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ABSTRACT.—A lightweight radiotelemetry system with a range of 80 km was used to monitor heart rate from free-ranging Herring Gulls on flights of up to 20 km. Heart rate varied from 130 beats/min in a resting bird to 625 beats/min for sustained flight. Soaring birds showed rates similar to those of birds sitting quietly on the ground. Simultaneous records of telemetered heart rate and intraspecific conflict on the nesting island revealed that cardiac acceleration preceded overt visual communication. Intensely aggressive behavior was accompanied by heart rates approaching those of sustained flight. Heart rate as a measure of metabolic cost indicates that the gull's behavioral adaptations for long-distance flight, food location and intraspecific communication result in major energy savings. Received 6 July 1976, accepted 10 December 1976.

The evolution of bird flight has required solving the interlocking problems of form, lightness and ability for intense muscular effort. Our knowledge of the physiological details of a bird in the air has of necessity been largely inferred. Wind tunnels have been used to obtain behavioral and physiological data from flying birds (Tucker 1968, 1972; Torre-Bueno 1976). Tethered birds and radiotelemetry systems with a range of a few hundred meters have also been used to monitor physiological parameters of flying birds (see Gessaman 1973a for several examples). Although these and other laboratory techniques yield valuable data, their extrapolation to natural conditions would be greatly facilitated by data telemetered from free-ranging animals undisturbed by an observer or experimental apparatus. We describe here the telemetry of heart rate from Herring Gulls (Larus argentatus) during flights of up to 20 km.

METHODS

We used a narrow bandwidth, high frequency (432 MHz) radiotelemetry system described by Lawson et al. (1976). The 50-g transmitter is attached to the birds with a nylon mesh harness; the birds preen the entire assembly under their feathers within an hour leaving only the 17-cm, ¼-λ whip antenna protruding. The transmitter operated continuously at full power (range up to 80 km) for 40 h and with reduced power (range 1–5 km) for 5 days. Physically small, high gain antennas (possible because of the short λ) were mounted on permanent tracking stations on hilltops, on mobile tracking stations on ships, on a large van, or were hand-held. Directional accuracy varies from ±10° for hand-held antennae to ±1° for fixed tracking sites (see Lawson et al. 1976).

Activity of the birds produced characteristic low frequency modulation of the transmitted signal; with this information plus data on position and received signal strength, we could reliably distinguish flapping flight, soaring, resting on the ground, and movement on the ground. The higher frequency modulation of the EKG was superimposed upon the behaviorally induced modulation by shifting the carrier frequency up to 1 kHz with an applied voltage from an EKG amplifier in the telemetry transmitter (see Lawson et al. 1976 for further detail). Each major contraction of the heart stood out as a distinctive “chirp” when a beat frequency oscillator was used to convert the received signal to audible frequencies.

The audio output of the telemetry receivers was recorded on one channel of a stereo tape recorder with the position and/or behavior of the bird recorded on the other channel. For recording long-term or long-distance flights we used two or three tracking stations simultaneously; for observations of the bird at close range a single station was used.
Fig. 1. Tachometer records of telemetered heart rate of free-living Herring Gulls under differing conditions. Logarithmic plot of instantaneous heart rate vs. time. a: A gull sitting quietly in the nesting colony. Record shows characteristic modulation correlated with breathing rate. b: Record from a gull startled by a quiet cough of an observer in a blind 10 m away. c: Heart rate during two short flights. Note gradual acceleration in heart rate before takeoff. Preflight acceleration is particularly evident in the second flight when the bird was startled by a shout from an observer 100 m distant. d: Terminal portion of an 8.5-km sustained flapping flight at an airspeed of about 40 km/hr (see text). Note similar heart rate deceleration in d and c. e: Record from a soaring or gliding gull. Note similarity to a, a record from a gull resting on land.
The double conversion superheterodyne receiver used a final I.F. of 455 kHz. We phase-locked to the received signal at this point in order to recover the original modulating EKG wave form on the bird. The excursions on such a signal from the major contraction of the heart (systole) shows as a distinctive pulse. In subsequent analysis from magnetic tape recordings we used the pulse to actuate an integrator that generated a linear ramp voltage starting with each heart beat. The next beat stopped the integration. The value of the arrested ramp became a measure of the time between beats.

The voltage was sampled and held, and the integration process was begun again. The result of the recording of these sampled voltages is a histogram whose elements represent the time between consecutive heart beats. We show such records in Fig. 1. They are inverted so they can be seen as pulse rate increasing upwards. The scale is non-linear because this rate is computed from the reciprocal of the period.

This is a true picture of instantaneous frequency because there is no electrical averaging between beats. Such records reveal frequency changes over intervals as short as three heart beats and can distinguish rapid increase in cardiac pacemaker rate from instantaneous doubling of the rate. The rate changes with breathing are an example of the added information that can be extracted from such tachometer records.

Gulls were captured on the nest at the greater Weepecket Island, 41°30′40″N, 70°44′30″W, 3 km WSW of Woods Hole, Massachusetts, as described in Williams et al. (1974). After anaesthesia with ether, the EKG lead (a #30 silver-plated wire with a short exposed end) was inserted under the breastbone through a #18 needle while we checked the strength of the EKG signal. When a sufficiently strong, clear signal was obtained, the needle was withdrawn, antiseptic applied, and the wire sutured in place. This procedure was rapid, in most cases lasting less than 15 min. The birds recovered from the anaesthesia in 10–20 min at which time they were capable of apparently normal flight, and with a single exception the birds gave no evidence of trauma from the operation.

For experiments involving long flights, the birds were captured, transported, and released several hours later in Vineyard Sound, 25–45 km ESE of the nesting area as described in Williams et al. (1974, fig. 2). After release from the ship, the position of the bird was determined by triangulation, from two or more tracking stations, as it flew to shore.

Birds released on the nesting island were captured on the nest. The electrode was implanted and the transmitter attached to the bird on the island, but out of sight of the nest area. The bird was allowed to recover in the vicinity of the nest while we watched from a blind.

After the birds had recovered and preened the transmitters under their feathers, it was difficult or impossible to identify the experimental bird visually among other gulls; for this reason most birds were marked with a spot of bright spray paint on the breast, head, or wing.

RESULTS

Resting.—A resting gull has a heart rate in the region of 130 to 250 beats/min. When there is behavioral activity such as looking about and preening the rate varies upwards to 300 or more for periods of 20 to 40 sec. Under both of these conditions there is 5–20% modulation of the heart rate that is synchronous with breathing (Fig. 1a). The latter occurs at 11–16/min. This apparently slow rate is about half that of a comparably-sized mammal. Such heart rate changes provide a way to monitor breathing of a resting bird without a special sensor. We checked this correlation on one bird by mounting a thermistor by the nares. This detected breaths by temperature changes in the incoming and outgoing air.

Behavior.—The behavior of four birds with EKG transmitters was studied for up to 3 days from a blind or (with binoculars) from a distance of 50–150 m. When birds were in the nesting colony the basic resting pattern was often interrupted by sudden increases in heart rate followed by a rapid return to the resting state. In some cases these were undoubtedly due to our presence. When we were in the blind a single cough or the slightest noise from a movie camera or tape recorder would cause a jump in heart rate similar to that shown in Fig. 1b. Often the birds had given no outward indication of alarm that we could observe at the time or in later analysis of cine films. The sensitivity of heart rate to external conditions was also noted several times during one day that we spent following a gull feeding 4–5 km away from the nesting island. At one point we watched the bird sitting on a telephone pole 100 m
away. A child moved toward the bird offering a bit of food. The bird watched, seemingly otherwise unconcerned, but its apprehension was signaled by a heart rate that accelerated from 160 to 440 beats/min and then returned to 200 as the child backed off.

Similar changes in heart rate were seen during interactions with conspecifics. Gulls on the nesting island frequently doubled their heart rates for a brief period as other birds approached. In two instances gulls that were being intensely threatened by other birds maintained accelerated, rapidly fluctuating rates of 250–450 beats/min for several minutes. Rapid changes in heart rate appeared to be produced by the approach of only certain other birds; for example, we watched a bird resting quietly on a rock as two other birds landed close to it. In neither case did the bird show any visual signs of agitation as the other birds approached. In the first case the heart rate did not change perceptibly, but in the second it increased rapidly to 400 as the other bird approached to about 20 m. The second bird then displaced the experimental bird from its place on the rock.

**Flight.**—Fig. 1c illustrates the change in heart rate during two short flights, one initiated by the observer. All records of flights showed similar patterns. The initial rise in heart rate before takeoff is rapid but not instantaneous, suggesting a linear increase in pacemaker activity rather than instantaneous doubling or tripling of the rate. Figure 1d shows the terminal portion of a record from a bird that flew toward shore in steady flapping flight for 15 min after release from the ship. The bird covered 8.5 km at a speed of 33 km/hr with an 18 km/hr crosswind. Vector addition of the speed relative to the ground and the speed of the wind indicates that the bird was moving through the air at an average speed of 42 km/hr. Three other birds released in the same area at other times made flights of 7.5–20 km, also at flight speeds of about 40 km/hr (see Williams et al. 1974). For all birds, the rapid acceleration of heart rate at takeoff was indistinguishable from the examples shown in Fig. 1c. Heart rate then climbed slightly for several minutes to values as high as 625 beats/min. Subsequent sustained flying for 15–30 min showed less than 3% change. The end of a flight (see Fig. 1d) initiated a rapid decrease in heart rate during which half of the flying rate was reached in about 12 sec. This rate of decrease was the same for a flight of 30 min as for one of 30 sec. Thus, a gull does not appear to be paying off a larger oxygen debt with a longer flight.

Figure 1e is a record from a soaring bird showing a heart rate of 230–260 beats/min with modulation due to breathing, as in Fig. 1a. After the birds reached shore using steady flight in a crosswind they rested and then took off moving along the shore utilizing updrafts for soaring (see Williams et al. 1974). Soaring flight was easily distinguishable by the lack of transmitter modulation due to wing beat. The birds were not sitting on the ground since the received signal strength indicated the transmitter was more than 10 m above ground and the positional data from tracking stations revealed that the birds were moving. Many other gulls were seen soaring in the same vicinity. The lowered rate of 230–300 beats/min for soaring birds represents what is probably a large energy saving of soaring over flapping flight.

**DISCUSSION**

Bird flight is unparalleled in animals for its sustained high energy expenditure (Tucker 1969, 1972). A single overwater flight may burn half of a bird’s weight in the form of stored mobile fat (Odum 1960, Nisbet et al. 1963). Although data are at
present limited, heart rate appears to be a relatively good predictor of metabolic rate in birds and mammals (Johnson and Gessaman 1973, Gessaman 1973b). Gulls are apparently able to reduce the cost of airborne travel greatly by soaring; the heart rate of a soaring bird is similar to that of an alert bird sitting quietly. Such data support the generalization that laboratory measurements of the metabolic cost of flight may indicate only maximum rates, while free-ranging birds often require less energy to cover a given distance. Gulls appear to have some latitude even during steady flapping flight, as we monitored heart rates from 480–625 beats/min during powered flight. Such changes may reflect variation in the amplitude of wingbeats, which we have often observed in gulls flying near ships.

The use of telemetered heart rate appears to offer many advantages in the study of energy budgets and behavior, if the proper techniques are employed. Our data on heart rate suggest clear physiological adaptations to the gull’s way of life. Gulls appear to anticipate a stressful situation or the need for flight by accelerating heart rate before the actual increase in activity. This contrasts sharply with fish, which when frightened may stop their heart for 10 to 20 sec (Kanwisher et al. 1974). Steady flight is costly; as shown by Williams et al. (1974), gulls will double the total distance traveled to take a route that allows soaring or gliding rather than steady flapping flight. Gulls under natural conditions obtain much of their food by searching beaches and shallow water from the air. They often do so by using the updraft from an onshore wind meeting a bank; the energy expenditure of this type of search behavior for the Herring Gull is much less than walking or flapping flight per unit area searched.

The evolutionary advantage of complex signaling behavior in gulls (Tinbergen 1972) is also apparent in studies of telemetered heart rate. Intense, aggressive interactions between conspecifics are accompanied by heart rates approaching that of flapping flight; any communication systems that reduce such interactions must constitute a significant energy saving.

As suggested by Gessaman (1973b), telemetered heart rate offers a technique to evaluate specific components of an energy budget in free-ranging animals. We believe such systems will also be of use in studies of respiratory physiology and behavior, but only if the telemetry system is designed for long-range, narrow bandwidth field use. FM systems designed for laboratory or hospital biomedical research appear ill-adapted to this purpose. The ability to monitor both physiology and naturalistic behavior in field studies offers great promise; one or two sensors certainly are not going to reveal the inner workings of an animal, but they help considerably.

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LITERATURE CITED


The American Ornithologists’ Union will hold its 96th Stated Meeting during the week of 14–18 August 1978 at the University of Wisconsin-Madison at the invitation of the Department of Wildlife Ecology and the Department of Zoology of the University of Wisconsin-Madison, the Wisconsin Society for Ornithology, and the Madison Audubon Society. A Circular of Information providing details of the meeting and a formal call for papers will be sent to the A.O.U. membership. Chairman of the Local Committee is Dr. Stanley A. Temple, Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706. Chairman of the Committee on Scientific Program is Dr. Ralph W. Schreiber, Natural History Museum, 900 Exposition Boulevard, Los Angeles, California 90007.