

Activity patterns, vocalizations, and site selection in nesting Blue-winged Teal

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Introduction

The Blue-winged Teal *Anas discors* breeds throughout the prairie pothole region of North America. Considerable data are available on its breeding biology (Bennet 1938; Sowls 1955; Glover 1956; Dane 1965). Little is known, however, about the female's behaviour during incubation and hatching or of the importance of microclimate in the evolution of nest site selection.

Lundy (1969) identified several important physical requirements for successful incubation of domestic fowl eggs, including temperature, humidity, and egg turning. For Mallard *Anas platyrhynchos* eggs, Romanoff and Romanoff (1972) found that no embryos survived continuous incubation below 35°C or above 40.5°C. Mayhew (1955) suggested that 65–75% relative humidity was optimal for incubation of Mallard eggs. Low humidity suppresses the removal of carbonic acid from the eggs, whereas extremely high humidities obstruct the uptake of oxygen through the egg shell (Baerends 1959). Successful hatching requires high humidity to prevent the membranes from drying and mechanically hindering hatching (Romanoff 1943). Frequent egg turning prevents the germinal disc or the embryo from adhering to the shell membrane (Lundy 1969) and counteracts temperature gradients within the egg (Drent 1973). Freeman and Vince (1974) provide a summary of incubation requirements of domestic fowl and other species.

Successful reproduction may be dependent upon selection of a nest site that provides camouflage for the female and an optimal microclimate for developing eggs. Optimal nest microclimate also may represent a less stressful environment for the incubating bird, reducing her energy cost.

The female may also meet the physical requirements for successful incubation through behavioural patterns, such as modification of nest attentiveness (presence at the nest) and intensity of incubation (contact with the eggs), that compensate for fluctuations in ambient temperature but also allow her to obtain sufficient food to support metabolism.

Finally, successful rearing requires communication between the female and brood

before departure from the nest. Imprinting is particularly critical in land-nesting waterfowl because young must follow the female to water to obtain food and respond to her alarm calls to avoid predation.

Methods

This study was conducted during June and July 1974, on Dewey's Pasture, a state-owned wildlife management area of about 400 acres (162 ha) in Clay County, north-western Iowa, USA. It is characterized by rolling uplands dominated by bluegrass *Poa pratensis* and semi-permanent interconnected ponds surrounded by sedge-meadow vegetation, predominantly *Carex* spp. This area supports a high nesting population of Blue-winged Teal and was the site of studies by Bennett (1938) and Glover (1956).

Microclimate at nest sites

Two methods were used to measure vegetation density. Percentage light penetration in the nest bowl was compared with the open sky directly above the nest with a Spectra, model Combi 500, light meter. A 'cover board' 2.5 cm wide × 1.0 m long, painted with alternating orange cm segments, was centred horizontally along the edge of the nest at litter level N, S, E, and W of the nest bowl. The number of orange segments visible at a distance of 1 m was recorded and summed from all four compass directions. Subjective assessments were made of vegetative characteristics, such as nests in clumps of vegetation or with a canopy. Mean vegetation height was measured with a metre stick. Slope of the site was determined by using a Brunton pocket transit, and distance to water was measured with a Toko split-image rangefinder. Wind velocities were measured with a Dwyer Wind Meter. Relative humidity was obtained by using an Aerological Research Inc. Humi-Tector, model 202. Temperatures were measured with a standard mercury thermometer.

Humidity in the nest bowl was recorded at 21 active nests during midday by placing the humidity probe among the eggs either after flushing the female or while she was absent.

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These readings were compared with ambient and site vegetation humidity readings.

Continuous recordings of temperature and humidity were obtained at one inactive nest in an upland site and one in a wet meadow site. Nest site temperatures were measured at ground level and 10 cm above the nest bowl with shielded, 15-cm probes of a Palmer thermograph. Ambient humidity was measured at a height of 5 cm, approximately 0.6 m from the nest bowl with a Brown hygrothermograph housed in a standard weather enclosure. Continuous ambient temperature recordings, daily rainfall, and wind velocity records were taken in a weather enclosure approximately 2 m above ground on a hill in the study area.

By using parametric analyses of variance, nest sites in upland and wet meadow vegetation were compared for differences in temperature, humidity, vegetative height and density, percentage light penetration, slope, and distance to water. Differences between ambient, nest site, and nest bowl humidities were determined by using parametric analyses of variance techniques for the 21 active nests (Snedecor and Cochran 1967).

Behaviour of female Teal during nesting

Absences and movements on the nest

Nest inattentiveness (time and length of absences) and movements on the nest were monitored for two females during laying, eight during incubation, and five during hatching. A microswitch, a 5-cm metal treadle and 5.0 × 1.6 × 1.9 cm plastic housing, was implanted in the nest bowl with 18-cm metal stakes. Double strand 20-gauge rubber coated wire extended to a 10-point Esterline Angus strip chart recorder (model A620T, style 80M) powered by a 6 V tractor battery. When the female moved, or left the nest, the microswitch activated the recorder pen. The recorder was placed 30 to 150 m from the nest and checked at least once a day.

Least squares regression analyses were performed to determine the relationship of the number of movements per hour, and the length and number of absences, to ambient temperature or stage of incubation.

Incubation temperatures

An index to temperatures of the eggs was obtained for three nests during incubation. Dummy eggs were constructed from Bantam chicken and Blue-winged Teal eggs. The fresh egg was opened at the blunt end with a scalpel and the contents removed. A temperature

sensitive radio-transmitter coated with beeswax was placed in the egg, after which the shell was filled with glycerol and sealed with epoxy. Glycerol is similar in density to albumen (glycerol 1.246 g/ml; albumen 1.035 g/ml) (Romanoff and Romanoff 1949) and the transmitter eggs gain and lose heat at rates similar to fresh eggs.

The transmitter produced a continuous signal that changed frequency with changing temperature. This signal was received by a loop antenna concealed in the vegetation surrounding the nest and relayed by 22-gauge, single strand wire to a Sony transistor radio, model TFM-3700W, which made the signal audible. A converter was used to transform the signal to one readable as numbers, corresponding to egg temperature, on a dial (Varney and Ellis 1974). Readings were taken at random times of the day between 05.00 and 22.00 hours. Least squares regression techniques were used to determine the relationship between the rate of heat loss of the egg and ambient temperature.

Activity budgets

Activities of females during absence from the nest, such as feeding, comfort movements, sleeping, loafing, and swimming were documented on two laying and four incubating females. A sampling interval was established by using a metronome timing device (Wiens *et al.* 1970). The timing device was set at a 12-second interval in accordance with a similar sampling interval established by Dwyer (1974). Females were observed with the aid of a 20-power spotting scope for a 1-hour period, or for the duration of their absence from the nest. Their activities were coded each time the tone sounded. Individual identification was attained by watching the females return to known nests, and/or by facial markings.

The proportion of each absence devoted to each activity was summed and analyzed by using parametric analyses of variance and group comparison techniques.

Vocalizations of nesting females

Vocalizations of females at their nests were recorded with the aid of an automatic timing unit devised and described by McBurney (1970). Each recorder consisted of two mechanical alarm clocks to stop and start the recorder, a relay system between the clocks that operated a tape recorder through its remote jack, and a 12 V battery that powered the relay system. Portable Sony model TC-900 recorders were used with 3-inch reels of

0.5 mil 'Scotch 200 or 290' magnetic tape for recording times of 30 and 50 minutes. Some 90-minute recordings were made on a portable Sony model TC-222A recorder with 5-inch reels of 1.0 mil 'Scotch 142' magnetic tape. Recording speed in all instances was 17 inches per second.

The microphone was attached to a stake approximately 13 cm above ground level by the nest bowl. An attempt was made to record at all hours between 04.00 and 23.00 hours, one to three times per day.

Calls were recorded at two nests during laying, five nests during incubation, seven nests during and after hatching, and three nests during departure of the female and brood. The number of vocalizations or calls per minute was determined. Differences in the frequency of vocalizations were tested with parametric analyses of variance and Student's *t*-test.

Vocalizations were analyzed visually by using a Kay Electric Company Sonograph, model 7029A, at F-L-1 and wide band settings.

Sounds from the embryos were recorded at six nests by using a Craig cassette recorder, model 2603 and 'Scotch 9' cassette magnetic tape. A microphone was placed among the eggs, and a 2-minute recording was made. To determine when embryos first vocalized, recordings were made from the 19th day of incubation through hatching on the 21st–23rd day.

Results

Microclimate at nest sites

Upland nests (68) were most commonly in bluegrass (Table 1). Of 33 nests in wet meadow vegetation, a greater number were found in sedge than in grasses or forbs (Table 1). In comparison with the acres of upland

(323 acres; 131 ha) and wet meadow vegetation (103 acres; 42 ha) available (Glover 1949), nests were located more frequently in wet meadow vegetation ($X^2 = 4.43$; $P < 0.05$).

Vegetation density at wet meadow nest sites was significantly greater than at upland nest sites ($P < 0.01$) (Table 2). Bue, Blankenship and Marshall (1952) also found that Blue-winged Teal nested in the most dense cover. Another measure of plant density, percentage light penetration, also indicated that density was greater for wet meadow nest sites than for nests in upland sites, but the difference was not significant. At 14 sites where vegetation density was low, nests were found in clumps of vegetation. Vegetation pulled over the nest to form a canopy was observed at 16 sites, as it had been in a large number of nests by Glover (1956). Mean vegetation height did not differ between wet meadow and upland sites, averaging 40.9 cm (Table 2). Glover (1949) observed a mean vegetation height of approximately 30 cm.

There was a greater difference between nest site and ambient relative humidity at wet meadow than at upland sites ($P < 0.05$) and a lesser difference between nest site and ambient temperature at wet meadow sites ($P < 0.01$) (Table 2).

Wind velocity in the nest bowl was low at all nest sites (Table 2).

Mean distance to water for all nests was 55 m (range 4.6 to 237.7 m) compared with 72.6 m found by Glover (1956) (Table 2).

Mean slope for all nest sites was only 3.1 degrees. A preference for level ground was also reported for Blue-winged Teal by Heiser (1971). The mean slope at upland nest sites was significantly greater because of the topography of the study area ($P < 0.05$) (Table 2).

Table 1. Composition of vegetation at upland and wet meadow nest sites of Blue-winged Teal, 1974.

Vegetation	Number	Upland		Wet Meadow	
		Number	%	Number	%
Bluegrass <i>Poa</i>	39		57.4	0	0.0
Bromegrass <i>Bromus</i>	11		16.2	0	0.0
Grass-forb	10		14.7	0	0.0
Forb	4		5.9	2	6.1
Other grass	3		4.4	0	0.0
Bluestem <i>Andropogon</i>	1		1.4	0	0.0
Sedge <i>Carex</i>	0		0.0	25	75.8
Grass-sedge	0		0.0	4	12.1
Sedge-forb	0		0.0	1	3.0
Reed canary <i>Phalaris</i>	0		0.0	1	3.0
<i>Total</i>	68		100.0	33	100.0

Table 2. Mean microclimatic and vegetative parameters of upland and wet meadow nest sites of Blue-winged Teal.

Parameter	Upland	Wet meadow	All nests	Range (all nests)
Vegetation density index ¹	23.4	10.9†	19.3	0.0– 82.0
% Light penetration	26.6	23.7	25.7	4.7– 85.7
Humidity difference ²	4.3	8.0*	4.6	0.0– 29.0
Temperature difference ³	1.8	0.7†	1.6	0.0– 6.1
Vegetation height (cm)	40.9	42.9	41.7	22.9– 71.1
Wind velocity (mph)	0.1	0.0	0.1	0.0– 2.0
Distance to water (m)	69.0	26.6†	55.0	4.6–237.7
Slope in degrees	4.1	1.1*	3.1	0.0– 20.0

¹ Index represents mean number orange cm segments summed over all four compass directions (N, S, E, W). Smaller index represents denser vegetation.

² Nest site vs. ambient relative humidity (%).

³ Nest site vs. ambient temperature (°C).

* Significant $P < 0.05$.

† Significant $P < 0.01$.

Table 3. Mean temperature and humidity at one upland and one wet meadow Blue-winged Teal nest site, and mean ambient temperature from the hilltop weather station.

Parameter	Upland		Wet Meadow	
	Mean \pm 1 SD	Range	Mean \pm 1 SD	Range
Nest site temperature (°C)	23.2 \pm 9.6	–5.0–46.1	22.1 \pm 8.2	–2.2–41.7
Ground temperature (°C)	17.8 \pm 4.6	2.2–32.2	18.1 \pm 2.2	8.3–28.9
Relative humidity (%)	68.8 \pm 12.3	34.0–95.0	76.2 \pm 13.1	34.0–100.0

Hilltop		
Parameter	Mean \pm 1 SD	Range
Ambient temperature (°C)	21.6 \pm 4.0	6.7–35.0

The female had some influence on the humidity in the nest bowl during incubation. Nest bowl humidity averaged 62.6%, and was significantly higher ($P < 0.01$) than the surrounding vegetation (57.5%) or ambient relative humidity (54.5%).

Table 3 presents microclimate parameters for the continuous recordings. Mean nest site temperature was lower and less variable at the wet meadow site. Temperatures at both sites averaged higher than ambient temperature and underwent the greatest variation recorded owing to the absorption and retention of solar radiation at the vegetation level (Rosenberg 1974). Ground temperatures were similar at both sites. The mean and variance of relative humidity were greater at the wet meadow site.

Behaviour of female Teal during nesting *Absences and movements on the nest*

The mean number of absences per day was 2.7 (range 1 to 5). Absences were observed at all hours, but were more common at 05.00 hours, shortly after sunrise, and at 15.00

hours ($X^2 = 212.26$; $P < 0.01$) (Figure 1), and rare between 20.00 hours and 04.00 hours. Recordings of absences at night may have been the result of instrumentation error. A tendency was found toward fewer absences per day at higher mean daily ambient temperatures ($r = 0.61$; $P < 0.01$).

The mean length of absence was 105 minutes. Longer absences were correlated with higher ambient temperatures ($P < 0.01$) (Figure 2). Total time off the nest averaged 289 minutes, one-fifth of the 24-hour period, and showed no relationship to mean daily ambient temperature or stage of incubation.

During incubation, the females moved on their nests an average of 6.2 times per hour. Caldwell (1971) found an average of 1.9 resettling movements per hour for incubating Mallard. The mean number of movements per hour was positively correlated with mean ambient temperature ($P < 0.01$) (Figure 3), indicating that the female possibly incubated more intensely at lower temperatures. Fewer movements occurred during mid-incubation ($P < 0.01$) (Figure 4).

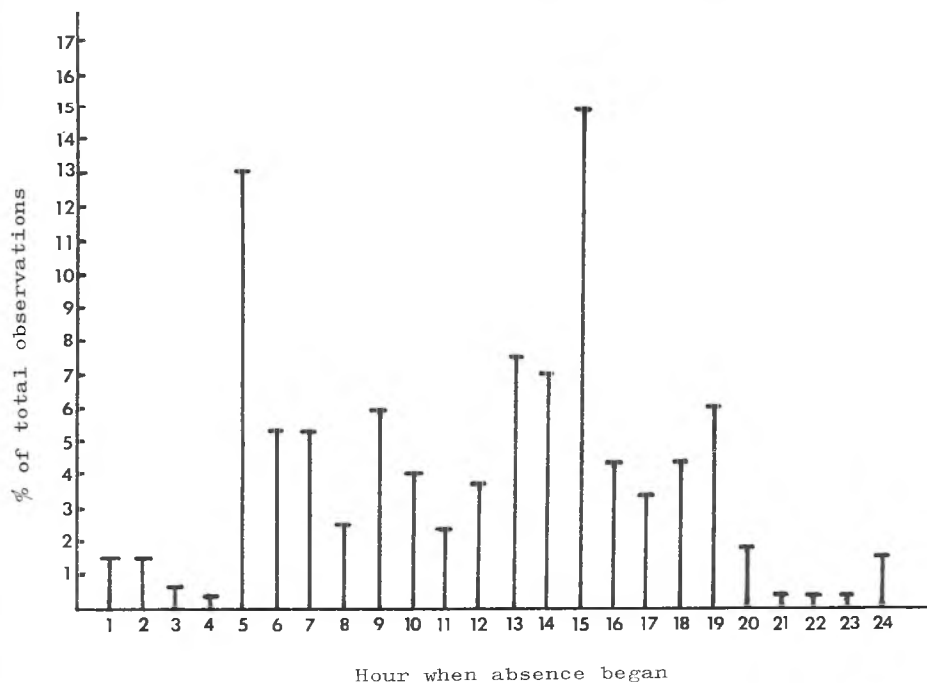


Figure 1. Nest absences of eight female Blue-winged Teal during incubation.

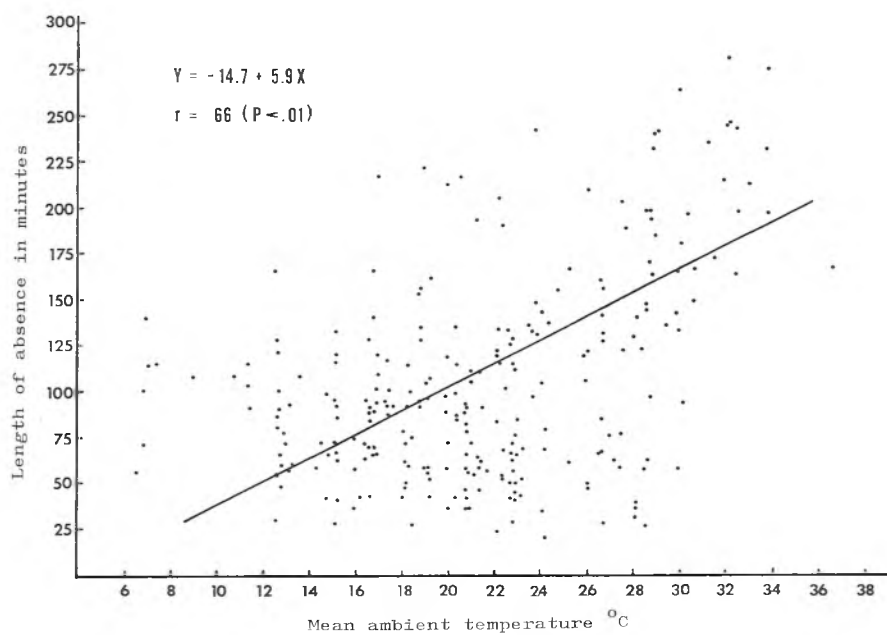


Figure 2. Relationship between length of absence and mean ambient temperature for eight incubating Blue-winged Teal females.

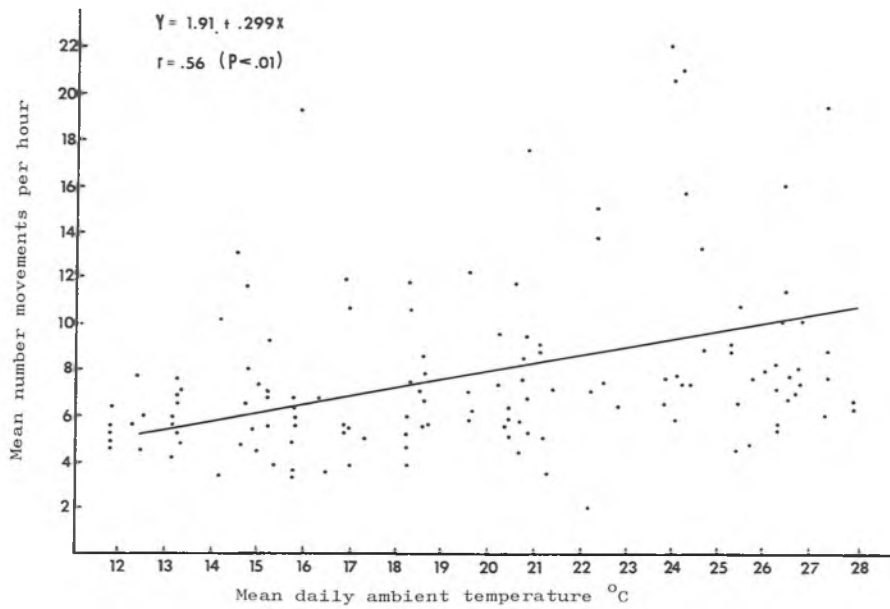


Figure 3. Relationship between the mean number of movements per hour (averaged over 24 hours) and mean daily ambient temperature for eight incubating Blue-winged Teal females.

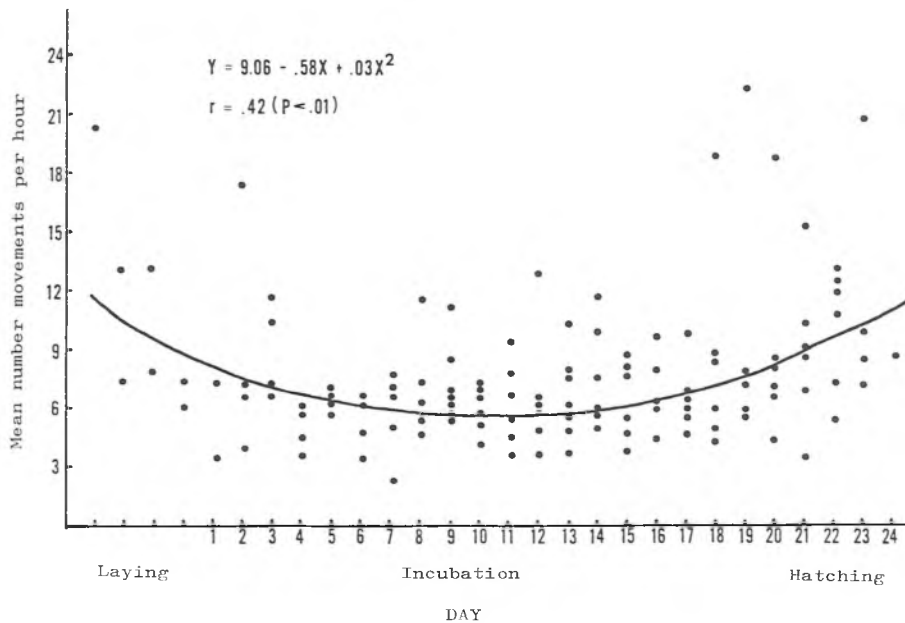
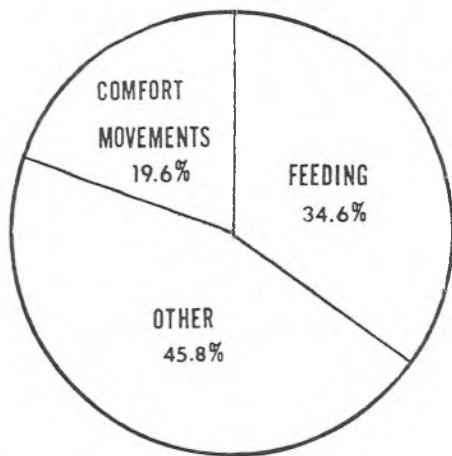
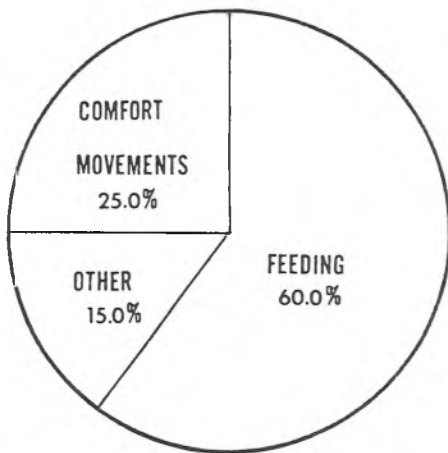


Figure 4. Relationship between the mean number of movements per hour (averaged over 24 hours) and stage of nesting for eight Blue-winged Teal females.



LAYING



INCUBATION

Figure 5. Activity budgets of two laying and four incubating Blue-winged Teal females during absences from the nest.

Incubation temperatures

Mean egg temperature during female attentive periods was $38.2 \pm 1.9^\circ\text{C}$. For absences of all lengths, the mean egg temperature fell to $35.6 \pm 2.8^\circ\text{C}$. Egg temperatures during absences fell exponentially, and more rapidly at lower than at higher ambient temperatures ($r = 0.85$; $P < 0.01$). When the female returned to the nest, egg temperatures increased rapidly.

Activity budgets

During laying, 27% of the day was spent at the nest site, compared with 80% during incubation. Off the nest, feeding was the most significant activity for both laying and incubating females ($P < 0.01$) (Figure 5). Activities other than feeding and comfort movements (sleeping, loafing, swimming) comprised a large percentage of a laying female's budget. When incubating, a greater amount of time was involved in feeding than in all other activities combined ($P < 0.01$). Incubating females spent a significantly greater amount of time feeding and significantly less time sleeping (0.2%), loafing (1.9%), and swimming (4.0%) than did laying females (sleeping 16.0%, loafing 12.1%, swimming 8.6%) ($P < 0.01$). There was no significant difference in the time spent in comfort movements when laying or incubating.

Vocalizations of nesting females

Three different vocalizations were recorded. A 'maternal' call (Gottlieb 1965), syllabified as *pup pup*, commonly occurred in sequences of two or three notes of short duration (Figure 6). Maternal calls, given with increasing frequency during late incubation, hatching, post-hatch, and departure, seemed to elicit contentment calls from the young. A 'trill' call, also observed for Blue-winged Teal by McKinney (1970), was given occasionally when the female returned to her nest after a short absence during the hatching period. This call, a series of rapid notes of short duration, also seemed to elicit contentment calls from the young. An 'alarm' call, observed during and after hatching, was given whenever a human approached. This call, one or more notes of longer duration than the maternal call, seemed to decrease the frequency of vocalizations among the brood.

No vocalizations were recorded for the laying females. Incubating females vocalized infrequently (0.01 per minute). The number of vocalizations increased significantly during hatching to two per minute ($P < 0.01$), and

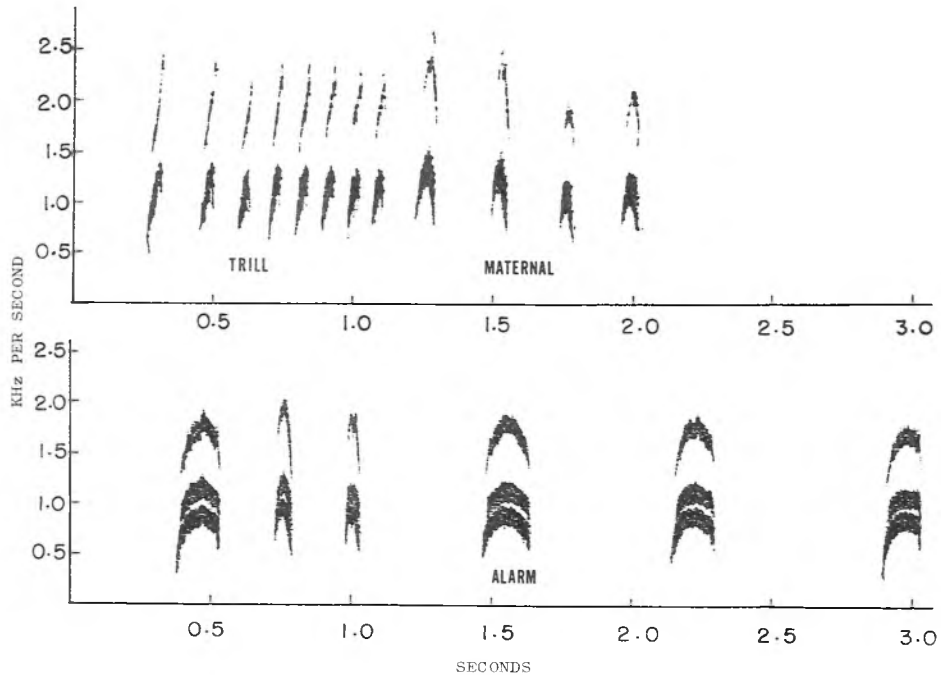


Figure 6. 'Trill', 'maternal', and 'alarm' calls of one female Blue-winged Teal at her nest. A trill call was preceded and followed by maternal calls.

again during the post-hatch period (22 per minute) ($P < 0.01$). On departure with the brood, the number of vocalizations increased dramatically to 146 per minute.

Rhythmic respiratory sounds and infrequent vocalizations from the embryos first became audible after the eggs had pipped and coincided with the significant increase in the number of vocalizations of the female.

Discussion

Microclimate at nest sites

Successful incubation may be augmented by nest site selection that takes advantage of favourable microclimates. Dense wet meadow vegetation not only provides camouflage, but also may offer a more favourable microclimate for incubation, reducing the female's energy cost of maintaining the eggs within the optimal temperature range. Wet meadow vegetation may also provide a more favourable moisture level for the developing eggs. The female, however, may have the greatest effect on the humidity in the nest bowl, providing moisture through the surface of the skin (Burke 1925), or by direct application of water brought back on the feathers (Caldwell 1971). Mayhew

(1955) suggested that female Mallard could bring water back to the nest on their feathers only if the nest was close to water. Thus the proximity of wet meadow nest sites to water may be advantageous.

Modification of the nest site may also result in improved microclimate for the developing eggs. Canopies built by the female, observed in several other species (Sowls 1955), possibly provide greater protection from aerial predators (Dwernychuk and Boag 1972), but also reduce penetration of solar radiation. Construction of a sunken nest bowl may effectively shield the eggs and prevent heat loss from the eggs during the female's absence (Huggins 1941).

Behaviour of female Teal during nesting

Successful incubation requires that the female maintains egg temperatures within an optimal range as well as maintains her own body metabolism. During absences from the nest, egg temperatures respond to the surrounding ambient temperature. The female seemingly adjusts the length and time of each absence in accordance with the temperature of her environment.

Increases in length of absence in response

to increasing ambient temperatures have also been observed in the Wood Duck *Aix sponsa* (Breckenridge 1956), Redhead *Aythya americana* (Low 1945), and Mallard (Caldwell 1971). Blue-winged Teal do not seem to make large adjustments in the total time off the nest in response to ambient temperature as found in the Wood Duck. This suggests that the female requires a certain amount of foraging time. This is met on cooler days without detrimental effects to the eggs by taking more absences of shorter duration.

Numerous absences in the afternoon also have been reported in the Mallard (Caldwell and Cornwell 1975), and follow high midday temperatures in the vegetation (Whitman and Wolters 1967) when the female's presence may be more crucial in preventing the eggs from reaching lethal high temperatures.

Periodic fluctuations in egg temperatures during the absences of the female can be beneficial to embryonic development. Balt and Cornwell (1972) reported an increase in hatching success in Mallard eggs given cold treatments at all stages of incubation. The chance, however, that a temperature decrease will be injurious to the embryo increases with the length of absence (Baerends 1959). Breckenridge (1956) also suggested that severe chilling could substantially increase the incubation period.

Although the stage of incubation did not seem to influence the inattentive behaviour of Blue-winged Teal, the amount of time absent may increase as incubation progresses in response to the increased energy output of the embryos. However absences became less frequent in Canvasbacks *Aythya valisneria* (Hochbaum 1944), and this may be due to the increased susceptibility of older embryos to low temperatures.

Less movement, resulting in more intense incubation at lower temperatures, may prevent body heat loss and egg chilling. At higher temperatures, increased movement may also cool the female (Caldwell and Cornwell 1975).

Much movement during laying probably reflects nest building. During early and late incubation, movement may correspond to egg turning behaviour, which is beneficial to embryonic development during these stages of incubation (Robertson 1961). Much movement during hatching also has been reported in the Mallard (McKinney 1952; Caldwell and Cornwell 1975) and Wood Duck (Breckenridge 1956). An increase in movements during hatching may be a response to the movements and vocalizations

of the embryos and may enhance the synchrony of the hatch (Vince 1966).

Numerous absences after sunrise probably reflect the need for food after the extended night attentive period, rather than a response to ambient temperature. The food consumed may be insufficient to replace the energy lost since Harris (1969) observed a progressive weight loss in Blue-winged Teal during laying and incubation. Incubating females have proportionately less absence time than when laying, so it may be important for them to minimize the amount of time spent in non-foraging activities.

Vocalizations of nesting females

Vocalizations may be easily located by predators because of their low frequency, repetitive nature and brief duration (Klopfer 1962). Lack of vocalizations during incubation has also been reported in the Blue-winged Teal by Collias and Collias (1956) and in the Mallard by Hess (1972).

Once hatching begins, however, communication between the female and hatching young becomes important. Vocalizations, seemingly in response to those of the embryos and their movements, may increase the hatching rate and promote synchronization of the hatch (Vince 1966; Hess 1972). In addition, communication between hatching young and the female enhances the imprinting process, assuring that during departure from the nest the following response of the young will be prompt and directed toward the biologically appropriate object (Collias and Collias 1956; Gottlieb 1965, 1968).

A gradual increase in frequency of vocalizations by the female as departure from the nest approaches has been reported in the Wood Duck and Mallard by Gottlieb (1965). He proposed that this increase in frequency of vocalizations prevented the young from habituating to the female call and so failing to respond during departure from the nest. Vocalizations of nesting females during hatching and post-hatching have been described for the Mallard (Gottlieb 1965; Abraham 1974), Wood Duck (Gottlieb 1965), Redhead (Weller 1959) and Canvasback (Collias and Collias 1956). Several different vocalizations also have been isolated in nesting Mallard (Abraham 1974).

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Summary

Wet meadow sites represented more favourable microclimates for nesting Blue-winged Teal *Anas discors* than upland sites because of the denser vegetation, higher humidity, and less extreme temperatures.

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Behaviour of incubating females was examined to determine how they modify their behaviour to provide an optimal environment for developing eggs while meeting their own food requirements. Absences and movements on the nest were monitored and rate of egg heat loss during absences obtained.

Absences were more common shortly after sunrise and after the high midday temperatures. Longer absences were correlated with higher ambient temperatures, but total time off the nest showed no clear relationship to mean daily ambient temperature.

More movement on the nest was also correlated with higher ambient temperatures, and with laying, early and late incubation, and hatching.

Feeding was the most significant activity during absence of both laying and incubating females and the latter spent significantly more time feeding.

Three different vocalizations at the nest were described during hatching: the 'maternal', the 'trill', and the 'alarm' call. Females vocalized infrequently during laying and incubation, but calling increased in response to the sounds and vocalizations from the hatching embryos, increasing dramatically at departure from the nest.

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