

THERMOREGULATORY BEHAVIOR OF ROCK DOVES ROOSTING IN THE NEGEV DESERT

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Abstract.—Free-living Rock Doves (*Columba livia*) were observed roosting throughout the day on ledges in a canyon in the Negev Desert. Potential thermoregulatory behaviors were recorded, including movement between sites in order to remain in the shade, the adoption of postures minimizing energy expenditure (and enhancing convective cooling), feather erection consistent with the cutaneous evaporation of water (and enhancing convective cooling) and elevated rates of blinking. These observations are consistent with recent laboratory studies on the heat balance of Rock Doves.

CONDUCTA DE TERMOREGULACIÓN EN INDIVIDUOS DE *COLUMBA LIVIA* EN EL DESIERTO DE NEGEV

Sinopsis.—Individuos silvestres de *Columba livia* fueron observados a través de las horas del día, mientras descansaban en salientes de un cañón del Desierto de Negev. Se tomó información sobre conducta potencial de termoregulación, que incluyó movimiento entre localidades para permanecer en el cobijo de la sombra, posturas para minimizar el gasto energético, (y mejorar el enfriamiento por convección), erección del plumaje en consistencia con la evaporación de agua cutánea (y mejorando el enfriamiento por convección) y una tasa elevada de parpadeo. Estas observaciones son consistentes con estudios recientes de laboratorio sobre el balance de calor en estas palomas.

The Rock Dove (*Columba livia*) possesses a wide repertoire of efficient cooling mechanisms and these enable it to survive and breed at temperatures that are lethal to some desert species. For example, a successful breeding colony was found by Marder and Gavrieli-Levin (1986) where the ambient temperature regularly exceeded 50 C in the middle of the day. After acclimation in the laboratory, these birds were able to maintain egg temperatures below 42 C during regular daily exposures of 4–6 h at 50–60 C (Arieli et al. 1988). Chukar Partridges (*Alectoris chukar*) cannot survive such temperatures for more than an hour or two (Marder 1983).

When ambient temperature is lower than body temperature, birds can cool by convection and by the evaporation of water from the respiratory tract, provided the relative humidity is sufficiently low. Convective heat loss is enhanced in pigeons by holding the wings out from the body and exposing the thinly feathered areas beneath (Butler et al. 1977, Hart and Roy 1967). Rapid shallow breathing (panting) and gular fluttering are employed to increase evaporative water loss from the upper respiratory tract and the pharynx/anterior oesophagus respectively (Ramirez and Bernstein 1976). Auricular feather erection may be used to facilitate the flow of heat away from the rita mirabile ophthalmicum (Gaunt 1980) thus enhancing brain cooling. Evaporation and convection from the corneal surface (Pinshow et al. 1982) and the buccopharyngeal mucosa (Bernstein

et al. 1979) can achieve the same effect. Heat loss also occurs in the Barbary Dove (*Streptopelia risoria*) from the inflatable oesophageal chamber via a special venous plexus in the subcutaneous tissue (Gaunt 1980). Apparently, this type of cooling does not occur in the Rock Dove even though it has a similar venous plexus (Zurovsky and Laburn 1987).

Most impressive of all, pigeons show efficient cutaneous evaporation of water (Smith and Suthers 1969), with as much as $14 \text{ mg H}_2\text{O g}^{-1} \text{ body weight h}^{-1}$ being lost by this route (74% of total water loss) at an ambient temperature of 35 C (Smith 1969, cited in Dawson 1984), at least in distressed birds. In unstressed birds, a cutaneous water loss of $1.7 \text{ mg H}_2\text{O g}^{-1} \text{ h}^{-1}$ occurred at temperatures of only 20 and 36 C, but rose to $6 \text{ mg H}_2\text{O g}^{-1} \text{ h}^{-1}$ at 40 C (Marder and Ben-Asher 1983). It is cutaneous water loss which is most important in enabling pigeons to acclimatize to environmental temperatures of 60 C (Marder and Arieli 1988, Marder and Gavrieli-Levin 1987).

Undisturbed non-incubating pigeons in the laboratory sometimes raise the back and rump feathers. Marder and Gavrieli-Levin (1987) and Marder and Arieli (1988) suggested that this opened up an avenue for water vapor movement from what was, on the basis of their measurements, the most intensive evaporating zone. Moore (1945) was one of the first to point out that elevated feathers were characteristic of very hot birds, though McFarland and Baher (1968) suggested that this kind of behavior in the laboratory was an artifact produced by the use of bright lights. Such feather postures have since been recorded for a number of species e.g., some sandgrouse, gulls, waders, coursers and falcons (Bartholomew and Dawson 1979, Simmons 1986, Thomas and Robin 1977), but it is not known in these cases whether it is associated with convective heat loss alone or in combination with cutaneous evaporation of water.

The present observations were made on roosting Rock Doves in the wild to determine what, if any, behavioral means were used to regulate temperature and to see if the feather postures associated with temperature control through convective heat loss and cutaneous evaporation of water were included. These birds possessed the light grey plumage typical of Rock Doves from this part of the Middle East (Goodwin 1983), but included a range of rump colors from light grey to white.

STUDY AREA AND METHODS

Observations were made at a rocky canyon (Ein Avdat), 500 m above sea level at the Wadi Zin in the Negev Desert, Israel. In this area, several hundred Rock Doves feed for several hours after dawn and before dusk on the cultivated fields of the Sede Boqer kibbutz, and roost during the rest of the day and during the night on ledges in Ein Avdat. The ledges offer shade from the sun and a degree of security from predators. Water is available from springs at the bottom of the canyon 20 m away. By moving to and from the roost while the sun is relatively low in the sky, the birds minimize the risk of overheating while flying. The distance between the fields and the canyon is about 5 km.

Observations were made using a 25× telescope positioned at the head of the canyon from where about 200 birds were visible. After some initial practice, observations were collected for several hours on different days in July 1987 and continuously throughout the day on the 24th. These observations have been pooled except where otherwise indicated. Temperature and relative humidity were measured at hourly intervals using a sling psychrometer in the shade. Wind strength and direction were estimated subjectively at the same time. Following this, every clearly visible dove was examined and its posture or activity recorded as one or more of the following: standing (and whether on one leg or two), sitting (and whether the wings were slightly extended or not). It was also noted whether the bird was in shade or exposed to the sun. Feather postures on each region of the body (rump, neck, crown, and coverts plus scapulars) were scored as follows: normal sleeked position (0), individual feather outlines just discernable (1), feathers at an angle to the body of about 30° (2) or 60° (3). A sample of the closest birds was then chosen and the time taken for 10 inspiration/expiration cycles (as indicated by rhythmical expansion and contraction of the body) was measured. These observations took just under an hour to make. I was unaware of the possible importance of the oesophagus to heat loss at the time these observations were made and so I did not look for oesophageal pulsation, though it would probably have been difficult to distinguish in the field (Gaunt 1980, Baumel et al. 1983). An overall index of the intensity of thermoregulatory activity was derived by assuming that the rate of heat loss was roughly equal to the area of skin exposed in different areas of the body. These in turn were estimated (from measurements on a live domestic pigeon) to be in the proportions rump 4, neck 2, coverts 1, crown 1. This might appear to underestimate the area of skin on the neck, but allows for the fact that the neck is withdrawn in roosting birds and the rump protruded (Fig. 1). These values were multiplied by the appropriate feather erection scores and summed. An arbitrary score of three was assumed for the additional benefit of spreading the wings. Thus the maximum possible score for a bird with all these feathers fully erected and wings spread was 27. The value for each bird was then expressed as a percentage of this maximum.

RESULTS

While roosting, the general feather and body postures adopted by Rock Doves were consistent with the suggestion that they are designed to enhance convective heat loss and the cutaneous evaporation of water. As temperatures increased, the birds tended to sit down more and the general levels of feather erection increased (Fig. 2, Table 1). When the observations were divided into three temperature ranges (<35.0, 35.0–37.5, >37.5 C), significantly more birds had higher scores at higher temperatures for all three regions of the body (association χ^2 , rump = 43.1, neck = 75.9, crown = 23.4, coverts = 39.5, $P < 0.001$ in all cases). The most extreme postures occurred during the hottest parts of the day, or following exertion caused by disturbance or spontaneous movement. In these pos-

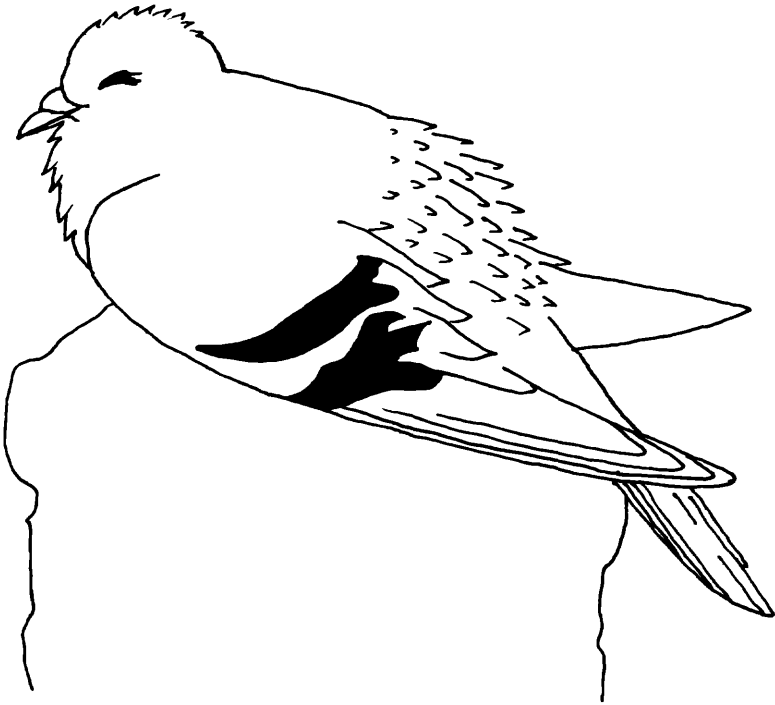


FIGURE 1. Rock Dove in roosting posture at high ambient temperature with splayed wings, drooping tail and elevated feathers on rump, neck, crown and scapular region.

tures, birds lay on the ledge with their tails flat on the ground and their rumps elevated (Fig. 1). The wings were also splayed out and allowed to rest on the ground. Although these postures are superficially similar to those employed when feather fluffing to increase insulation, as illustrated by Marder et al. (1989), they differ in that large gaps were opened up between the feathers. Such gaps existed on all the above mentioned regions of the body and the feathers were sometimes erected to an angle of 90°. Quite often, the tail was allowed to droop over the edge of the ledge, presumably to enhance air circulation. Wind was force 0–1 (Beaufort scale) throughout most of the day, but rose to 2–3 between 1800 and 1900 hours.

Above 35 C the increase in feather erection was particularly marked (Fig. 2). During the hottest part of the day, between 1400 and 1700 hours, about half of the birds were standing, but very few of them were standing on one leg compared with the rest of the day. Both legs thus provided potential avenues for heat loss at the time of highest ambient temperature. The remaining birds were sitting down, and these had, on average, significantly higher feather erection scores than those which were standing (median test, $\chi^2 = 23.3$ $P < 0.001$). This excludes birds that

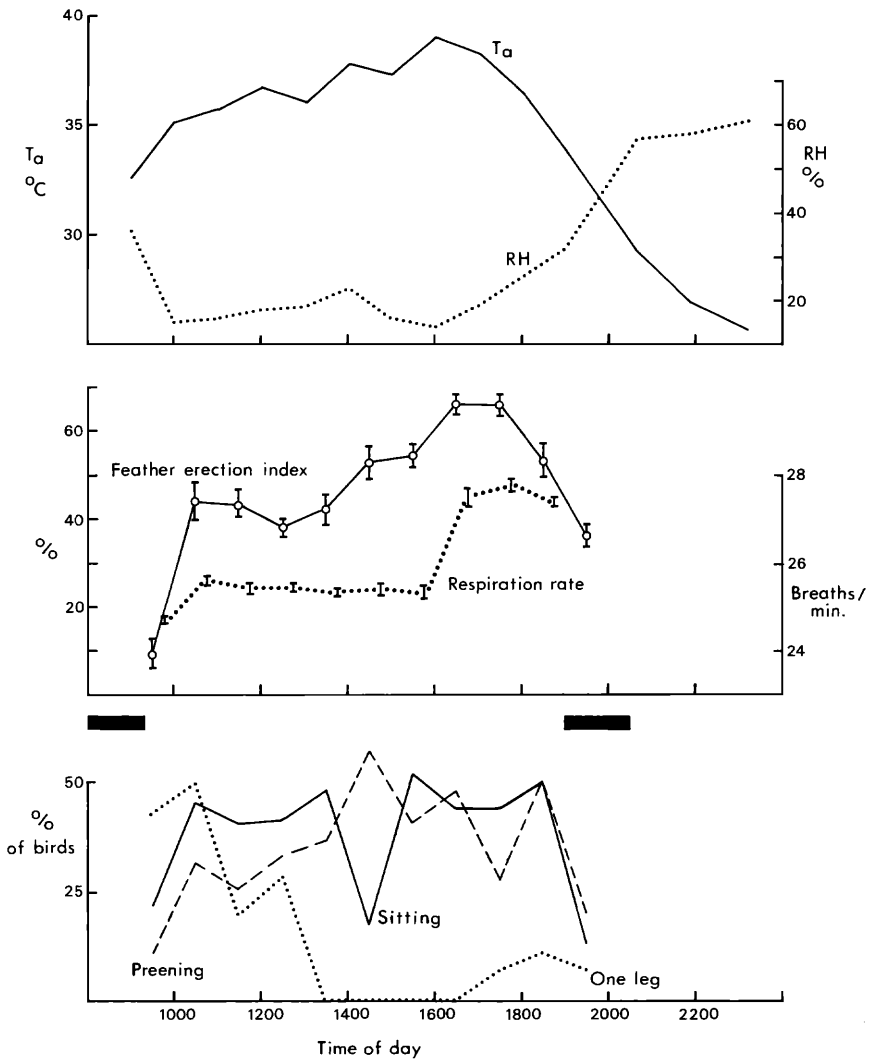


FIGURE 2. Variation in thermoregulatory behavior of roosting Rock Doves in relation to the time of day and ambient conditions. Temperature (T_a) and relative humidity (RH) are shown at the top, feather erection (%) and respiration (breaths/min) in the center, and the percentages of birds preening, sitting or standing on one leg at the bottom (the latter may sum to >100 because preening birds sometimes stood on one leg). The filled bars indicate the periods when the doves were arriving from, and departing to, the feeding areas.

TABLE 1. Average intensity of various cooling postures in the Rock Dove at different times of the day.

Time	Feather erection scores				Percentage of birds with wings spread
	Rump	Nape	Crown	Scapulars	
0900	0.19	0.13	0.00	0.00	50
1000	1.79	1.29	0.50	0.64	50
1100	1.45	1.30	0.60	0.75	73
1200	1.44	1.31	0.19	0.56	50
1300	1.47	1.59	0.35	0.65	54
1400	1.75	1.67	0.33	0.83	100
1500	1.81	1.63	0.25	1.06	100
1600	2.54	1.85	0.54	1.08	100
1700	2.11	2.22	1.00	1.06	100
1800	1.84	1.58	0.58	0.63	100
1900	1.00	1.08	0.17	0.42	100

were preening because the great majority of these were standing up with feathers only erected on the part of the body that they were preening. The peak of preening activity occurred just prior to the move to the other side of the canyon (see below), and there was a further peak prior to the birds' departure to the feeding areas (Fig. 2).

There were just four incidents of disturbance or movement during the course of the day on which the roost was continually monitored. At 1011 hours, an Egyptian Vulture (*Neophron percnopterus*) glided low over the canyon. This caused all the birds to adopt a standing alert posture for a few minutes until the vulture disappeared from view. At 1025 hours a Sooty Falcon (*Falco concolor*) flew around the lip of the canyon causing some of the doves on the more open higher ledges to take flight for several minutes. The falcon made another circuit at a lower level making several shallow-angled stoops at doves in flight. Although it appeared to make contact with two individuals, it did not succeed in catching any. During this disturbance, the displaced birds tried to land on ledges lower down in the canyon, but most were driven off by the birds already occupying them. The falcon left after about 6 min and during the next half hour or so the vacated higher ledges were gradually reoccupied. Feather erection scores were somewhat elevated immediately after this, but declined during the next 2 h despite rising temperatures (Fig. 2).

Between 1300 and 1600 hours the birds moved across to ledges on the other (west) side of the canyon as the sun began to shine onto their existing sites. At 1600 hours, I had to take up a new position and from this new observation point observed several birds with elevated respiration rates. Presumably these were birds which had just flown across the canyon. The birds were in the air for a much shorter period (just a few seconds) during this change over, than they were when the Sooty Falcon disturbed them, but this was the time at which a peak ambient temperature of 39 C was reached. At 1335 hours a few birds on the larger ledges were

disturbed by an Ibex (*Capra ibex*), which was moving along the ledges eating Ibex droppings.

For most of the time, the birds avoided the sun, and on the more exposed ledges had to change positions to do so. During the hottest part of the day, a few individuals stopped roosting and flew up from the lower part of the canyon and laid down in spreadeagled positions with one wing and part of the tail exposed to full sunlight. Their posture during this sunning activity was quite different from that during cooling. Apart from being in the sun rather than in the shade, one or both wings were spread fully and less feather erection was visible. Sunning is believed, amongst other things, to play a role in facilitating ectoparasite removal (reviewed by Simmons 1986).

There was a greater tendency for birds to have their eyes open during the hottest parts of the day. In the morning and afternoon, when ambient temperature was less than 36 C, the birds had their eyes closed, provided they were undisturbed, blinking them open at intervals to monitor their surroundings as many other birds do (Lendrem 1984). In the middle of the day, however, the reverse occurred with birds keeping their eyes open for longer and blinking them at regular intervals presumably to moisten them. The rate of blinking at 39 C (30 blinks s^{-1}) was just significantly higher than it was at 36 C (21 blinks s^{-1}) ($t = -3.07$, $df = 10$, $P < 0.05$). This may have served to increase cooling.

Panting was only observed after flights, and no gular fluttering was seen. Respiration rates declined throughout the morning, rose after the birds relocated and then dropped thereafter (Fig. 2). Immediately after relocation, much more rapid rates of about 50 min^{-1} (panting) were observed. These rates soon decreased to just under 28 min^{-1} , but remained at this slightly elevated level (compared with those measured in the morning) until the birds left. Butler et al. (1977) showed that pigeons, which probably hyperventilate in flight for cooling purposes, accelerate their ventilation rates to nearly 600 min^{-1} once the flight is over in order to continue to dissipate heat in the absence of forced convection. They measured resting respiration rates of 20 min^{-1} .

DISCUSSION

Dorsal feather erection and body posture appear to play an important role in temperature dissipation in roosting Rock Doves in the wild. At the temperatures observed here, the exposure of the skin may have been beneficial merely because it facilitated convective cooling. The most intense cooling behaviors, however, were observed following the short flight, which occurred during the hottest part of the day at a temperature of 39 C, and it seems likely that cutaneous evaporation of water was taking place then. Approximately half the water evaporation of Rock Doves is via this route even at 30 C (Arad et al. 1987). Other suggested functions of such feather erection, namely to act as a sunshade (Bartholomew 1966) or conversely to expose the skin deliberately to the sun (Simmons 1986), clearly did not apply in the present situation because the birds remained

in the shade. The results are also suggestive of the use of the cornea as an evaporative surface, because the rate of blinking increased by 40% between ambient temperatures of 35 C and 39 C. The value at 35 C was exactly the same as that recorded by Lendrem (1984) for single Barbary Doves in the absence of predators.

A recumbent body posture can contribute to thermal economy by minimizing muscular heat output. This is presumably one reason why Rock Doves sit down more as it gets hotter. There could of course be an additional benefit if the surface on which they are lying is cool. There is no indication, however, that this was the case in these Rock Doves as there was no greater tendency for them to sit down in the mornings, when they were on ledges that had been shaded all day, than there was in the afternoon when they were on ledges that had been in sunlight all day (association $\chi^2 = 0.02$, $P > 0.10$). The fact that sitting birds had higher feather-erection scores than those that were standing may have been because they did not have the legs available for convective cooling. This seems unlikely, however, because more birds tended to sit down as it became hotter, and they could presumably have stood up at any time had it been advantageous to do so. It seems more plausible that these birds were hotter than those that were standing either because of greater recent activity (such as sunning, preening, or other movement), or because they were roosting on less favorable ledges (either because these were warmer or had a poorer air circulation).

These observations also point to some of the factors that are of importance in roost site selection. The best sites offer freedom from disturbance and predation as well as a favorable microclimate. In this case, such sites are likely to be the isolated, deeper ledges towards the bottom of the canyon. Nearly all birds have to use two sites during the course of the day, one on each side of the canyon. Those that are able to obtain the best ledges may have the added benefit of being able to afford to expose themselves to very high temperatures during sunning (because their initial body temperatures are lower) and thereby help reduce their parasite burdens. They may also be able to leave somewhat earlier for the feeding grounds during the evening because they are cooler.

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LITERATURE CITED

- ARAD, Z., I. GAVRIELI-LEVIN, U. EYLATH, AND J. MARDER. 1987. Effect of dehydration on cutaneous water evaporation in heat-exposed pigeons (*Columba livia*). *Physiol Zool.* 60:623-630.
- ARIELI, A., L. PELTONEN, AND J. MARDER. 1988. Reproduction of rock pigeon exposed to extreme ambient temperatures. *Comp. Biochem. Physiol.* 90A:497-500.

- BARTHOLOMEW, G. A. 1966. The role of behavior in the temperature regulation of the masked booby. *Condor* 68:523-535.
- BARTHOLOMEW, G. A., AND W. R. DAWSON. 1979. Thermoregulatory behavior during incubation in Heerman's gulls. *Physiol. Zool.* 52:422-437.
- BAUMEL, J. J., A. F. DALLEY, AND T. H. QUINN. 1983. The collar plexus of subcutaneous veins in the pigeon, *Columba livia*, its association with oesophageal pulsation and gular fluttering. *Zoomorphol.* 102:215-239.
- BERNSTEIN, M. H., I. SANDOVAL, M. B. CURTIS, AND D. M. HUDSON. 1979. Brain temperature in pigeons: effects of anterior respiratory bypass. *J. Comp. Physiol.* 129B: 115-118.
- BUTLER, P. J., N. H. WEST, AND D. R. JONES. 1977. Respiratory and cardiovascular responses of the pigeon to sustained level flight in a wind-tunnel. *J. Exp. Biol.* 71: 7-26.
- DAWSON, W. R. 1984. Physiological studies of desert birds: present and future considerations. *J. Arid Environ.* 7:133-155.
- GAUNT, S. L. L. 1980. Thermoregulation in doves (Columbidae): a novel esophageal heat exchanger. *Science*, NY 210:445-447.
- GOODWIN, D. 1983 (3rd ed.) Pigeons and doves of the world. Cornell Univ. Press, Ithaca, New York. 363 pp.
- HART, J. S., AND O. Z. ROY. 1967. Temperature regulation in flight in pigeons. *Amer. J. Physiol.* 213:1311-1316.
- LENDREM, D. W. 1984. Sleeping and vigilance in birds, II. An experimental study of the Barbary dove (*Streptopelia risoria*). *Anim. Behav.* 32:243-248.
- MARDER, J. 1983. Cutaneous water evaporation. II. Survival of birds under extreme thermal stress. *Comp. Biochem. Physiol.* 75A:433-439.
- , AND Y. ARIELI. 1988. Heat balance of acclimated pigeons (*Columba livia*) exposed to temperatures up to 60°C T_a . *Comp. Biochem. Physiol.* 92A:165-179.
- , ———, AND J. BEN-ASHER. 1989. Defense strategies against environmental heat stress in birds. *Israel J. Zool.* 36:81-75.
- , AND J. BEN-ASHER. 1983. Cutaneous water evaporation—I. Its significance in heat-stressed birds. *Comp. Biochem. Physiol.* 75A:425-431.
- , AND I. GAVRIELI-LEVIN. 1986. Body and egg temperature regulation in incubating pigeons exposed to heat stress: the role of skin evaporation. *Physiol. Zool.* 59:532-538.
- , AND ———. 1987. The heat acclimated pigeon: an ideal physiological model for a desert bird. *J. Appl. Physiol.* 62:952-958.
- McFARLAND, D. J., AND E. BAHER. 1968. Factors affecting feather posture in the Barbary dove. *Anim. Behav.* 16:171-177.
- MOORE, A. D. 1945. Winter night habits of birds. *Wilson Bull.* 57:253-260.
- PINSHOW, B., M. H. BERNSTEIN, G. E. LOPEZ, AND S. KLEINHAUS. 1982. Regulation of brain temperature in pigeons: effects of corneal convection. *Amer. J. Physiol.* 242: R577-R581.
- RAMIREZ, J. M., AND M. H. BERNSTEIN. 1976. Compound ventilation during thermal panting in pigeons: a possible mechanism for minimising hypocapnic alkalosis. *Fed. Amer. Soc.* 35:2562-2565.
- SIMMONS, K. E. L. 1986. The sunning behavior of birds. Bristol Ornithological Club, Bristol, United Kingdom. 119 pp.
- SMITH, R. M. 1969. Cardiovascular, respiratory, temperature and evaporative water loss responses of pigeons to varying degrees of heat stress. Ph.D. thesis. Indiana Univ., Bloomington, Indiana.
- , AND R. SUTHERS. 1969. Cutaneous water loss as a significant contribution to temperature regulation in heat stressed pigeons. *Physiologist* 12:358.
- THOMAS, D. H., AND A. P. ROBIN. 1977. Comparative studies of thermoregulatory and osmoregulatory behavior and physiology of five species of sandgrouse (Aves: Pteroclididae) in Morocco. *J. Zool.*, London 183:229-249.
- ZUROVSKY, Y., AND H. P. LABURN. 1987. The effects of ligation of the oesophagus on body and brain temperature in pigeons. *Comp. Biochem. Physiol.* 87A:959-962.

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