

METABOLIC RESPONSES OF MOURNING DOVES TO SHORT-TERM FOOD AND TEMPERATURE STRESSES IN WINTER

DONALD L. IVACIC AND RONALD F. LABISKY

THE Mourning Dove (*Zenaidura macroura*) breeds throughout Illinois, but usually migrates southward from the state in autumn. Band recoveries indicate that the majority of doves traversing Illinois in autumn reside during the winter in states bordering the Gulf of Mexico (Hanson and Kossack, 1963). However, small numbers of Mourning Doves, either resident breeders or migrants, often winter in contingents within the species' northern breeding range (McClure, 1943; Chambers et al., 1962), including northern and central Illinois (Hanson and Kossack, 1963); these wintering doves are frequently subjected to severe temperature stresses and food shortages. To illustrate, those doves that wintered in the vicinity of Urbana, Illinois (Latitude 40° 10' N.), in 1970 were subjected to temperature fluctuations of 17° C and 26° C within 8- and 32-hour periods, respectively, on 20 and 21 February. Furthermore, severe storms that deposit glaze or as much as 6 inches of snow, or both, may occur as many as five times each winter in northern and central Illinois (Changnon, 1969), and may frequently render the seed-eating dove's staple winter foods unavailable.

The findings of many investigators of bird metabolism (Kendeigh, 1944; Seibert, 1949; Dawson and Tordoff, 1959; Misch, 1960; Veghte, 1964; and Pohl, 1969) have indicated that acclimatized birds maintain a relatively constant body temperature by increasing their metabolic expenditures as the ambient temperature decreases. Two recent studies, however, have indicated that Mourning Doves, when subjected to decreasing ambient temperatures, exhibited reductions in metabolic rate and body temperature (R. F. Labisky, unpubl. rept.; Hudson and Brush, 1964).

The objectives of this study were to determine: (1) the short-term metabolic responses of Mourning Doves exposed, without food, to rapidly changing ambient temperatures that extended both above and below their usual acclimatized temperature range in winter; and (2) the survival responses of doves of different sex and age exposed to the stresses of low ambient temperatures and the absence of food.

METHODS

The Mourning Doves used in this study were captured in stationary bait traps on the Max McGraw Wildlife Foundation near Dundee, Illinois, during early June 1969. Adults and juveniles were separated on the basis of plumage characteristics, and banded; sex of the birds was determined by internal examination at the conclusion of the tests. The

birds were confined near Urbana, Illinois, throughout the summer, autumn, and winter in a 3.6 × 3.6 × 2.1-m outdoor pen, during which time they were fed water and Purina Mixed Pigeon Grains ad libitum. The doves were subjected to experimentation within the period extending from 19 December 1969 to 25 February 1970. The mean maximum and minimum daily temperatures in Urbana during these months were, respectively: December, 1.4° C and -5.1° C; January, -3.4° C and -12° C; and February, 2.5° C and -7.5° C.

Metabolic rates of doves, as indicated by their rates of oxygen consumption, were determined at ambient temperatures of 10°, 0°, -10°, and -18° C. Consumption of oxygen was ascertained by measuring the amount of oxygen needed to maintain oxygen equilibrium in the 8-liter metabolic chambers used to contain the doves individually during the tests; each system remained open to air flow except during measurement. The chambers were kept in a thermostatically controlled cold room. Each chamber contained a commercial carbon dioxide absorbant (Ascarite) and a desiccant (Drierite) to absorb carbon dioxide and water, respectively. The quantity of pure oxygen that was passed into the closed system during the consumption trials was recorded on an oxygen spirometer for 15 minutes at each experimental temperature; the most stable period of 10 consecutive minutes within the 15-minute interval was used as a measure of the rate of oxygen consumed by the test dove. Rates of oxygen consumption are expressed as cubic centimeters of oxygen consumed per gram body weight per hour ($\text{cc O}_2\text{-g}^{-1}\text{-hr}^{-1}$) under conditions of standard temperature (0° C) and atmospheric pressure (760 mm Hg).

Experimental trials were conducted in the following manner: four doves (two adults and two juveniles) were captured from their outdoor roosts at the onset of darkness and transported to the indoor facilities; there, they were weighed and permitted to rest briefly before being placed in the metabolic chambers. The chamber temperature at the initiation of the experimental cycle, which began at 5 P.M., was 10° C (Fig. 1). Temperatures were lowered, beginning at 6 P.M., approximately 5° C per hour from the initial 10° C to a low of -18° C; the latter was reached at 1 A.M. Three hours were required to reduce the temperature of the cold room from -10° C to -18° C, the lower limit of the cold room. Temperatures were held constant at -18° C from 1 A.M. to 8 A.M. at which time light was restored; the experimental temperature was then raised at the rate of 5° C per hour until the initial temperature of 10° C was reached at 2 P.M. The doves were held at 10° C for 3 hours, or until 5 P.M. (darkness), and then resubmitted to a second identical 20-hour experimental cycle (Fig. 1). Measurements of oxygen consumption were taken under conditions of darkness at 10° C (6 P.M.), 0° C (8 P.M.), -10° C (10 P.M.), -18° C (1 A.M.), -18° C (7 A.M.), and under conditions of light at -18° C (8 A.M.), -10° C (10 A.M.), 0° C (12 N), and 10° C (2 P.M.). Thus, the experimental photoperiod consisted of 9 hours of light (8 A.M. to 5 P.M.) and 15 hours of darkness; this photoperiod approximated the photoperiod of the winter-acclimatized doves, which averaged 9 hours and 27 minutes of daylight, i.e., 7:15 A.M. (sunrise) to 4:52 P.M. (sunset).

The birds were not fed during the 2 days of experimental cycles. The range of experimental ambient temperatures, the photoperiod, and the absence of food were designed to simulate the exposure of wild doves to a winter storm (i.e., a sharp decrease in temperature accompanied by snow or glaze, or both, which could prevent the obtainment of food by the doves). The doves thus entered the second cycle (at darkness) of decreasing ambient temperatures in a 24-hour fasted state.

Initial body weights of doves were recorded from birds with moderately full crops, whereas final weights were taken after the doves had been fasted throughout the 44-hour experiment. The rates of oxygen consumption were computed for each dove at

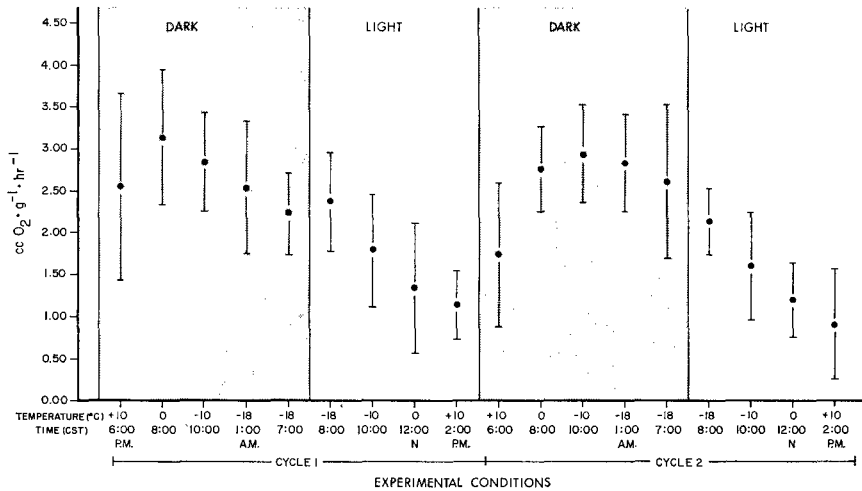


FIG. 1. Oxygen consumption (STP) of all doves (20) during the 44-hour experiment. Circles denote means; vertical lines designate standard deviations.

each test interval after adjustment had been made for a linear loss in body weight between the beginning and end of the 44-hour experiment. Hence, only metabolic rates of doves that survived the experiment, as well as a 24-hour postexperimental period, are reported in this paper; furthermore no individual dove was subjected to an experimental trial more than once during the course of study. The decision to use a linear projection

TABLE 1
MEAN BODY WEIGHTS (G) OF WILD, CAPTIVE DOVES BEFORE AND AFTER EXPOSURE TO 44 HOURS OF EXPERIMENTAL AMBIENT TEMPERATURES WITHOUT FOOD

Age and Sex	Number	Initial Weight (g)	Final Weight (g)	Weight Loss	
				(g)	Percent
Juvenile males	3	136.8 ± 17.3 ^a	106.1 ± 3.1	30.7 ± 3.1	22.4 ± 2.3
Juvenile females	7	128.9 ± 7.5 ^b	98.6 ± 7.5	30.8 ± 5.8	23.5 ± 4.5
Adult males	3	143.9 ± 7.6 ^{b,c,d}	112.7 ± 7.4 ^f	31.2 ± 1.3	21.7 ± 0.9
Adult females	7	130.2 ± 4.0 ^c	102.2 ± 3.9 ^f	28.0 ± 3.6	21.5 ± 2.8
All males	6	140.4 ± 10.5 ^e	109.4 ± 10.5	31.0 ± 2.1	22.1 ± 1.5
All females	14	129.6 ± 6.9 ^{d,e}	100.4 ± 8.9	29.2 ± 5.6	22.5 ± 4.3
All juveniles	10	131.3 ± 9.4	100.8 ± 10.1	30.4 ± 4.8	23.2 ± 3.7
All adults	10	134.3 ± 8.1	105.4 ± 7.6	29.0 ± 3.1	21.6 ± 2.3

^a Standard deviation.

^{b,c,d,e,f} All combinations of means, within columns, were tested for significant differences by *t* analyses; those means followed by the same letter are significantly different ($P < 0.05$).

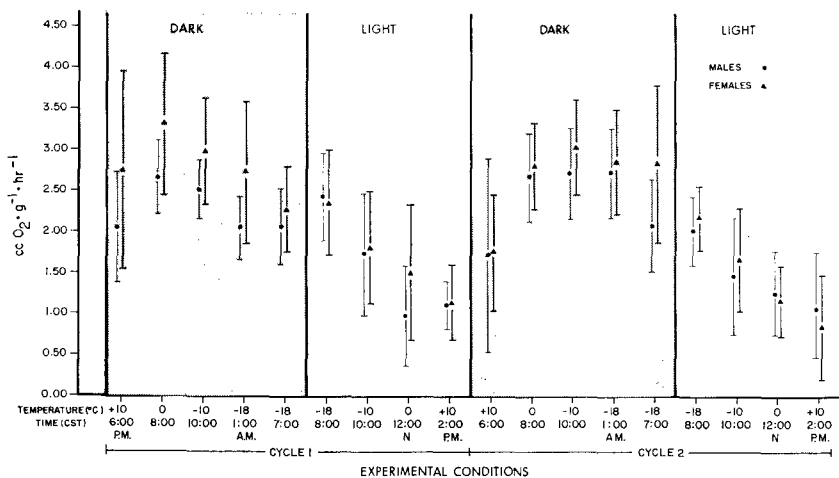


FIG. 2. Comparison of oxygen consumption (STP) of six males (three adults, three juveniles) with 14 females (seven adults, seven juveniles). Symbols denote means; vertical lines designate standard deviations.

of weight loss was considered valid, inasmuch as the weight losses for the doves studied averaged (with attending standard deviations) 18.0 ± 3.6 g and 29.7 ± 4.1 g after 29 and 44 hours of experimentation, respectively. Those metabolic rates measured before the effects of fasting were operative—specifically during the first four test intervals of the first cycle—are the products of counterbalancing factors; the reduction in rates due to those contributions to body weight attributable to metabolically inert components, such as crop contents and alimentary wastes, are principally offset by an increase in rates through specific dynamic action resulting from digestion. The rationale of counterbalancing factors was substantiated by the finding that the overall consumption of oxygen by doves during the first cycle did not differ significantly ($P > 0.05$) from that during the second cycle.

Temperatures in the cloaca and in the pectoral muscle of two doves were measured simultaneously, at each test interval during the 44-hour experiment, with 30-gauge copper-constantan thermocouples, and recorded to the nearest 0.1° C on a battery-operated potentiometer.

The null hypothesis, in all tests for determination of statistical significance, was accepted or rejected at the 0.05 level of probability. When *t* analyses were used to test for differences between means, appropriate adjustments were made for unequal samples and dissimilar variances.

RESULTS

Weight losses.—The initial mean weights of males, 140.4 g, were 8 percent heavier than those of females, 129.6 g (Table 1). Body weights of adults were similar to those of juveniles, averaging 134.3 g and 131.3 g, respectively. Among specific sex and age groups, significant differences in body weight

TABLE 2

MEAN OXYGEN CONSUMPTION cc O₂ (g body weight)⁻¹·hour⁻¹ OF DOVES AT THE DIFFERENT AMBIENT TEMPERATURES TO WHICH THE BIRDS WERE EXPOSED WITHOUT FOOD DURING THE 44 HOURS OF EXPERIMENTATION. OXYGEN MEASUREMENTS ARE CORRECTED FOR STP.

Age and/ or Sex	Time (CST) Temp °(C)	6 P.M.	8 P.M.	10 P.M.	1 A.M.	7 A.M.	8 A.M.	10 A.M.	12 N	2 P.M.
		10	0	-10	-18	-18	-18	-10	0	10
Cycle 1										
Juvenile males (n = 3)		1.57 (0.36)*	2.66 (0.69)	2.42 (0.51)	1.90 (0.49)	2.00 (0.63)	2.18 (0.62)	1.42 (0.17)	0.79 (0.69)	0.87 (0.16)
Juvenile females (n = 7)		3.36 (1.11)	3.44 (1.09)	3.00 (0.80)	2.29 (0.47)	2.21 (0.41)	2.30 (0.57)	1.79 (0.72)	1.89 (0.93)	1.33 (0.42)
Adult males (n = 3)		2.58 (0.49)	2.71 (0.17)	2.64 (0.17)	2.23 (0.17)	2.14 (0.33)	2.68 (0.37)	2.04 (0.76)	1.18 (0.57)	1.35 (0.13)
Adult females (n = 7)		2.18 (1.04)	3.20 (0.61)	2.95 (0.49)	3.16 (0.96)	2.21 (0.63)	2.41 (0.74)	1.82 (0.69)	1.10 (0.45)	0.96 (0.45)
All juveniles (n = 10)		2.83 (1.26)	3.21 (1.02)	2.83 (0.75)	2.17 (0.49)	2.15 (0.47)	2.26 (0.55)	1.68 (0.70)	1.56 (0.98)	1.18 (0.41)
All adults (n = 10)		2.30 (0.90)	3.05 (0.56)	2.86 (0.44)	2.89 (0.91)	2.19 (0.54)	2.49 (0.64)	1.88 (0.68)	1.13 (0.46)	1.08 (0.41)
All males (n = 6)		2.08 (0.67)	2.68 (0.45)	2.53 (0.36)	2.06 (0.38)	2.07 (0.46)	2.43 (0.53)	1.73 (0.74)	0.98 (0.61)	1.11 (0.29)
All females (n = 14)		2.77 (0.12)	3.32 (0.86)	2.98 (0.64)	2.72 (0.86)	2.28 (0.51)	2.35 (0.64)	1.81 (0.68)	1.50 (0.82)	1.14 (0.46)
All doves (n = 20)		2.56 (1.10)	3.13 (0.81)	2.84 (0.60)	2.52 (0.80)	2.21 (0.49)	2.37 (0.59)	1.78 (0.67)	1.34 (0.78)	1.13 (0.41)

occurred between adult males and juvenile females and between adult males and adult females, the males being heavier than the females.

Weight losses among doves exposed to the 44-hour experimental trial without food were similar both between ages and sexes (Table 1). Interestingly, proportionate weight losses among the sex and age groups were the lowest and least variable for adult males, and the greatest and most variable for juvenile females; the difference, however, was not statistically significant.

Metabolic expenditures.—The doves did not progressively increase their oxygen consumption (and hence, metabolic expenditures) as ambient tem-

TABLE 2—Continued

Age and/ or Sex	Time (CST) Temp. °(C)	6 P.M.	8 P.M.	10 P.M.	1 A.M.	7 A.M.	8 A.M.	10 A.M.	12 N	2 P.M.	Mean Sums
		10	0	-10	-18	-18	-18	-10	0	10	
Cycle 2											
Juvenile males (n = 3)		1.29 (0.50)	2.36 (1.05)	2.40 (0.48)	2.50 (0.32)	2.07 (0.72)	1.79 (0.34)	1.61 (1.09)	1.39 (0.32)	1.33 (0.95)	32.50 ^{b,c} (5.62)
Juvenile females (n = 7)		2.01 (0.63)	2.89 (0.43)	3.39 (0.61)	3.21 (0.72)	3.13 (1.18)	2.10 (0.44)	1.55 (0.63)	1.34 (0.43)	0.65 (0.45)	42.18 ^{b,d} (4.42)
Adult males (n = 3)		2.14 (1.64)	3.00 (0.65)	3.03 (0.50)	3.00 (0.63)	2.11 (0.51)	2.25 (0.38)	1.32 (0.03)	1.12 (0.71)	0.81 (0.32)	38.33 (5.34)
Adult females (n = 7)		1.51 (0.75)	2.72 (0.62)	2.68 (0.24)	2.58 (0.26)	2.55 (0.62)	2.26 (0.36)	1.77 (0.67)	0.97 (0.36)	0.89 (0.59)	37.86 (5.05)
All juveniles (n = 10)		1.79 (0.66)	2.73 (0.44)	3.10 (0.73)	2.99 (0.70)	2.81 (1.14)	2.01 (0.42)	1.57 (0.72)	1.36 (0.38)	0.95 (0.80)	39.28 (6.48)
All adults (n = 10)		1.70 (1.05)	2.80 (0.60)	2.79 (0.35)	2.67 (0.43)	2.42 (0.60)	2.26 (0.35)	1.64 (0.59)	1.02 (0.45)	0.87 (0.50)	38.00 (4.35)
All males (n = 6)		1.72 (1.18)	2.68 (0.54)	2.72 (0.56)	2.74 (0.53)	2.09 (0.56)	2.02 (0.41)	1.47 (0.71)	1.26 (0.51)	1.07 (0.69)	35.42 ^d (5.81)
All females (n = 14)		1.76 (0.46)	2.81 (0.71)	3.04 (0.58)	2.86 (0.63)	2.84 (0.95)	2.18 (0.39)	1.66 (0.63)	1.16 (0.43)	0.84 (0.64)	40.02 ^c (4.80)
All doves (n = 20)		1.74 (0.85)	2.77 (0.51)	2.94 (0.58)	2.83 (0.59)	2.61 (0.91)	2.13 (0.40)	1.60 (0.64)	1.19 (0.44)	0.91 (0.65)	38.64 (5.42)

^a Standard deviation.

^{b,c,d} All combinations of mean sums were tested for significant differences by *t* analyses; those followed by the same letter are significantly different ($P < 0.05$).

peratures decreased from 10° to -18° C during the first cycle (Figs. 1-3; Table 2). The greatest oxygen consumption by doves occurred at 0° C of the first cycle, i.e., during the first exposure to a decreasing temperature gradient and darkness. Oxygen consumption decreased successively at -10°, at -18° C, and during the holding period of 7 hours at -18° C in darkness. Oxygen consumption increased slightly at -18° C after the lights were turned on at 08:00, but then decreased progressively in response to the steadily increasing temperature gradient (-10° C to 10° C) during the subsequent 6 hours. Oxygen consumption during the second experimental cycle followed a pattern similar to that observed during the first cycle (Figs. 1-3; Table 2).

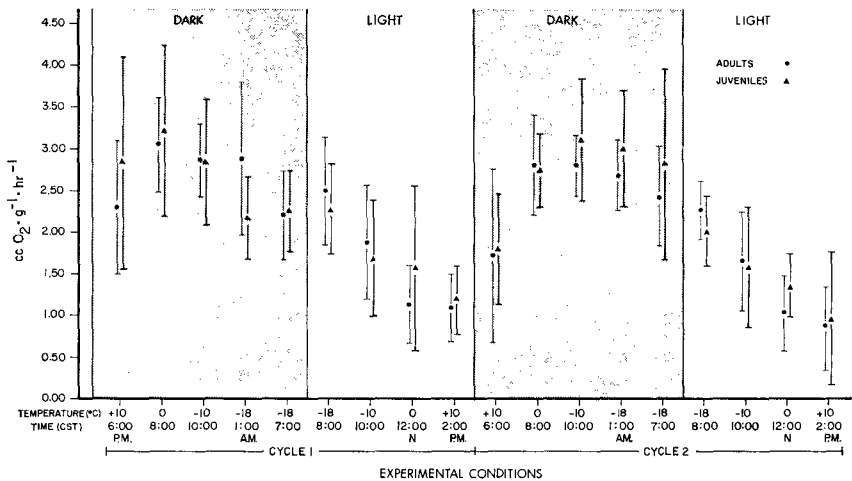


FIG. 3. Comparison of oxygen consumption (STP) of 10 adults (three males, seven females) with 10 juveniles (three males, seven females). Symbols denote means; vertical lines designate standard deviations.

In fact, among the nine measurement periods common to both cycles, the mean consumption of oxygen by doves, sex and age ignored, differed significantly ($P < 0.05$) only under conditions of darkness at 10°C , i.e., the first test of each cycle. In the final analysis, however, there was no significant difference ($P > 0.05$) between the total consumption of oxygen by doves during the first and second cycles. The diurnal pattern of oxygen consumption by the doves subjected to this experiment is best described by a non-linear model (Fig. 4).

The differences between the rates of oxygen consumption during darkness and a decreasing temperature gradient (excluding the measurement at -18°C , 7 A.M.) and those during light and an increasing temperature gradient were significant ($P > 0.05$) for both cycles, singly and combined. In fact, the rates of oxygen consumption, all doves and both cycles considered, differed significantly ($P < 0.05$) for each test temperature (10° , 0° , -10° , and -18°C) between conditions of darkness and light, being greater in darkness in all cases; the direction of the temperature gradient was ignored in these comparisons. These observations suggested that the rate of oxygen consumption was influenced either by light or by the direction of the temperature gradient, or both.

To investigate the relationship of light and ambient temperature to metabolic expenditures, three birds (juvenile males) were tested under a reverse

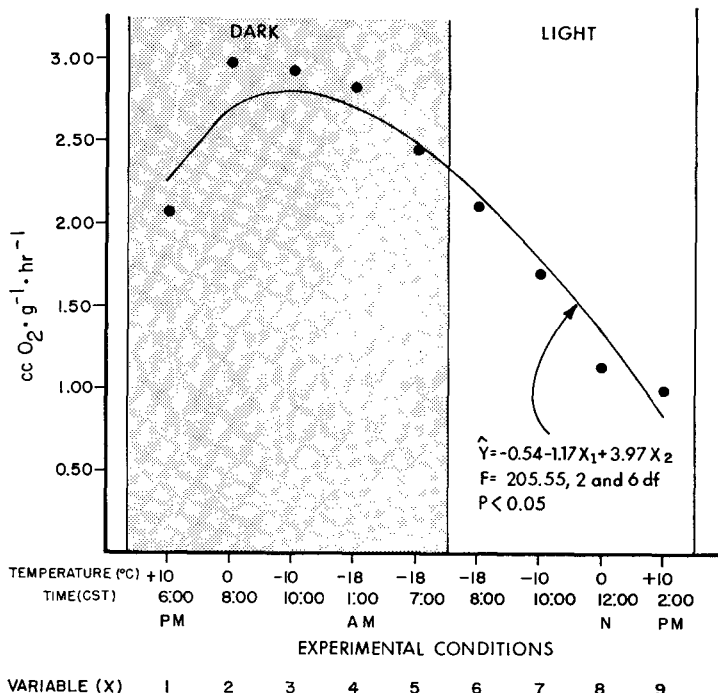


FIG. 4. Diurnal pattern of oxygen consumption (STP) of all doves (20) subjected to a simulated 2-day winter storm in the absence of food; cycles 1 and 2 were combined for this analysis. These data yielded significant departures from linearity ($P < 0.05$).

cycle of light and temperature; that is, temperatures were decreased during light and increased during darkness. These birds showed the same pattern of response to increasing and decreasing temperatures as those juvenile males functioning in the light-temperature conditions of the standard experimental trial employed in this study (Fig. 5). Oxygen consumption by these doves differed significantly ($P < 0.05$) between conditions of light and decreasing temperatures and those of darkness and increasing temperatures, being greater under the former conditions. These findings indicated that the metabolic expenditures of doves were more in response to ambient temperatures than to light. However, an increased response to light is indicated by the greater oxygen consumption during the period of decreasing temperatures and light of this particular test, when compared with the period of decreasing temperatures and darkness of the standard test; this difference was statistically significant also ($P < 0.05$). This latter response reflects the additive effects of light and decreasing temperature on metabolic rates.

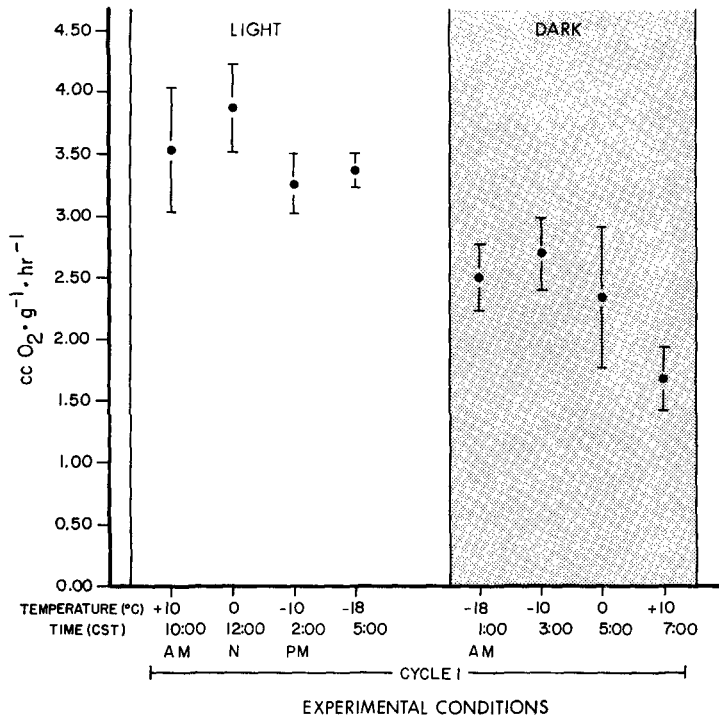


FIG. 5. Oxygen consumption (STP) of three, juvenile male doves subjected to 20 hours of a reversed light-temperature gradient (temperature decreased during light, increased during darkness). Circles denote means; vertical lines designate standard deviations.

The patterns of metabolic responses of doves exposed both to increasing and to decreasing ambient temperatures were related strongly to the direction of the ambient temperature gradient, and not just to temperature per se (Figs. 1-4). In fact, once the directional gradient of either increasing or decreasing ambient temperature was operative, the metabolic responses of the doves were seemingly in anticipation of continuing predictive changes along the thermal gradient.

Female doves had rates of oxygen consumption that exceeded those of males in 15 of 18 tests, but the overall difference between the sexes was not statistically significant (Table 2; Fig. 2). Neither was the rate of oxygen consumption by juveniles significantly different from that of adults. However, rates of oxygen consumption by juvenile males were significantly different—in this case, lower—from juvenile females and from all females, age ignored (Table 2).

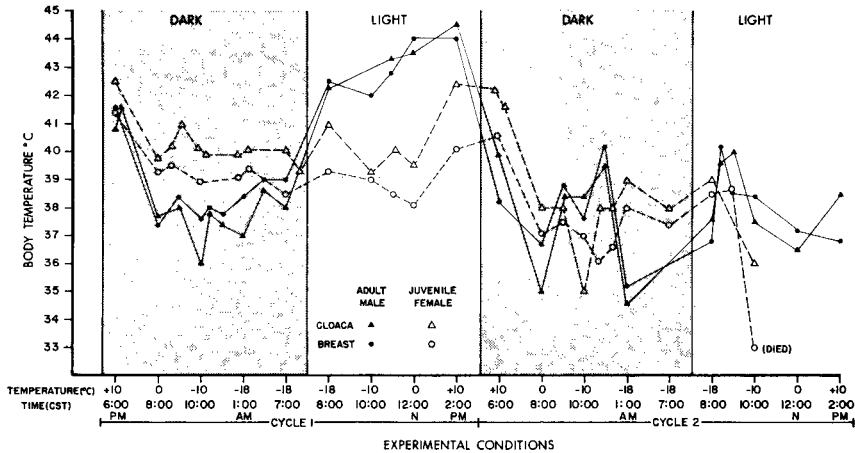


FIG. 6. Cloacal and pectoral temperatures of two doves, fitted with thermocouples, during the 44-hour experiment.

An analysis of variance, testing the mean sums of oxygen consumption at the 18 test temperatures by sex and age groups, revealed a significant interaction between sex and age ($P < 0.05$), although neither the difference due to sex alone nor to age alone was significant ($P > 0.05$).

Body temperature.—Our measurements of body temperature of doves, being limited to one adult male and one juvenile female, were meager. The adult male, however, exhibited noticeably greater flexibility than the juvenile female in reducing body temperature under conditions of declining ambient temperatures, and in increasing body temperature under conditions of ascending ambient temperatures (Fig. 6). Furthermore, the thermoregulatory ability of the juvenile female appeared to decline rapidly after 36 hours of exposure to the simulated winter storm, in the absence of food. The cloacal temperature of the adult male ranged from 34.5° to 44.5° C, whereas that of the juvenile female ranged from 35.2° to 42.5° C. The normal daytime body temperature of a resting Mourning Dove is 41.5° C; the nighttime temperature is about 2 degrees lower (Bartholomew and Dawson, 1954).

The relationship between body temperature and oxygen consumption was principally inverse for the doves exposed to the conditions of this experiment (Figs. 1–6), which propounded the presence of a compensatory feedback mechanism.

Survival ability.—Several doves were deliberately exposed to the previously described experimental cycles until they succumbed. Two juvenile males died after 36 and 67 hours of experimentation, losing, respectively, 31.7 g (24.3

percent) and 42.4 g (30.4 percent) of their initial body weight. Two adult females died after 62 and 72 hours of exposure, with respective weight losses of 32.7 g (26.8 percent) and 35.6 g (28.0 percent). One adult male lost 48.2 g (33.5 percent) prior to death after 108 hours of exposure.

DISCUSSION

Although many investigators have studied the effects of lowered ambient temperature on metabolic rates and body temperatures of birds (Kendeigh, 1944; Steen, 1957; Dawson, 1958; Misch, 1960; Hart, 1962; and Pohl, 1969), most have used a series of stable temperatures to measure the metabolic rates; only a few workers have measured metabolic rates under conditions of fluctuating ambient temperatures (Veghte, 1964; Pohl, 1969).

This study was designed specifically to measure the short-term metabolic responses of winter-acclimatized Mourning Doves to the food and temperature stresses placed on them by a simulated winter storm. Oxygen consumption was measured as ambient temperatures were decreased progressively from 10° C to -18° C in darkness, and then increased progressively to 10° C in light during each day of a 2-day experiment; food was not available to the doves during the 44-hour experimental trial.

The doves, under the prescribed experimental conditions, showed a greater metabolic response to directional gradients of either increasing or decreasing ambient temperatures than to actual temperatures. The rate of oxygen consumption was greater, and significantly different ($P < 0.05$), under a decreasing temperature gradient and darkness than under an increasing temperature gradient and light (Figs. 1-4). Furthermore, the rate of oxygen consumption by doves exposed to cycles of decreasing temperature and light and of increasing temperature and darkness, conditions opposite of those in the standard cycles, was dependent principally on ambient temperature gradients and not on light (Fig. 5). Thus, we concluded that rising or falling temperature gradients had a greater effect on oxygen consumption, under the experimental conditions of this study, than did either ambient temperatures per se or light.

The doves in this study did not exhibit the usual straight-line dependency between metabolic rates and decreasing ambient temperatures as reported for small birds by other investigators (Kendeigh, 1944; Seibert, 1949; Dawson and Tordoff, 1959; Misch, 1960; and West, 1962). In the present study, doves showed an increase in oxygen consumption as ambient temperatures decreased from 10° C to -10° C in darkness (Fig. 4), but then showed a decrease in oxygen consumption as the temperature decreased to -18° C and as the duration of exposure to the latter temperature increased. Thus,

we believe that Mourning Doves, when exposed to the stresses of low ambient temperatures and the absence of food during winter, possess a physiological mechanism that allows them to substantially reduce their body temperature and, correspondingly, their metabolic expenditures. These conclusions are supported by the findings of R. F. Labisky (unpubl. rept.) and Hudson and Brush (1964), who studied the metabolic requirements and body temperatures of Mourning Doves in response to decreasing ambient temperatures. Labisky showed lower metabolic rates at 4° C and -1° C than at 10° C in three species of winter-acclimatized small birds, including the Mourning Dove. Although such a pattern of decreased oxygen consumption might be interpreted as indicative of exhausted glucose reserves, Labisky, after testing the birds at 4° C and -1° C, restored the ambient temperature to 10° C and found that the metabolic rate of the doves reverted to its earlier value at the same temperature; the decrease in oxygen consumption at low ambient temperatures was therefore not attributable to a depletion of energy reserves. Labisky hypothesized that the apparent mechanism that allowed the doves and other small birds to reduce their body temperature and metabolic requirements when ambient temperatures were frigid and food was scarce would have positive survival benefits to the species so exposed to winter adversities.

Hudson and Brush (1964) reported that metabolic expenditures, body temperatures, and cardiac rates of Mourning Doves were lowered when the birds were subjected to reduced ambient temperatures. They therefore concluded that below the lower critical temperature (30° C) for the dove, body temperature decreased with a resultant decrease in the value of thermal conductance; hence, a conservation of metabolic effort was executed. (Thermal conductance is the metabolic rate divided by the difference between the body temperature and the ambient temperature: $C = MR/T_B - T_A$.)

All the physiological measurements that we recorded for the doves subjected to simulated winter storms, i.e., low ambient temperatures coupled with the absence of food, suggested that Mourning Doves wintering in the northern regions of the U.S. possessed sex- and age-associated differences as regards their potential survival ability. To illustrate, among the four sex and age groups of doves exposed to the 44-hour experimental trial, adult males were initially the heaviest and proportionately lost the least body weight, whereas juvenile females were the lightest and lost proportionately the most weight (Table 1). And in the endurance tests, heavier doves, in general, survived longer than lighter doves; one adult male, the heaviest dove subjected to the endurance tests, survived 108 hours of testing prior to death, or 38 hours longer than his nearest competitor. Observations, though only meagerly substantiated, hinted that adult doves possessed a greater ability to thermoregulate

under conditions of alternately decreasing and increasing ambient temperatures (Fig. 6)—thereby conserving energy—than did juveniles. Therefore, adult doves (particularly males) because of the influence of age or superior weight, or both, seemed better equipped physiologically than juveniles (particularly females) to withstand the rigors of northern winters.

These findings of differences in the survival abilities of doves offer a potential explanation for the changes in sex and age structure that occur among flocks of doves wintering north of their normal winter range. To illustrate, Chambers et al. (1962), who studied flocks of doves wintering in northern Missouri, found that between November and March, changes in age ratios favored adults and changes in sex ratios favored males. Explanations for changes in sex and age structure among such wintering flocks of doves have included: a higher autumnal migration rate among juveniles than among adults (Austin, 1951; Tomlinson et al., 1960); a greater attachment to northern breeding sites by adults than by juveniles (Chambers et al., 1962); a greater tendency for males to winter farther north than do females (Quay, 1951); and a higher mortality rate among juveniles than among adults (Austin, 1951). Our findings indicate that one of the major factors contributing to the skewness toward males in sex ratios and toward adults in age ratios among flocks of Mourning Doves wintering in the northern U.S. is related to physiological differences in the survival ability among doves of different sex and age.

SUMMARY

Winter-acclimatized Mourning Doves were subjected to a photoperiod and an ambient temperature range designed to simulate conditions of a severe winter storm, common to central Illinois. Metabolic rates were recorded for two daily cycles of decreasing temperatures (10° C to -18° C) in darkness and increasing temperatures (-18° C to 10° C) in light; the doves were fasted throughout the 44-hour experiment.

Juvenile doves had higher metabolic rates than adults, and females had higher rates than males, but neither difference was statistically significant ($P > 0.05$). The metabolic rates of doves were greater during exposure to decreasing ambient temperatures and darkness than during exposure to increasing ambient temperatures and light, the difference being statistically significant ($P < 0.05$). The doves responded metabolically more to the directional temperature gradient than to either actual ambient temperature or light.

The consumption of oxygen by doves did not follow a straight-line increase with concurrent declines in ambient temperatures. Oxygen consumption was not only less at -18° C than at -10° C (in darkness), but also diminished with extended exposure at -18° C. These observations suggested that Mourning Doves employed a physiological mechanism (perhaps reduced body temperature) to decrease their metabolic expenditures at low ambient temperatures; the mechanism permits the conservation of energy and thus augments survival.

The potential survival ability of doves exposed to simulated winter storms was related

to sex and age attributes. Adult doves (particularly males), because of their age or greater weight, or both, were better equipped physiologically than juveniles (particularly females) to survive the stresses of low ambient temperatures without food. Thus, among Mourning Doves wintering in the northern and central U.S., the autumn-to-spring changes in sex ratios and in age ratios, which usually favor males and adults, respectively, probably reflect the differential survival abilities of the sex and age cohorts.

ACKNOWLEDGMENTS

Sincere appreciation is extended to the staff of the Max McGraw Wildlife Foundation, Dundee, Illinois, for their assistance in capturing the doves for study. S. Charles Kendeigh, University of Illinois, Urbana, and Sheldon Lustick, The Ohio State University, Columbus, generously offered advice on the technical presentation of the findings. Helen C. Schultz and Glen C. Sanderson, Illinois Natural History Survey, Urbana, offered editorial suggestions.

LITERATURE CITED

- AUSTIN, O. L., JR. 1951. The Mourning Dove on Cape Cod. *Bird-Banding*, 22:149-174.
- BARTHOLOMEW, G. A., JR., AND W. R. DAWSON. 1954. Body temperature and water requirements in the Mourning Dove, *Zenaidura macroura marginella*. *Ecology*, 35: 181-187.
- CHAMBERS, G. D., H. M. WIGHT, AND T. S. BASKETT. 1962. Characteristics of wintering flocks of Mourning Doves in Missouri. *J. Wildl. Mgmt.*, 26:155-159.
- CHANGNON, S. A., JR. 1969. Climatology of severe winter storms in Illinois. *Illinois State Water Surv. Bull.* 53.
- DAWSON, W. R. 1958. Relation of oxygen consumption and evaporative water loss to temperature in the Cardinal. *Physiol. Zoöl.* 31:37-48.
- DAWSON, W. R., AND H. B. TORDOFF. 1959. Relation of oxygen consumption to temperature in the Evening Grosbeak. *Condor*, 61:388-396.
- HANSON, H. C., AND C. W. KOSSACK. 1963. The Mourning Dove in Illinois. *Illinois Dept. Conserv. Tech. Bull. No. 2*.
- HART, J. S. 1962. Seasonal acclimatization in four species of small wild birds. *Physiol. Zoöl.*, 35:224-236.
- HUDSON, J. W., AND A. H. BRUSH. 1964. A comparative study of the cardiac and metabolic performance of the dove, *Zenaidura macroura*, and the quail, *Lophortyx californicus*. *Comp. Biochem. Physiol.*, 12:157-170.
- KENDEIGH, S. C. 1944. Effect of air temperature on the rate of energy metabolism in the English Sparrow. *J. Exp. Zool.*, 96:1-16.
- MCCLURE, H. E. 1943. Ecology and management of the Mourning Dove, *Zenaidura macroura* (Linn.), in Cass County, Iowa. *Iowa Agr. Exp. Sta. Res. Bull.* 310: 355-415.
- MISCH, M. S. 1960. Heat regulation in the Northern Blue Jay, *Cyanocitta cristata bromia* Oberholser. *Physiol. Zoöl.*, 33:252-259.
- POHL, H. 1969. Some factors influencing the metabolic response to cold in birds. *Federation Proc.*, 28:1059-1064.
- QUAY, T. L. 1951. Mourning Dove studies in North Carolina. *North Carolina Wildl. Resources Comm.*
- SEIBERT, H. C. 1949. Differences between migrant and non-migrant birds in food and water intake at various temperatures and photoperiods. *Auk*, 66:128-153.

- STEEN, J. 1957. Food intake and oxygen consumption in pigeons at low temperatures. *Acta Physiol. Scandinavica*, 39:22-26.
- TOMLINSON, R. E., H. M. WIGHT, AND T. S. BASKETT. 1960. Migrational homing, local movement, and mortality of Mourning Doves in Missouri. *Trans. 25th N. Amer. Wildl. and Nat. Resources Conf.*, 253-266.
- VECHTE, J. H. 1964. Thermal and metabolic responses of the Gray Jay to cold stress. *Physiol. Zoöl.*, 37:316-328.
- WEST, G. C. 1962. Responses and adaptations of wild birds to environmental temperature. *In Comparative Physiology of Temperature Regulation, Part 3*, J. P. Hannon and E. Viereck (Ed.) *Arctic Aeromed. Lab.*, pp. 291-333.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF ILLINOIS, URBANA, ILLINOIS (PRESENT ADDRESS: DEPARTMENT OF BIOLOGICAL SCIENCES, ROCK VALLEY COLLEGE, ROCKFORD, ILLINOIS 61111) AND SECTION OF WILDLIFE RESEARCH, ILLINOIS NATURAL HISTORY SURVEY, URBANA, ILLINOIS 61801, 25 MAY 1972.

ANNOUNCEMENT

The Nuttall Ornithological Club is sponsoring a symposium, "Avian Energetics," as part of its centennial celebration. This symposium will be presented on 10 October 1973 in conjunction with the 91st Stated Meeting of the American Ornithologists' Union at Provincetown, Cape Cod, Massachusetts. Speakers will include Robert E. Ricklefs (reproductive strategies of birds in relation to energetics), William A. Calder (energetics and size in birds), James R. King (seasonal allocation of energy resources by birds), and Vance A. Tucker (energetics of avian flight). George A. Bartholomew, S. Charles Kendeigh, and Eugene P. Odum will participate as discussants. The symposium has been organized and will be chaired by William R. Dawson. The entire symposium will be published by the Nuttall Club. For further information contact: Nuttall Ornithological Club, c/o Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.