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That birds are homeotherms is demonstrated by their ability to maintain a relatively constant body temperature over a wide range of ambient temperatures. An important component of this ability to maintain a constant body temperature in a cold environment is the feather layer. Birds have been shown to acclimate to cold by increasing their plumage 20-30 percent and, hence, increasing their insulation (Kendeigh, 1934; Scholander, et al., 1950; West, 1962). Hutchinson (1954) states that oil secreted by uropygial (preen) glands maintains the ability of the feathers to shed water and, therefore, aids in maintaining the insulating layer.

Since feathers are so important for minimizing heat loss, anything that will decrease their insulative efficiency will increase the thermal conductance and the lower critical temperature. Baldwin and Kendeigh (1932) clipped feathers off of Eastern House Wrens (*Troglodytes aedon aedon)* and observed a decrease in body temperature. Brush (1965) obtained similar results in the California Quail (*Lophortyx californicus)*, thus indicating the necessity of feathers for minimizing thermal conductance and maintaining a constant body temperature.

Kessler, et al. (1968) observed mass deaths of Cowbirds *(Molothrus ater ater),* Bronzed Grackles (*Quiscalus quiscula aeneus*), and Starlings (sturnus *vulgaris)* after a driving rainstorm with concomitant low ambient temperatures (10°C). Under similar circumstances Jogi (1968) reported mass deaths of swallows (*Riparia riparia, Delichon urbica,* and *Hirundo rustica)* in Estonia. Apparently the driving rain had destroyed the insulating quality of feathers, and with low ambient temperatures the birds succumbed to hypothermia. Caslick and Stowers (1967) and Stickley, et al. (1971) used a surfactant to remove the preen gland oil from the Red-winged Blackbird *(Agelaius phoeniceus phoeniceus)* and exposed them to low ambient temperatures and wetting, which resulted in a large number of deaths. The surfactant reduced the surface tension of the preen oil, allowing water to penetrate through the feathers to the skin, thus destroying the insulative quality of the feathers. More recently this technique of wetting the bird with surfactant has been used as a means of controlling blackbird populations.

Environmental physiologists have long been interested in the effects of temperature on bird energetics (Calder and King, 1974). More recently, interests have changed from just the influences of temperature on energetics to the synergistic effects of temperature, wind, humidity, and solar radiation (Lasiewski, et al., 1966; Lustick, 1969, 1970; Gessaman, 1973). If we are to understand energy flow through a population of birds, then, we must know how every environmental stress affects the birds energy requirement. Since wetting may be an important environmental stress which can affect bird energetics and survival, the following study was conducted to examine two questions: 1. What are the effects of wetting on bird energetics and survival over a range of ambient temperatures from 5° to 40°C? 2. Are there seasonal differences in a bird's ability to withstand the detrimental effects of wetting?

METHODS AND MATERIALS

Starlings (*sturnus vulgaris*) and Bronzed Grackles *(Quiscalus quiscula aeneus)* were trapped in large funnel traps on The Ohio State University campus. One hundred Starlings and 155 Grackles were captured from June through September, and 35 Starlings and 15 Grackles were captured between 26 December and 21 March. After capture, the birds were maintained in the laboratory in individual cages on a 12 hour photoperiod and received food and water *ad libitum.* Birds were tested within two days after capture to avoid acclimation to laboratory temperatures (16-25°C).

The method used for determining oxygen consumption and body temperature (Tb) has been previously described (Lustick, 1970). All animals were weighed to the nearest 0.1 gram before each test, and body temperature was determined at the end of each experiment. Peak and low rates of oxygen consumption within the hour test period were determined for totally-wet, summer-acclimatized birds over an ambient temperature (T_a) range of 5° to 40°C; for totally-wet, winter-acclimatized birds, over a T_a range of 5° to 15°C. Birds were considered totally wet when held up to the neck in a 0.5 percent detergent solution for one minute. Birds were weighed prior to wetting and just after wetting to determine the

amount of water on them. Cooling rates in degrees C per minute were determined directly by inserting a thermocouple 1 cm into the cloaca of a wet bird at the desired T_a. Body temperature was then recorded continuously on a Leeds and Northrup potentiometer. The test lasted for one hour or until the bird succumbed, whichever came first.

Heart rate as a function of T_b was determined for the totally-wet summer-acclimatized Starling. Body temperature (T_b) and heart rate were simultaneously monitored by use of a leeds and Northrup potentiometer and Harvard Biograph Model 2120, in conjunction with Narco Bio-systems Bio-tachometer BT 1200. Since shivering was intense in the wet birds (masking the heart rate), it was necessary to implant electrodes between the furcula of the bird to obtain a clear electrocardiographic signal.

The conduction velocity of the sciatic nerve as a function of temperature (15° to 40°C) was determined. The birds were lightly anesthetized with 0.02 cc of nembutal, and the sciatic nerve was removed from along the femur and placed in physiological saline. The bird was then given an overdose of nembutal. Next, the nerve was placed in a temperature-controlled nerve chamber with a known distance between recording electrodes. The temperature of the nerve chamber was controlled by adjusting the water temperature around it (in water jacket). The nerve chamber was connected to a Grass SA-9 stimulator and a Tetronix Model 122 preamplifier in conjunction with a Tetronix Model 5403 oscilloscope. The sweep speed (500 µu/cm), frequency of stimuli (10/s), intensity of stimuli (1.7 volts) and sensitivity of oscilloscope (100 mV/cm) were kept constant for each test. The temperature in the nerve chamber was monitored with a Yellow Springs Telethermometer.

RESULTS

Starlings

The thermal neutral zone of dry, summer Starlings extended from a T_a of 22.5° to approximately 38°C. Below a T_a of 22.5°C, the oxygen consumption increased linearly according to the least squares regression equation $Y = 4.42 - 0.09X$. Within the zone of thermal neutrality the oxygen consumption remained relatively constant at approximately 2.35 cc $0_2 \, g^{-1} Jhr^{-1}$. The mean value for thermal conductance below thermal neutrality was 0.125 cc $0_2 \, g^{-1} hr^{-1} C^{-1}$.

In totally-wet, summer-acclimatized birds, the peak oxygen consumption attained increased linearly between an ambient temperature of 40°C and 25°C, as expressed by the equation, $Y = 17.4 - 0.36X$ (Fig. 1). Between the ambient temperatures of 25°C and 20°C the peak oxygen consumption remained relatively constant (8.3 cc $0_2 \, g^{-1} hr^{-1}$). declining with decreasing T_a below 20°C to a minimum of 4.7 cc $0_2 \, g^{-1} hr^{-1}$ at a T_a of 5°C (Fig. 1). The minimum oxygen consumption increased from a T_a of 40°C to 30°C, remained relatively constant between 30° and 20°C, and then dropped off rapidly to zero at 5°C, indicating that the summer-acclimatized Starling could no longer maintain a high level of heat production below a T_a of 20°C. It should be pointed out that the lower critical temperature of totally-wet birds was shifted up to a T_a of 40°C.

The peak oxygen consumption of totally-wet, winter-acclimatized, Starlings was significantly higher ($P<0.05$) than that of the summer-acclimatized wet birds (11.5 cc $0_2 \, g^{-1} hr^{-1}$ compared to 8.3 cc $0_2 \, g^{-1}$) (Fig. 2). In fact, at the three test temperatures (5°, 10°, and 15°C) the minimum winter oxygen consumption was higher than the peak summer oxygen consumption at the same temperature.

Summer-acclimatized, dry birds maintain a relatively constant body temperature (40°C) over a range of ambient temperatures from 5° to 35°C with a slight increase at a T_a of 40° to 41.6°C. Surviving totally-wet, summer-acclimatized Starlings could maintain their T_b above 35°C only at T_as exceeding 20°C. At a T_a below 20°C the body temperature dropped to a minimum of 21.6 at a T_a of 5°C. The surviving totally-wet, winter-acclimatized birds were able to maintain their T_b above 34°C at a T_a as low as 10°C indicating that the winter bird is acclimatized. The T_b from which the summer and winter-acclimatized Starlings could restore homeothermia on their own when placed at room temperature was approximately 27°C.

The cooling rate (C°/min) of totally-wet, summer-acclimatized Starlings increase linearly from a T_a of 20° to 5°c and may be expressed by the equation $Y = 0.97 - 0.037X$ (Fig. 3). The totally-wet, winter-acclimatized Starlings had a significantly lower ($P<0.05$) cooling rate at all the test temperatures (Fig. 3). A line fitted by the method of least squares to data on winter-acclimatized birds is expressed by the equation $Y = 0.43 - 0.03X$.

The winter-acclimatized Starlings were significantly (P<0.05) heavier than the summer-acclimatized Starlings (79.3 ± 1.2 compared to 67.3 ± 1 g), and mass seemed to be an important factor to survival. At most of the test temperatures studied, it was the heavier bird that survived. Not only was mass important to survival, but the amount of water on the bird was equally as important to survival. Birds with water equivalent to less than 20 percent of their body mass on them usually survived the one-hour test period. The survival rate of summer-acclimatized wet birds decreased from 25 percent at 15°C to none at 5° and 10°C. The interesting fact is that in winter-acclimatized birds the survival rate for the one-hour test period never dropped below 88 percent even at a T_a of 5°C. In other words, survival at 5°C in winter-acclimatized birds was greater than surviv-al at a T_a of 20°C (60 percent) in summer-acclimatized birds.

The heart rate in both wet summer-and winter-acclimatized birds decreased linearly from a maximum of 630 beats/min at a T_b of 37°C to 0 beats/min at body temperature of 16°C and may be expressed by the equation, $Y = -465.4 + 28.9X$. The heart rate exhibits a Q_{10} of 2.1 between a T_a of 25° and 35°C.

The conduction velocity of the sciatic nerve decreased linearly with decreasing tem-perature from a maximum 55 m/s at 40°C to 0 m/s at approximately 18°C and may be express-ed by the equation, $Y = -46.8 + 2.6X$. The Q_{10} between 30° and 40°C is 1.9.

Grackles

The thermal neutral zone was not sharply defined, but oxygen consumption was minimal between 22.5°C and 38°C. Below an ambient temperature of 22.5°C the oxygen consumption increased linearly and may be expressed by the equation ($Y = 3.78 - 0.07X$). Between 35° and 40°C oxygen consumption increased slightly. The standard oxygen consumption within the zone of thermal neutrality is approximately 2.2 cc 0_2 g-^{1} hr-^{1}. The mean value for thermal conductance below thermal neutrality was 0.10 cc O_2 g-^{1}hr-^{1}C-^{1}.

In totally-wet summer-acclimatized birds the peak oxygen consumption increased linear-ly between an ambient temperature of 40°C and 25°C and can be expressed by the equation $Y = 15.03 - 0.32X$ (Fig. 4). Between an ambient temperature of 25° and 5°C, the peak oxygen consumption remained relatively constant. The minimum oxygen consumption increased linear-ly from 40° to 20°C and then decreased, indicating that below an ambient temperature of 20°C the birds could no longer sustain a high level of oxygen consumption (heat production). Like the Starling, the lower critical temperature for a wet Grackle is shifted up to 40°C. The maximum attainable mean oxygen consumption rate for a wet simmer-acclimatized Grackle was approximately 8.0 cc O_2 g^{-1}hr^{-1}.

The peak oxygen consumption of totally-wet winter-acclimatized birds was not sig-nificantly different from that of totally-wet summer-acclimatized birds (Fig. 4). The major difference between summer and winter wet birds was in the minimum oxygen consumption at an ambient temperature of 10°C. While in summer-acclimatized wet birds the minimum oxygen consumption decreased drastically, it was not significantly different (P<0.05) from the peak oxygen consumption in the winter-acclimatized birds (at 10°C). At an ambient temperature of 5°C there is no significant difference in oxygen consumption between summer and winter wet birds.

Summer-acclimatized dry birds maintain a relatively constant body temperature (40°C) over a range of ambient temperatures from 5° to 30°C. Above a T_a of 30°C, the body tem-perature increases to a maximum of 43.5°C at an ambient temperature of 40°C. Totally-wet summer-acclimatized Grackles could maintain their body temperatures above 36°C only at ambient temperatures of better than 25°C. At T_as below 25°C the body temperature dropped to a minimum of 22°C at T_as of 5° and 10°C. As with minimum oxygen consumption, at a T_a of 10°C, the wet winter-acclimatized Grackles had a higher body temperature (27.7°C) than wet summer-acclimatized birds, 21.2°C. There was no significant difference in body tem-perature between totally-wet summer-and winter-acclimatized birds at 5°C. The body tem-perature below which a Grackle could not survive when returned to room temperature (20-25°) was approximately 25°C.

The cooling rate of totally-wet summer-acclimatized birds (C°/min) increased linearly from a mean of 0.15 C°/min at an ambient temperature of 20°C to a mean of 0.653 C°/min at an ambient temperature of 5°C. A line fitted to the data by the method of least squares is expressed by the equation $Y = 0.759 - 0.032X$ (Fig. 5). The figure includes some data collected in 1972 (23 summer-acclimatized wet birds at 10°C) to show the consistency in measuring cooling rates. The totally-wet winter-acclimatized birds had significantly lower cooling rates at an ambient temperature of 10°C and a lower cooling rate at 5°C (Fig. 5).

As with the Starlings the winter-acclimatized Grackles were approximately 20 grams (107.8 g) heavier than the summer-acclimatized birds (87.9 g). At most test temperatures where birds survived the hour test period, the surviving birds were heavier. As with the Starlings birds with less than 2.0 percent of their body weight of water on them usually survived the one-hour test.

Survival decreased with decreasing ambient temperature in both the totally-wet summer and winter-acclimatized birds. It should be pointed out that survival at 10°C in winter-acclimatized birds was similar to that of summer-acclimatized birds at 20°C. In summer-acclimatized wet birds there was 100 survival at T_as above 20°C.

The heart rate decreased linearly from a maximum of 615 beats/min at a T_b of 40°C to 0 beats/min at approximately a T_b of 14°C. A line fitted to the data by the method of least squares is expressed by the equation Y = -316 + 23.19X, with a correlation coefficient of 0.96.

The conduction velocity of the sciatic nerve decreased linearly with decreasing temperature from a maximum of 42 m/s at 40°C to 0 m/s at 16°C. Again a line fitted to these data by the method of least squares is expressed by the equation Y = -28 + 1.76X with r = 0.85.

DISCUSSION

As expected, both a dry Starling and Grackle can easily maintain homeothermia over a range of T_as (5° - 40°C). The oxygen consumption within thermal neutrality 2.35 and 2.2 cc 0_2 $g^{-1} hr^{-1}$ for a Starling and Grackle, respectively, and the thermal conductance below thermal neutrality 0.125 and 0.10 cc O_2 $g^{-1} hr^{-1} C^{-1}$ for a Starling and Grackle, respectively, agree closely with the values predicted by Lasiewski and Dawson (1967) for a 67 and 88 g bird and Herreid and Kessel (1967) for a 67 and 88 g bird, respectively.

In the Starling and Grackle, as with the Red-winged Blackbird and Brown-headed Cowbird (unpublished date), the lower critical temperature for a wet, summer-acclimatized bird is shifted up approximately 20C°(to 40°C), indicating that the wet bird must increase its metabolism at all ambient temperatures below 40°C if it is to maintain its body temperature. The facts that the insulative quality of the feathers has been destroyed by wetting and in a wet bird 40°C is the lower critical temperature compared to approximately 20°C for a dry bird suggest that the feathers are the main means of changing thermal conductance (rate of heat loss) within thermal neutrality.

The major means the summer-acclimatized birds have for increasing their heat production below thermal neutrality is shivering, since non-shivering thermogenesis has not been demonstrated in adult birds (Hart, 1963; West, 1965; Dawson and Hudson, 1970). Although increased activity would increase heat production, it would probably increase heat loss by convection and increased blood flow to the periphery. The maximum metabolic rate attained by a wet, summer-acclimatized Starling and Grackle was approximately 8.0 cc 0_2 $g^{-1} hr^{-1}$ and is 3.6 times higher than that of a resting summer bird at thermal neutrality. Dawson and Hudson (1970) have stated that shivering can increase the standard metabolic rate 3 to 5 fold.

Rosenmann and Morrison (1972) using a He-02 atmosphere found that the Common Redpoll (*carduelis = Acanthis flammea L.*) could increase its metabolism 5.5-fold above resting metabolism at thermal neutrality. This is in agreement with our findings. If one makes the assumption that the standard metabolic rate for a winter-acclimatized bird in thermal neutrality is the same as that for summer birds, then the winter Starlings also exhibit a 5-fold increase. The drop in T_b in these birds, which leads to a drop in metabolism, a drop in nerve conduction and heart rate, is a circular event and self-defeating as far as survival is concerned, since a drop in nerve conduction and heart rate lead to a further drop in metabojism and body temperature. A similar response in nerve conduction to temperature was demonstrated by Chatfield, et al. (1952) in chickens and gulls and by Chatfield, et al. (1948) in mammals.

No Starling recovered once its T_b dropped to approximately 27°C. It would take a totally-wet summer Starling with a T_b of 40°C at a T_a of 5°C approximately 17 minutes to cool to a T_b of 27°C. With a drop in T_b of only 5C°, nerve conduction drops as much as 24 percent. Below a T_a of 15°C, only 25 percent of the totally-wet summer Starlings were able to maintain their T_b above 27°C for an hour, which would indicate that 15°C is close to the temperature below which a totally-wet, summer-acclimatized Starling could not survive an hour. Although as with the Red-winged Blackbird, Common Grackle, and Brown-headed Cowbird, a T_a below 10°C is most detrimental to survival.

The peak metabolism of totally-wet winter-acclimatized Starlings was higher (11.5 cc $O_2 g^{-1}hr^{-1}$ compared to 8.3 cc $O_2 g^{-1}hr^{-1}$ for wet summer birds), and thus their heat production is greater (3442 cal/bird-hr compared to 2558 cal/bird-hr at T_a of 10°C). Pohl and West (1973) found a similar result in the Common Redpoll when comparing winter to summer-acclimatized birds. Some of this increased heat production and decreased heat loss (smaller surface area to volume ratio) is because the winter Starlings are heavier. The higher heat production caused by increased oxygen consumption in larger birds means a lower cooling rate and a greater survival at low ambient temperature. The mean cooling rate at a T_a of 5°C in totally-wet winter-acclimatized Starlings was 0.28 compared to 0.76 C°/min for totally-wet summer Starlings. This means that in winter-acclimatized Starlings it takes at least 46 minutes for the body temperature to drop to 27°C. Within the one-hour test period in winter-acclimatized Starlings, the survival rate was 88 percent at a T_a of 5°C. In fact, cooling rates in totally-wet winter-acclimatized Starling was as low as 0.08 C°/min at a T_a of 5°C, meaning that it would take 162 (2.7 hr) minutes of continued wetting for the Tb to reach 27° and a zero survival rate.

Hart (1962) noticed Increased resistance to cold In winter-acclimatized Starlings and suggested that an enhancement of metabolic capacity occurs in these birds during the colder part of the year, although he did not demonstrate it. Our study demonstrates a remarkable ability to acclimatize (by metabolic means) in the Starling. The Grackle acclimatized only slightly to winter conditions, the survival rate at 5°C being 11 percent in summer-acclimatized birds compared to 25 percent for winter-acclimatized birds. The actual physiological mechanism by which these birds are acclimatizing is yet to be verified, although several hypothesis can be set forth as to how these birds have adjusted.

1. It is possible that the winter birds caught in Columbus migrated from more northern areas. Kendeigh and Blem (1974) and Hudson and Kimzey (1966) have shown that more northern populations of the same species have a higher metabolic rate and a lower zone of thermal neutrality.

2. Although non-shivering thermogenesis has not been demonstrated in the adult bird (Dawson and Hudson, 1970) It has been demonstrated by Wekstein and Zolman (1968) and Freeman (1970) in neonate fowl. Also Barnett (1970) found winter-acclimatized House Sparrows (*passer domesticus)* had higher rates of metabolism in the brain and muscle tissues and lower rates In the liver than summer-acclimatized birds. In this same study, laboratory cold-acclimated birds had higher rates of metabolism in liver and muscle while brain remained unchanged. Barnett suggested the possibility of non-shivering thermogenesis occurring In isolated tissues. Slonim (1971) found similar elevated rates of tissue metabolism in brain, heart, and liver of cold acclimatized House Sparrow, Rock Dove *(columba livia)* and the Bullfinch *(pyrrhula pgrrhula)*. Calder and King (1974) state that the relationship between tissue metabolism and intact animal metabolism is unclear and suggest that more evidence regarding non-shivering thermogenesis be obtained. Since the winter-acclimatized Starling has a higher metabolic rate on the per gram basis, it is possible that they may have a form of non-shivering thermogenesis. The slight acclimatization seen in the winter Grackles could be explained on weight increase alone, especially since the peak metabolic rate of the winter birds was not significantly higher than that of the summer birds.

3. There may be an increased ability to shiver (Pohl and West, 1973) and/or a change in the muscle fiber's ability to produce heat (Parker and George, 1974).

4. There may be increased energy reserves and a concomitant increased ability for the mobilization of substrate or different metabolic pathways which generate more heat and less ATP.

In both the summer- and winter-acclimatized wet birds, both weight and the amount of water on the birds were important to survival. The heavier birds and those with less water on them than 20 percent of their body mass were most often the ones to survive.

This study points out that wetting is extremely detrimental to bird survival and stresses the evolutionary significance of the preening behavior. It also points out an area in avian energetics that needs further research, the physiological mechanisms of seasonal acclimatization, especially since It seems to vary from species to species (Kendeigh, 1949; Davis, 1955; West, 1960; Lustick, 1975).

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DISCUSSION

Question: According to the winter data that came out of the 1975 Tergitol spraying in Tennessee, they killed about 40% Starlings, almost 40% Grackles, and very few others. Was this possibly due to the fact that it was so cold that you were killing any bird present?

Lustick: It was freezing that day. They kept water going with fire trucks, hoses, and all kinds of things. If you keep water on them for 3 hours, you're going to kill all of them, even at their lowest cooling rate. If they dry themselves off, they will survive.

H. Good: Do you have any data on effects of wind velocity?

Lustick: Wind velocity; would have a tremendous effect, but in our chamber we didn't have wind. We're doing a study now on the effects of wind just on roosting. Why do birds pick a nice pine roost? Basically we found that a half a million bird roost, by going into pine trees and avoiding a 15 km/hr wind, saves an equivalent of 3½ T of corn a day or 11 million calories.

Dyer: I believe it is very easy to make a case against roost control. I have long opposed this massive killing based on the fact that we may encounter secondary reactions that we don't know about. The beneficiary of this whole massive action might be the Starling, and that's the last thing we want to happen. I thought we couldn't get to the Starlings in the first place because they would be in urban roosts where they couldn't be sprayed. It looks to me like the Starling will survive. That coupled with potentials for food competition indicates that if we release the Starling from competition in the SE, very likely we'll have greater survival overall in the Starling. We'll change nominal mortality rates drastically and very well could create a new niche, so to speak. We'll have more problems than before. I really like your data for it points out how potential problems may become realities;

Question: Did you notice any differences in reactions related to sex or age in any of the birds you worked with?

Lustick: The only thing we were really interested in was size; we didn't check sex or age. We were interested in adults, and we went mainly be weight. We have male and female data (except for Starlings), but we never analyzed it in that way.
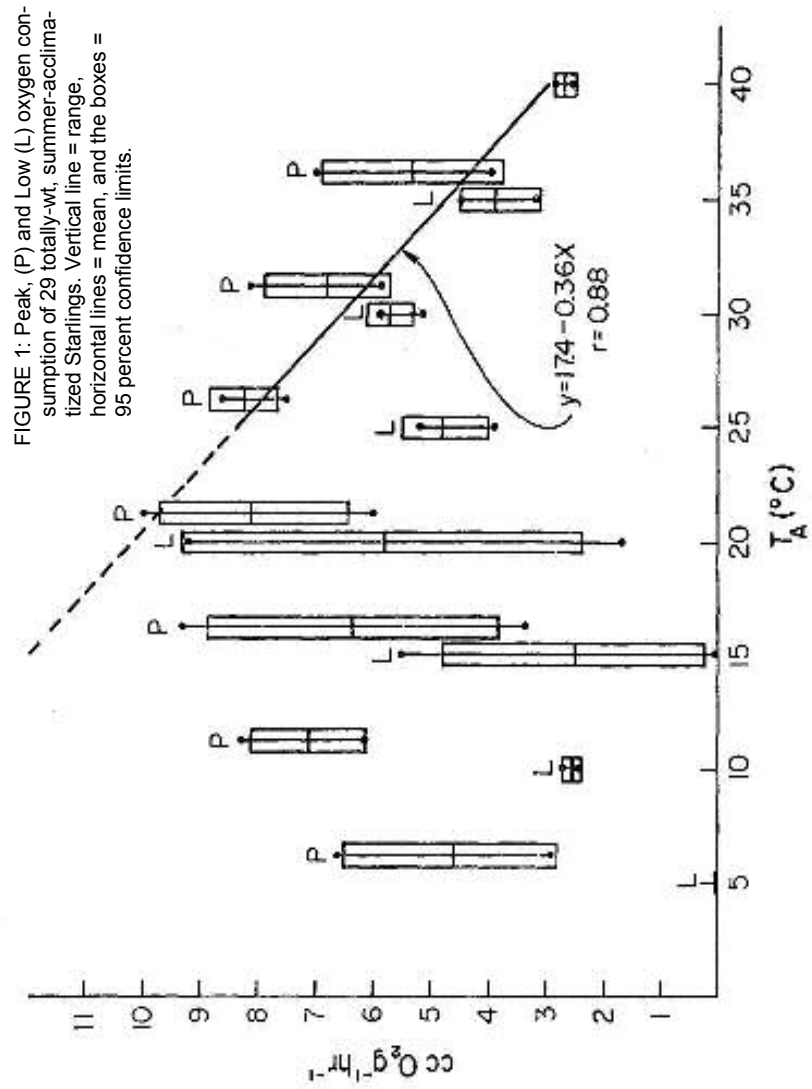
FIGURE 1: Peak, (P) and Low (L) oxygen consumption of 29 totally-wt, summer-acclimatized Starlings. Vertical line = range, horizontal lines = mean, and the boxes = 95 percent confidence limits.
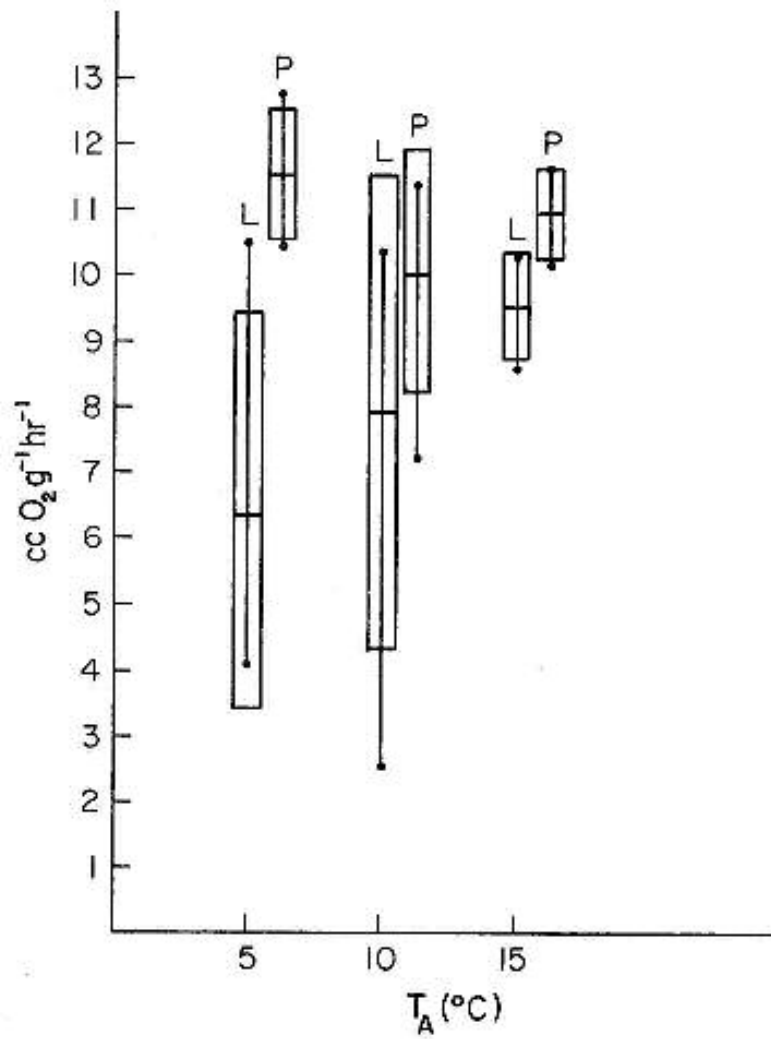
y=174−0.36X
r=0.88

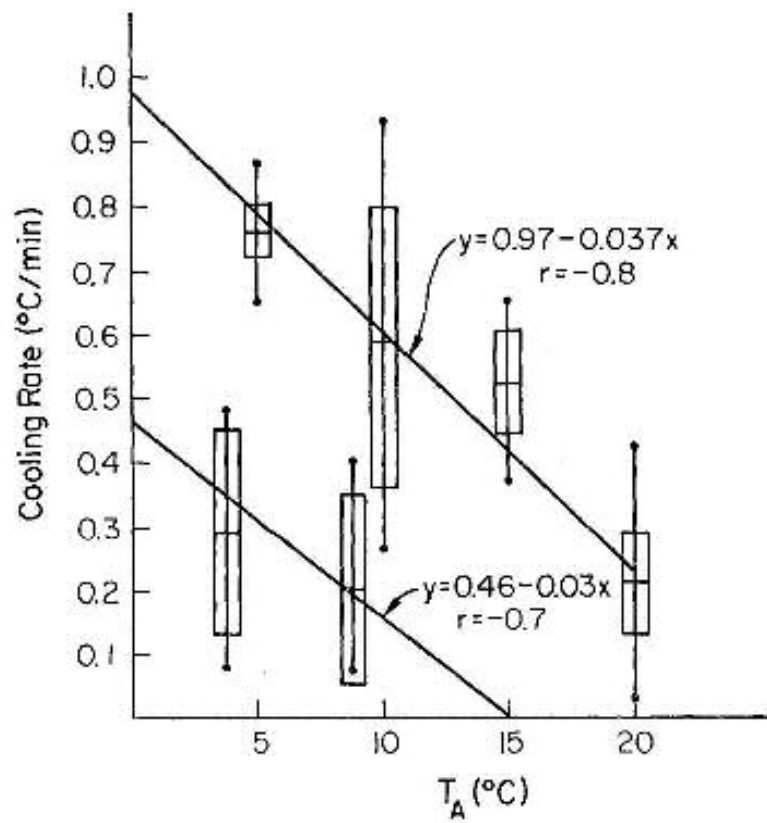FIGURE 2: Peak (P) and Low (L) oxygen consumption of 12 totally-wet, winter-acclimatized Starlings. Symbols as previously described.
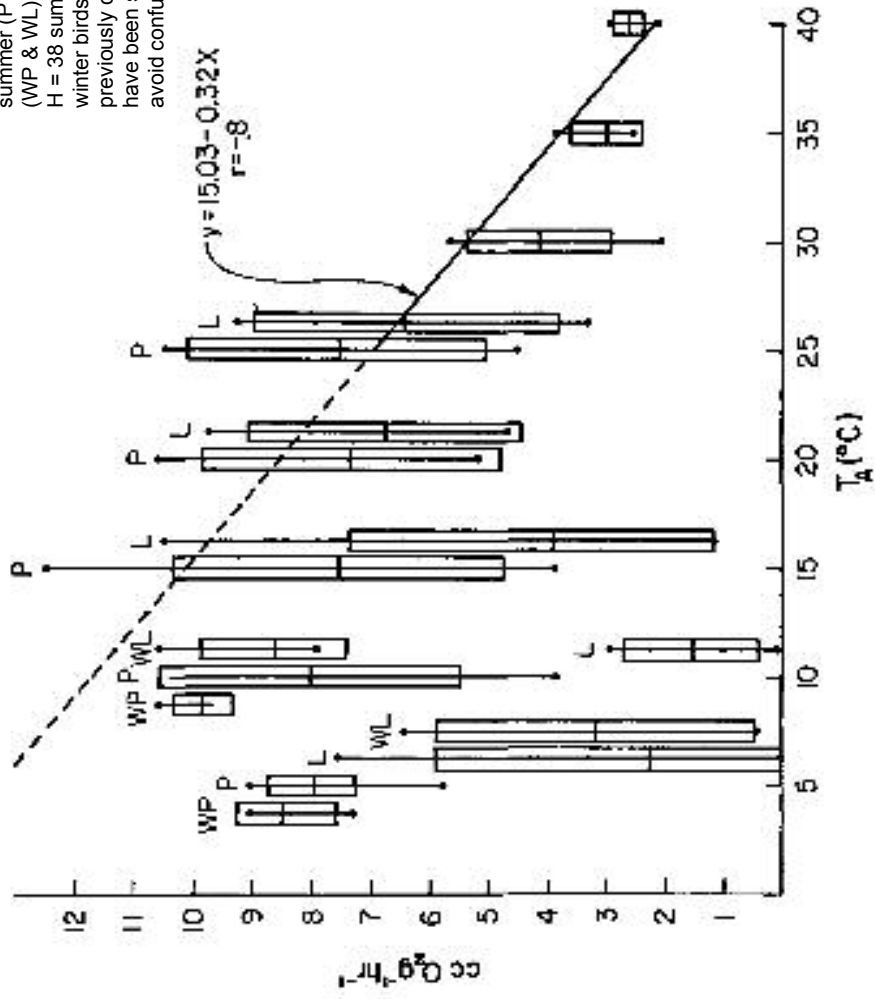
FIGURE 3. Cooling rates of 16 totally-wet, summer (upper line) and 12 winter-acclimatized (lower line) Starlings. Symbols as previously described.

FIGURE 4: Peak and low oxygen consumption of totally-wet summer (P & L) and winter (WP & WL) acclimated Grackles. H = 38 summer birds and 8 winter birds. Symbols as previously described. Boxes have been shifted over to avoid confusion.
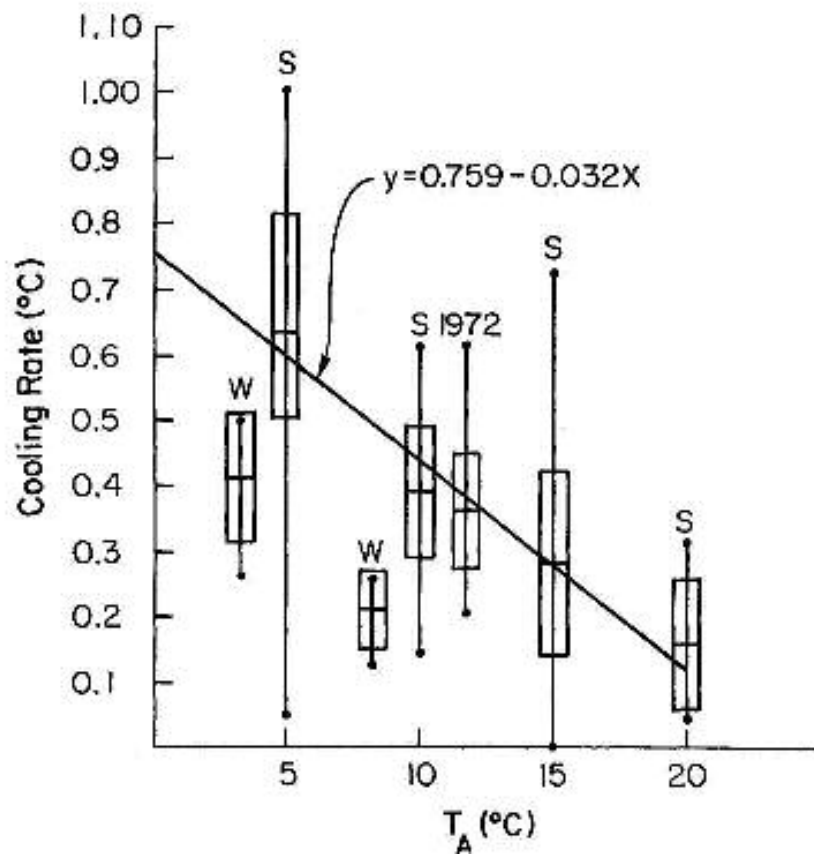
FIGURE 5. Cooling rates of totally-wet summer (S) and winter (W) acclimated Grackles. At 10C there is data from both 1972 and 1974. Winter data shifted to left to avoid confusion. N = 21 summer, and 8 winter.