The Auk 112(3):564-570, 1995

HUMIDITY LEVELS IN PIED FLYCATCHER NESTS MEASURED USING CAPSULE HYGROMETERS

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ABSTRACT.—We used plastic capsules that were perforated at one end and filled with silica gel to measure the water vapor pressure (P_N) in nests of Pied Flycatchers (*Ficedula hypoleuca*) during 1992 And 1993. Nest humidity measured daily for 7 to 16 consecutive days of incubation in 31 nests averaged 2.1 kPa or 15.7 torr (range 1.8-2.5 kPa). Humidity varied greatly from one nest box to another and within individual nests, but did not affect the rate of egg water loss or hatching success. Nest humidity often was significantly correlated with variations in ambient humidity. Large clutches had significantly lower average P_N than small ones. In general, nest humidity was low at the beginning of incubation, rose during midincubation, and remained elevated thereafter. *Received 8 December 1994, accepted 6 February 1995.*

EGGS THAT LOSE ABNORMAL AMOUNTS of water during incubation frequently do not hatch (Snyder and Birchard 1982, Carey 1986). Since egg water loss depends in part upon differences between the water-vapor pressure in the egg and in the air around it (Landauer 1967, Lomholt 1976, Rahn and Paganelli 1990), humidity levels of nest air can affect hatching success, particularly under harsh environmental conditions (e.g. Grant 1982). Even though the water-vapor pressure (P_N) commonly varies in the nest (Howey et al. 1984, Kern 1987, Kern et al. 1990) and is not apparently regulated (Walsberg 1980, 1983), it may be responsible for otherwise unexplainable hatching failure and its measurement may be therefore of considerable practical importance.

However, few direct measurements of P_N were made before the late 1970s when Rahn et al. (1977) introduced the egg hygrometer. Since that time, many such measurements have been made, particularly in nests of birds which lay large eggs (Rahn and Paganelli 1990). Egg hygrometers can be used to measure humidity in nests of such large species because it is relatively easy to install a screw cap in large, thick-shelled eggs in order to add or remove desiccant. Such eggs are robust and readily accepted by an incubating bird as part of its clutch. It is, however, difficult to make hygrometers from eggs of small birds because of the egg's small size and thin shell. It is possible to seal desiccant into a small egg, but it cannot be replaced when it becomes waterlogged, and removing water from it by gently heating the egg in an oven may change the shell's water-vapor conductance (Kern et al. 1990).

Faced with the drawbacks of using desiccant-filled eggs to measure humidity in the nests of small birds, we developed another hygrometer that is small enough to use in their nests, that is virtually unbreakable, and in which desiccant can be replaced at will. In principle, it is the same as that used by Rahn et al. (1977)—a porous shell containing desiccant. In this case, however, the shell is a plastic capsule, one end of which has been perforated so that water vapor can penetrate and bind to the desiccant inside. This hygrometer is like an egg hygrometer in the sense that it provides one value of nest humidity representing conditions that presumably exist throughout a set period of time, usually 24 h. If there are marked changes in water-vapor levels in a nest during that period, as sometimes happens (Howey et al. 1984, Kern and Knapic 1991), neither hygrometer will record the variations. Our capsule hygrometer is unlike an egg hygrometer, however, in the sense that it measures the quantity of water in nest air, whereas an egg hygrometer does not because 20 to 30% of its porous surface is often in contact with the skin of the incubating adult and such contacts can be an important source of water vapor (Handrich 1989).

Using these capsule hygrometers, we measured humidity levels in the nests of Pied Flycatchers (*Ficedula hypoleuca*) during 1992 and 1993, not only because few such measurements exist for cavity-nesting birds, but also to see if P_N affected egg water loss and hatching success.

We describe how the hygrometers were made and present information about water-vapor levels in flycatcher nests during each day of incubation.

METHODS

Capsule hygrometers.—Hygrometers were made from replacement capsules for model TM transmitters (Mini-Mitter Company, Sunriver, Oregon). These capsules are cylindrical (1 cm in diameter) and consist of a tubular cap into which a hollow plug fits. We cut the plug down to a length of about 0.5 cm in order to shorten the overall length of the hygrometer to 2.0 to 2.3 cm. Six evenly spaced holes were made in the top of the capsule with a 25-gauge hypodermic needle. For a desiccant, we used silica gel (Tel-tale brand, mesh 6-16, Fisher Scientific, Pittsburgh, Pennsylvania). Since the top of the capsule was semitransparent, it was possible to see the silica gel inside and to determine approximately how much water it had adsorbed (anhydrous silica gel is deep purple; as water combines with the gel, its color changes to light blue; when it is waterlogged, the gel is colorless). The desiccant should be changed daily because of the amount of water that it adsorbs in a 24-h period.

We filled about 75% of the capsule with silica gel (350-500 mg). The hollow plug was lined inside and out with Clingfilm, so that a layer of it was between the two parts of the capsule when they were connected. We used the wooden handle of a dissecting needle to push Clingfilm into the hollow center of the plug. The two parts of the capsule were then fitted together, the dessicant was shaken down into the plug, and excess Clingfilm was cut off with a scalpel blade. Clingfilm did not provide a complete seal between the cap and the plug, but made it easier to take them apart. The junction between the two parts of the capsule was sealed with electrician's tape. In our experience, Scotch Super 33+ vinyl electrical tape (3M Electrical Products, Austin, Texas) works particularly well.

When necessary, the length of the capsule hygrometer was reduced even further (to 1.7 cm) by not using the plug, but simply sealing desiccant into the cap. In this case, we filled the capsule completely with silica gel (550-600 mg), covered the open end with a small piece of Clingfilm cut to fit, and sealed the end with electrician's tape.

We determined the water-vapor conductance of capsule hygrometers by putting them in a small, closed container over water at a constant temperature. The capsules were weighed beforehand and then at approximately 12-h intervals for 1 to 1.5 days. Their conductance was determined using the formula (Ar et al. 1974):

$$G_{\text{water}} = \dot{M}_{\text{water}}/(P_o - P_i), \tag{1}$$

where G_{water} is the water-vapor conductance of the capsule (in mg day^{-1} kPa^{-1}), $\dot{M}_{\text{water}}$ is the change in the capsule's mass (the amount of water taken up) per day (in mg day^{-1}), P_o is the water-vapor pressure of the environment outside the capsule (in kPa), and P_i is the water-vapor pressure inside the capsule. Because the capsule was filled with silica gel, P_i was 0 kPa and the equation reduced to

$$G_{\text{water}} = \dot{M}_{\text{water}}/P_o. \tag{2}$$

Since the capsules were sealed in a small container over water, we assumed that the atmosphere around them was 100% saturated with water vapor. Under these conditions, P_o is directly related to water temperature and can be obtained from Weast (1975).

We calibrated the capsules before and after each field season. Their conductance values, even after they had been used repeatedly, changed less than 10%: by an average of −1.8% (range −11.5 to 8.5%, n = 32 capsules) in 1992; and 6.3% (range 2.9 to 11.1%, n = 40 capsules) in 1993.

The amount of water taken up by the silica gel in the capsule hygrometers depends on P_o. In environments that were 100% saturated with water (P_o ca. 3.9 kPa), the mass of the silica gel increased by an average of 5.2% per day (range 3.9 to 6.1%, n = 35 capsules). Under typical ambient conditions in the field (P_o ca. 1.6 kPa), the increase was only 2.0% per day (range 1.6 to 2.4%, n = 25 capsules).

Values of water-vapor pressure obtained using these capsule hygrometers corresponded closely to those obtained with a hygrothermograph (calibrated with a sling psychrometer and a precision thermometer). We averaged ambient vapor pressure measured at 2-h intervals over a 24-h period with a hygrothermograph and compared that value with the vapor pressure measured concurrently by 25 capsule hygrometers. The difference between the values provided by the hygrothermograph and 13 capsules without plugs averaged 0.04 kPa. The value from the hygrothermograph and the average P_o obtained from 12 capsules with plugs were identical. The coefficients of variation were 4.8% for capsules without plugs and 1.9% for those with plugs.

Sealed capsules were essentially impervious to water vapor. Six unperforated capsules were filled with silica gel, sealed, and kept in a 100% humidified atmosphere at 30°C (P_o = 4.2 kPa); they gained less than 1 mg over a three-day period. Two groups of perforated capsules (n = 26 and 45) were sealed and kept at a P_o of about 1.3 kPa; they gained on average only 1.7 and 0.6 mg, respectively, over periods of six to seven days.

Field measurements.—During 1992 and 1993, we measured humidity levels in nest boxes occupied by incubating Pied Flycatchers, as well as in unoccupied nest boxes, in Llanwrthwl woods, 1.5 km north of Newbridge-on-Wye, Powys, south-central Wales (52°N, 3°W).

TABLE 1. $\dot{M}_{water}$, P_N, and hatching success in Pied Flycatcher nests as function of clutch size. Values in parentheses are ranges and sample sizes.

Clutch size (no. eggs)	$\dot{M}_{water}$ (mg day^{-1})	P_N (kPa)	Days of incubation during which P_N measured	Hatching success (percent of eggs)
5	22.2 ± 1.7 (22.0-25.6, 5)	2.12 ± 0.20 (1.93-2.48, 7)	9-14	83 (60-100, 7)
6	—	2.32 ± 0.13 (2.23-2.52, 4)	7-10	88 (67-100, 4)
7	23.1 ± 3.1 (19.4-27.2, 7)	2.07 ± 0.11 (1.87-2.19, 9)	11-14	73 (43-86, 8)
8	—	2.08 ± 0.05 (2.00-2.15, 5)	10-14	80 (50-100, 5)
9	24.0 ± 5.6 (17.3-26.7, 6)	1.95 ± 0.13 (1.84-2.20, 6)	11-16	57 (33-89, 6)

Capsule hygrometers were made and calibrated (as described above) at the Llysdinam Field Centre (of the University of Wales College of Cardiff) in Newbridge-on-Wye, weighed to the nearest 0.1 mg on a Mettler microbalance, and buried in a sealed container of silica gel until they were used. They were embedded in the walls of flycatcher nests with the perforated ends exposed to nest air underneath the clutch. After approximately 24 h in the nest, they were removed, sealed in Clingfilm, and returned to the field station where they were reweighed.

By exchanging capsules daily, we were able to measure P_N on each of 7 to 16 days of incubation in 31 nests (6 in 1992 and 25 in 1993). All of the birds used in our study except one (which had a sterile clutch) hatched their eggs and reared broods successfully.

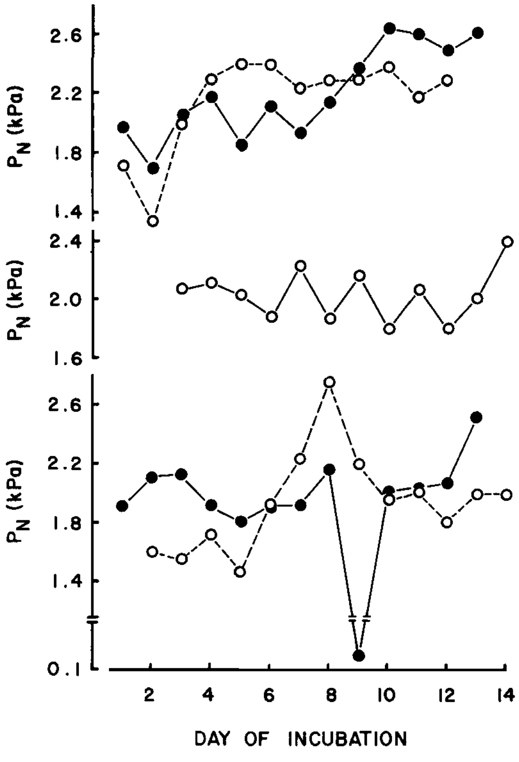

Fig. 1. Day-to-day variation of P_N in nests of five incubating Pied Flycatchers.

In 1993, we also measured ambient vapor pressure (P_I) in the woods with hygrometer capsules placed in empty nest boxes at the study site. These capsules were treated in the same way as those placed in occupied nest boxes.

Nest and ambient water-vapor pressures (in kPa) were determined from the mass (in mg day^{-1}) gained by the capsules when they were in a nest box and their water-vapor conductance (in mg day^{-1} kPa^{-1}), using the general formula

$$P = \dot{M}_{water}/G_{water}. \quad (3)$$

In 1993, we also weighed the eggs in 18 clutches two or three times during the incubation period to see if the rate at which they lost water (i.e. mass) depended on the humidity in the nest. In each case, the eggs were briefly removed from the nest box (we replaced them with clay eggs) and transported to the field centre, where they were weighed to the nearest 0.1 mg with a Mettler microbalance. Usually, the eggs were out of the nest box for less than 2 h. We have ignored the small amount of mass that they lost while in transit. Weighing times were three to six days apart.

Data were examined statistically with student t-tests, regression analyses, and analyses of variance followed when necessary by Student-Newman-Keuls multiple-range tests (Zar 1974).

RESULTS

During 7 to 16 days of incubation, water-vapor levels in nest boxes averaged 2.1 ± SD of 0.07 kPa (range 1.8 to 2.5 kPa; Table 1). Large clutches had significantly lower average P_N than small ones (clutch size versus average P_N, $r^2 = 0.18$, $P < 0.02$, $n = 31$ nests). Hatching success did not depend on the average humidity level in the nest box ($r^2 = 0.06$, $P > 0.1$, $n = 30$ nests) or on the maximum change that occurred in the

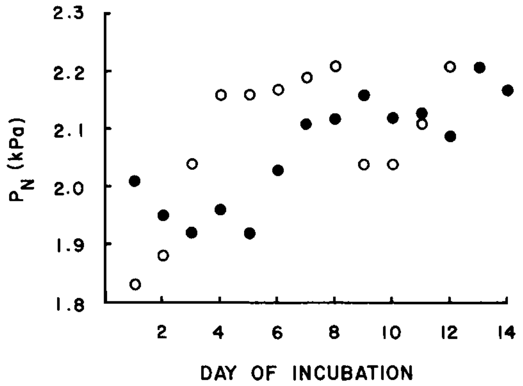

Fig. 2. Daily average P_N in representative nests of Pied Flycatchers.

P_N of the nest during incubation ($r^2 = 0.005$, $P > 0.5$, $n = 30$ nests). Day-to-day variations in P_N were different from one nest to another (Fig. 1). In some cases, P_N rose more or less steadily during the incubation period, but in others, it declined during midincubation, or included one or more pronounced, but brief changes. Even with such differences, P_N and P_I were significantly correlated in 16 of 25 nests in 1993 ($r^2 =$ 0.35 to 0.92). Humidity levels were on average 0.5 ± 0.1 kPa higher in occupied nest boxes than in empty ones.

There was no significant relationship between the average P_N in individual nests and the rate at which eggs in the clutch lost water ($r^2 = 0.09$, $P > 0.1$, $n = 18$ nests), even though daily values of P_N within individual nests varied on average 0.8 ± 0.2 kPa and, in some cases, as much as 1.3 kPa.

In general, P_N was low at the onset of incubation and rose as incubation continued (Fig. 2). In 1992, it rose sharply during the first few days of incubation and remained reasonably constant thereafter. In 1993, however, it remained low through day 5 of incubation, and then rose steadily through day 14. Average daily P_N (in kPa) and day of incubation were linearly related:

$$P_N = 1.937 + 0.020 \text{ Day} \qquad (4)$$

($r^2 = 0.47$, $P < 0.001$, $n = 26$).

DISCUSSION

As Table 2 illustrates, humidity levels in the nests of small birds increase as the nest cup becomes more enclosed. Open-bowl nests, which are presumably well ventilated, commonly have low values of P_N, whereas domed and cavity nests with more stationary air masses, have higher values. Underground burrows, which are poorly ventilated and in which the atmosphere is nearly saturated with water vapor, have still higher values. Levels of water vapor in the nest boxes of Pied Flycatchers are consistent with this general picture (Table 2). However, the humidity in flycatcher nests is no higher than that in the open-bowl nests of some passerines that breed in xeric environments, specifically House Finches (*Carpodacus mexicanus*) and Phainopeplas (*Phainopepla nitens*; Walsberg 1983). Such seemingly anomalous condi-

TABLE 2. Relationship between P_N and nest type among small birds.

Species	Type of nest	P_N (kPa)	Source
Barn Swallow (*Hirundo rustica*)	Open bowl	1.2	Birchard and Kilgore (1980)
Common Canary (*Serinus canarius*)	Open bowl	1.6	Kern (1987)
		1.3–2.8	Kern and Knapic (1991)
House Finch (*Carpodacus mexicanus*)	Open bowl	1.7	Walsberg (1983)
Phainopepla (*Phainopepla nitens*)	Open bowl	2.1	Walsberg (1983)
Song Sparrow (*Melospiza melodia*)	Open bowl	2.1	Kern et al. (1990)
Red Bishop (*Euplectes orix*)	Domed woven (grass) nest	2.1	Woodall and Parry (1982)
Great Tit (*Parus major*)	Nest box	2.4 (2.0–2.9)	Lomholt (1976)
Prothonotary Warbler (*Protonotaria citrea*)	Nest box	2.1[a]	Blem and Blem (1994)
Pied Flycatcher (*Ficedula hypoleuca*)	Nest box	2.1 (1.8–2.5)	This study
Bank Swallow (*Riparia riparia*)	Tunnel	2.7	Birchard and Kilgore (1980)
European Bee-eater (*Merops apiaster*)	Tunnel	2.9–4.0	White et al. (1978)

[a] Calculated from average values of nest temperature and relative humidity.

tions have been observed before. Walsberg (1980), for example, in reviewing what was known about P_N up to 1980, noted that the average P_N of desert species was higher than that of nondesert species (2.8 vs. 2.5 kPa). Grant (1982) discovered that the P_N of several species of Charadriiformes breeding under extremely hot, dry xeric conditions was an unexpectedly high 2.7 to 3.3 kPa.

Walsberg (1983, 1985) showed, both by changing P_N experimentally and by observing natural changes in the nest's microclimate during the breeding season, that P_N in *wild* birds affects egg water loss, a relationship long since known for domesticated birds (Murray 1925, Romanoff 1929); the higher the humidity, the lower the $\dot{M}_{\text{water}}$.

It has been argued that this is precisely why P_N is so important (Rahn et al. 1977, Morgan et al. 1978, Rahn and Paganelli 1990). Uncharacteristic degrees of egg water loss cause abnormal embryonic development and reduce hatching success. High water loss may interfere with formation of the chorioallantoic membrane (Snyder and Birchard 1982), reduce embryonic growth rates (Simkiss 1980a, b), or block late stages of embryogenesis (Carey 1986). Low water loss prevents fully developed chicks from pipping successfully (Walsberg and Schmidt 1992). In domestic fowl (*Gallus*; which may not be representative of birds in general), the embryo is particularly sensitive to egg water loss during early development (Snyder and Birchard 1982) and percent hatch is highest when eggs lose only 6 to 12% of their mass (i.e. water) during incubation (Landauer 1967, Lundy 1969).

Wild species appear to show much more tolerance to variations in egg water loss and P_N during incubation than chickens (Carey 1986); natural fluctuations in both, between and within species, can be quite large (Hoyt 1979, Walsberg 1980, Howey et al. 1984, Kern 1987, Kern et al. 1990, Kern and Knapic 1991). Some evidence suggests that even domestic fowl will tolerate marked variations in $\dot{M}_{\text{water}}$, provided they occur during late incubation (Simkiss 1980a, b, Snyder and Birchard 1982).

Several factors besides P_N can influence egg water loss, including the G_{water} of the egg shell and the nest-related behaviors of incubating birds. Walsberg (1980) developed a model that examines the relative importance of such factors. The model indicates that P_N is not very important; changes would need to be extreme to push $\dot{M}_{\text{water}}$ to lethal limits. By contrast, the egg's G_{water} seems to be much more important and in an evolutionary sense is generally adapted to the environmental conditions under which a species nests. It is high in wet nests and mesic habitats (e.g. Lomholt 1976, Birchard and Kilgore 1980, Davis et al. 1984), but low in xeric habitats (Grant 1982) and at all but the highest altitudes (Leon-Velarde et al. 1984, Carey et al. 1987, 1989). Furthermore, it often increases during incubation concurrent with the embryo's increasing demands for oxygen (Kern et al. 1992).

The fact that daily values of P_N within and among flycatcher nests were so varied (Fig. 1) suggests that: (1) P_N is not closely regulated by the birds; (2) no particular level is optimal for all nests, as has now been demonstrated for many other species (Walsberg 1980, 1983, Howey et al. 1984, Andersen and Steen 1986, Kern 1987, Kern et al. 1990, Kern and Knapic 1991); and (3) normal variations in P_N do not have serious effects on egg water loss, as Walsberg's (1980) model predicts. We were not, for example, able to demonstrate a relationship between P_N and egg water loss for Pied Flycatchers, perhaps because natural variations in P_N were not large enough to produce substantial changes in $\dot{M}_{\text{water}}$. Extreme differences in P_N from day to day of incubation averaged only 0.8 kPa and did not exceed 1.3 kPa in any nest. By contrast, much greater elevations in P_N of 1.5 to 1.6 kPa reduced egg water loss in Walsberg's (1983, 1985) studies. Furthermore, P_N was only about 0.5 kPa higher than P_I at our study site, and the fractional mass loss of the flycatcher egg during incubation would have increased only 2% had P_I and P_N been the same. In addition, hatching success was not significantly affected by the average P_N in the nest during incubation, or by the degree of change in P_N during incubation.

Based on values of $\dot{M}_{\text{water}}$ in our study (Table 1), the egg would lose approximately 23% of its mass during a typical 13-day incubation period. This fractional mass loss is somewhat higher than we have found in our previous work with Pied Flycatcher eggs (14.2%; Kern et al. 1992), but still within the 10 to 23% range reported for other species (Rahn and Ar 1974, Ar and Rahn 1980, Rahn and Paganelli 1990).

Nest-humidity levels were low when incubation began, increased during midincubation, and remained high until the chicks hatched (Fig. 2). It is also during mid- and late incubation that the G_{water} and $\dot{M}_{\text{water}}$ of Pied Flycatcher eggs are elevated and the egg's mass loss is most pronounced (Kern et al. 1992). This could be a cause-and-effect situation in which the eggs become more water permeable and lose more water, which remains in the confines of the nest cup elevating P_N, or it could indicate changes in the nest-related behavior of the incubating bird that add water to the nest or prevent water loss. The fact that P_N was significantly lower in large clutches than in small ones, in distinct contrast to the situation in bantam hens (*Gallus domesticus*; Andersen and Steen 1986), argues against the first possibility. The fact that egg water loss did not depend on P_N is evidence against the second possibility. The birds do, however, sit very tightly near the end of the incubation period, which could explain why P_N is elevated then.

Ar (1990) suggested recently that P_N is not regulated directly, but nonetheless stays relatively constant because an incubating bird regulates egg temperature (T_e) closely. That does not seem to be true for Pied Flycatchers (Figs. 1 and 2). If P_N depended on T_e in Pied Flycatchers, T_e would be higher during the second half of the incubation period than it is during early incubation. In a previous study (Kern et al. 1992), however, we found no significant changes in T_e during the incubation period.

In both years of our study, P_N was, as expected, highest when hatching occurred. Hatching should contribute water vapor to the nest, since 20 to 40% of the egg's total water loss occurs during external pipping (Ar and Rahn 1980, Whittow 1982, Sotherland and Rahn 1987).

ACKNOWLEDGMENTS

We thank: Fred Slater, warden of the Llysdinam Field Centre, who is a constant source of help to us during our field seasons; the Llysdinam Trust for providing facilities at the centre; Pat Tantrum on whose property we work; and C. R. Blem and two anonymous reviewers for their thoughtful comments on an earlier draft of our paper. This research was conducted under license SB:7:93 issued to R.J.C. and M.D.K. by the Countryside Council for Wales in Bangor. M.D.K. was supported by a grant from the Howard Hughes Foundation and faculty development funds from the College of Wooster.

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