulse-discharging gymnotoids (*12*) in which it was noted that local variations in the peak powers of EOD's are matched by local changes in receptor tuning characteristics. Alternative proposals are (i) that steroids directly influence both the EOD-generating circuitry and receptor tuning and (ii) that steroids act directly on receptors, altering their tuning characteristics; the fish then modifies its discharge to match the best frequencies of its electroreceptors. Elucidation of the mechanism involved will shed light on the more general question of tuning in other vertebrate hair cells (*13*).

J. HARLAN MEYER
Scripps Institution of Oceanography, A002, La Jolla, California 92093

HAROLD H. ZAKON
Neurobiology Unit, Scripps Institution of Oceanography, A001, and Department of Neurosciences, University of California, San Diego, La Jolla 92093

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8. Aquariums were kept at 26° ± 0.2°C throughout the experiment by means of solid-state temperature controllers. Resistivity of the water was 1 kilohm-cm and pH was 6.5 to 7.0. The fish were maintained on a 12-hour light cycle.
9. Pulses (2 to 6 Hz) were passed through a stimulus isolation unit before entering the tank via the two carbon rods. Durations ranged from 0.2 to 20.0 msec, with the standard pulse being 1.0 msec. Amplitudes ranged from 1 to 20 mV/cm. The water in the tank was of the same resistivity, temperature, and pH as the water in the fish's home aquarium.
10. By utilizing a large-field stimulus and averaging, we recorded extracellular receptor potentials of many receptors from a patch of skin. This provides a consistent measure of receptor tuning, since the receptors are so similarly tuned in this species. Tuning, as determined by the oscillation frequency, is in very good agreement with the best frequencies of electroreceptive primary afferents (H. H. Zakon and J. H. Meyer, in preparation).
11. Saline solutions given to control animals consisted of two drops of Tween 80 per 50 ml of Ringer (6.48 g NaCl; 0.15 g KCl; 0.29 g $CaCl_2 \cdot 2H_2O$; 0.12 g $MgSO_4$; 0.084 g $NaHCO_3$; 0.06 g NaH_2PO_4 per liter of distilled water). DHT solutions were prepared by homogenizing DHT in the saline solution. Tween 80 was added to the saline to aid in the suspension of the steroid. Injections, consisting of 0.1 ml of saline or DHT solution (5 μg/g), were started 2 days after the baseline frequency determinations and were given for five consecutive days. A second series of five injections was given 2 days after the second determination of oscillation frequency.
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Computer-Assisted Mapping of Pyroclastic Surges

Abstract. *Volcanic hazard maps of surge boundaries and deposit thickness can be created by using a simplified eruption model based on an "energy line" concept of pyroclastic surge and flow emplacement. Computer image-processing techniques may be used to combine three-dimensional representations of the energy relations of pyroclasts moving under the influence of gravity (defined by an "energy cone") with digital topographic models of volcanoes to generate theoretical hazard maps. The deposit boundary and thickness calculated for the 18 May 1980 eruption of Mount St. Helens are qualitatively similar to those actually observed.*

Maps of volcanic hazards provide a basis for making policy decisions regarding public safety during times of impending volcanic crises. A useful map is one that is produced by methods that are (i) reliable (the data base should accurately reflect the distribution of products from all hazardous phenomena recorded by outcrop patterns of prehistoric events, and observed phenomena of historic eruptions), (ii) applicable (an understanding of the phenomena should be sufficient to predict the distribution of products of renewed activity given adequate assumptions regarding the magnitude of the event, location of the vent,

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