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EFFECTS OF MOISTURE ON EGGS AND HATCHLINGS OF LOGGERHEAD SEA TURTLES (CARETTA CARETTA)

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ABSTRACT: Ten clutches of eggs from Caretta caretta were divided into subsamples and incubated in sand containing one of five percentages of moisture: 0, 25, 50, 75, and 100. The percent hatch was greatest at 25% moisture and significantly less at higher and lower levels of moisture. Incubation time was significantly longer at 75 and 100% moisture than at drier conditions. Measurements of hatching carapace length decreased significantly with each increase in moisture treatment after 25%. Hatchling plastron lengths were greatest at 25% moisture and significantly smaller in other levels of moisture. Hatchling mass and carapace width measurements did not differ between treatments. Thus, 25% moisture was the optimum level for maximum percent hatch and hatchling size. The average moisture content of the sand in natural nests of Caretta on the beach was 18%. The hydric environment in areas frequented by nesting loggerhead turtles generally coincided with the optimum conditions required for proper egg development. Proper moisture conditions are necessary for maximum hatching success and, therefore, are important in the maintenance of a turtle egg hatchery.

Key words: Caretta; Sea turtle; Egg; Hatchling; Sand; Moisture; Hatchery

The eggs of many chelonian species are noncleidoic, meaning that they are dependent on uptake of moisture from the environment for successful development (Needham, 1966). Studies in both natural habitats and in the laboratory have demonstrated that many species of turtles, including marine turtles, have flexible-shelled eggs which exchange water with the surrounding substrate and atmosphere (see review by Packard and Packard, 1988).

Eggs of marine turtles incubated in hatcheries are not always maintained at the moisture levels found in nature, and this difference could affect hatching results (McGehee, 1979). Because all species of sea turtles are considered threatened or endangered in the United States of America, and to some degree in other countries, conservation efforts that include incubating eggs in hatcheries could ultimately affect the long-term survival of the species. The purpose of this study was to determine the extent to which moisture during incubation affects eggs and hatchlings of loggerhead sea turtles, Caretta caretta, and to delineate the optimum moisture level for incubation as an aid to hatchery activities.

MATERIALS AND METHODS

Eggs were collected from nesting loggerhead sea turtles on Merritt Island, Florida, during 1977. Handling of the eggs was kept to a minimum. All eggs were packed in plastic buckets with beach sand within 12 h after deposition and were kept in a hatchery, an aluminum house trailer on Merritt Island. Each egg mass was surrounded by 4–5 cm of sand on all sides. Air temperature in the hatchery was not controlled, and all eggs were subject to the
same temperature fluctuations. Hatchery temperatures taken between 25 June and 30 August 1977 ranged from 26.5–34.0°C and averaged 27.8°C (SD = 3.7, n = 74). Ten clutches were selected for experimentation in the hatchery. Each clutch was divided into five subsamples of at least 20 eggs each. Subsamples were incubated in buckets of sand containing one of five different moisture contents: 0, 25, 50, 75, and 100% saturation. Preliminary studies indicated that the 25% moisture treatment was most likely to yield the highest percent hatch; when a clutch consisted of >100 eggs (i.e., more than 20 eggs/subsample), the remaining eggs were placed with the 25% moisture subsample in order to produce and save as many hatchlings as possible of this threatened species. Therefore, subsamples incubated at the 25% moisture level contained from 20–56 eggs. In all other treatments, subsamples contained 20 eggs each. Eggs from different clutches were not mixed. Once the eggs were packed in buckets with sand, they were not disturbed until hatching.

The level of moisture for each bucket of sand was attained by adding measured amounts of water to dry sand. The amounts of water were derived from the constant required for 100% saturation, which I defined by the following method. Beach sand was thoroughly dried in a drying oven at 60°C for 24 h. After drying, 100 g of sand were placed in a small plastic bag, which was tied securely, and a corner of the bag was perforated with several pinholes. The bag of sand was suspended over a beaker of 100 g distilled water with the perforated corner submerged in the water for 12 h; water was drawn up into the sand by capillary action. The water that remained in the beaker was measured, thus indicating the amount of water required to saturate 100 g of dry sand. Four trials produced identical results yielding a value of 24 g water/100 g sand or 0.24 as a constant. The grain size of beach sand used in this study was generally consistent.

For the experiment, the 0.24 value was used in the preparation of five batches of sand containing 0, 25, 50, 75, or 100% moisture saturation. Beach sand was dried in a drying oven at 60°C for 24 h, and the amount of water calculated to bring a known amount of dry sand to the desired percent moisture was added. Each subsample (20–56 eggs each) was packed in sand of the appropriate percent moisture in a plastic bucket with drainage holes in the bottom. Each bucket was then weighed to the nearest 0.1 kg. The buckets were reweighed two or three times weekly until hatching. Any loss of weight was assumed to be due to loss of moisture. Moisture levels were maintained by sprinkling distilled water on the sand until the bucket was restored to its original weight. No compensation was made for water which had been taken up by the eggs.

The gravimetric water content of the sand used in the experiment was related to water potential by use of a suction cell apparatus as described by Klute (1986). A sample of sand was placed on a porous plate in a funnel connected by a hose to a burette containing water; thus, the sand was in hydraulic contact with the water through the porous plate. By changing the difference in height between the level of the sand sample and the water level in the burette, a water potential curve was constructed. The curve was used to estimate the water potential in kPa for each level of moisture used in the experiment, ranging from approximately −10 kPa for 0% moisture to 0 kPa for 100% moisture (Table 1).

To determine the moisture level of nests of Caretta in the natural habitat, samples of sand were collected from inside 20 nests as the nesting turtle began laying eggs. The nests were chosen haphazardly. The sand was taken from the approximate middle of the nest chamber wall, and care was taken to avoid contact with oviposition fluids. Sand samples of 100 g from each nest were weighed, were thoroughly dried in a drying oven at 60°C for 24 h, and were reweighed to determine the amount of moisture lost. Moisture content of the sand was calculated by using the 0.24 constant for saturation, described previously.

Hatchlings were weighed to the nearest 0.1 g. The following linear measurements were taken with vernier calipers to the nearest 0.1 mm as an assessment of hatching morphology: carapace length, carapace width, and plastron length. A maximum of 20 hatchlings was measured from
each subsample. After measurement, the hatchlings were released to the ocean.

Hatching success or percent hatch was defined as the percent of turtles that hatched from a clutch or subsample of eggs and were successfully released to the ocean; these hatchlings had the potential to survive and reproduce. This category did not include the few turtles that hatched and died before release. Incubation time for each subsample was defined as the number of days from the date deposited to the date of first pipping.

Data were analyzed for population normality by means of $Q$-$Q$ correlation coefficient and for homogeneity of variances using Bartlett's test. If the assumptions of normality and homogeneity of variance were met, the data were tested by parametric analysis of variance. In one case, measurements of hatching carapace width, these assumptions were not approximated; these data were analyzed by the Kruskal-Wallis test, a nonparametric analysis of variance.

One-way analysis of variance was used to test for differences among moisture treatments in hatching success (all percentages were analyzed after arcsine transformation), in percent of dead hatchlings and in incubation time. Hatching morphology data (except carapace width) were tested for differences in effects of treatment and clutch by two-way analysis of variance (mixed model). The alpha level was 0.05; 95% confidence intervals were used as multiple range tests to indicate where significant differences occurred between treatments.

Egg mass can vary from clutch to clutch, and differences in egg mass can affect the results of incubation (e.g., Morris et al., 1983; Packard et al., 1987). To determine any relationships between egg mass and hatch results, a random sample of 20 eggs was taken from each clutch after deposition and before experimental manipulation. The eggs were weighed to the nearest 0.1 g as an assessment of mass and then were replaced in the clutch. To test for interclutch variation, clutches were analyzed by one-way analysis of variance for differences in egg masses. Mean egg mass for each clutch was tested by regression analysis for correlation with mean values for hatch results from each clutch (i.e., percent hatch, incubation time, hatching weight, carapace length, carapace width, and plastron length).

**Results**

Egg data and hatch results by clutch are presented in Table 2. Egg masses varied significantly among clutches ($F_{a,160} = 198.68$, $P < 0.0001$). Egg mass was not correlated with percent hatch ($r = 0.44$, $n = 10$, $P = 0.21$) or incubation time ($r = 0.35$, $n = 10$, $P = 0.33$). However, there were significant positive correlations of egg mass with hatching mass ($r = 0.75$, $n = 10$, $P = 0.01$), carapace length ($r = 0.71$, $n = 10$, $P = 0.02$), carapace width ($r = 0.85$, $n = 10$, $P = 0.002$), and plastron length ($r = 0.66$, $n = 10$, $P = 0.04$).

All hatch results by treatment are displayed in Table 3. Hatching success of *Caretta* eggs was significantly affected by moisture content of the sand used for incubation ($F_{4,65} = 24.09$, $P < 0.0001$). Percent hatch was highest for eggs incubated at 25% moisture saturation and progressively lower for eggs incubated at 50, 75, and 100% moisture. Hatching results from eggs kept at 25 and 50% saturation were not significantly different from each other, nor were those from eggs kept at 0 and 50% (Table 4). Eggs incubated at 0% moisture produced a hatch success significantly lower than those at 25%. Percent hatch for eggs kept at the 75 and 100% moisture levels was significantly lower than for those maintained at drier conditions. Percentage of dead hatchlings did not differ significantly among treatments ($F_{4,65} = 1.61$, $P = 0.19$).

Incubation time for eggs of *Caretta* was influenced significantly by percent moisture of the substrate ($F_{4,65} = 8.14$, $P < 0.001$). Eggs kept at 75 and 100% moisture
required significantly more time to hatch than did eggs incubated at lower levels of moisture (Table 4).

Data for hatching mass did not differ among moisture treatments ($F_{4,36} = 3.48$, $P = 0.06$) but varied significantly among clutches ($F_{9,304} = 76.85$, $P < 0.0001$) and exhibited a treatment × clutch interaction ($F_{36,304} = 4.14$, $P < 0.0001$).

Carapace lengths of hatchlings differed significantly by treatment ($F_{4,36} = 7.83$, $P < 0.0001$) as well as by clutch ($F_{9,304} = 43.95$, $P < 0.0001$), and there was a significant treatment × clutch interaction ($F_{36,304} = 2.09$, $P < 0.001$). Carapace lengths differed among treatments except in the 0% and 25% moisture levels (Table 4). The measurements decreased with each increase in moisture treatment.

Carapace widths of hatchlings did not come from a normal distribution nor were the variances homogeneous; therefore, the assumptions necessary for analysis of variance were not met. A Kruskal-Wallis test showed that these data did not vary between treatments ($H = 2.17$, $P > 0.70$).

Analysis of variance of hatching plastron lengths indicated significant differences among moisture treatments ($F_{4,36} = 21.08$, $P < 0.0001$) and among clutches ($F_{9,304} = 42.34$, $P < 0.0001$); additionally, there was a treatment × clutch interaction ($F_{36,304} = 4.06$, $P < 0.0001$). Hatchlings from the 0%, 75%, and 100% moisture treatments did not differ from each other in plastron lengths but were significantly smaller than the turtles from the 25% and 50% moisture levels (Table 4). Turtles from the 25% moisture level had significantly longer plastrons than all others.

The mean moisture content of the sand taken from the 20 nests of Caretta in the natural habitat was 4.2 g moisture (SD = 1.1) per 100.0 g sand, or a ratio of 4.2/95.8 which equals 0.0438. This value, when divided by the 0.24 constant, yielded an average of 18.3% moisture saturation in the nests of Caretta sampled on Merritt Island. Values for the 20 nests ranged from 8.5–31.4% saturation.

**DISCUSSION**

Although the present study indicated that hatch results can be affected by variations among clutches and egg mass (i.e.,

<table>
<thead>
<tr>
<th>Hatchling no.</th>
<th>Hatching mass ± SD (g)</th>
<th>Hatching time ± SD (day)</th>
<th>Incubation temperature ± SD (°C)</th>
<th>Incubation duration ± SD (day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>38.2 ± 1.8</td>
<td>38.5 ± 0.9</td>
<td>38.6 ± 1.3</td>
<td>38.6 ± 1.3</td>
</tr>
<tr>
<td>2</td>
<td>38.6 ± 1.2</td>
<td>38.4 ± 1.5</td>
<td>38.5 ± 1.4</td>
<td>38.5 ± 1.4</td>
</tr>
<tr>
<td>3</td>
<td>38.0 ± 1.0</td>
<td>38.0 ± 1.1</td>
<td>38.0 ± 1.2</td>
<td>38.0 ± 1.2</td>
</tr>
<tr>
<td>4</td>
<td>38.4 ± 1.4</td>
<td>38.2 ± 1.4</td>
<td>38.1 ± 1.5</td>
<td>38.1 ± 1.5</td>
</tr>
<tr>
<td>5</td>
<td>38.2 ± 1.3</td>
<td>38.3 ± 1.3</td>
<td>38.3 ± 1.4</td>
<td>38.3 ± 1.4</td>
</tr>
<tr>
<td>6</td>
<td>38.5 ± 1.2</td>
<td>38.4 ± 1.5</td>
<td>38.5 ± 1.4</td>
<td>38.5 ± 1.4</td>
</tr>
<tr>
<td>7</td>
<td>38.6 ± 1.0</td>
<td>38.0 ± 1.1</td>
<td>38.0 ± 1.2</td>
<td>38.0 ± 1.2</td>
</tr>
<tr>
<td>8</td>
<td>38.4 ± 1.4</td>
<td>38.2 ± 1.4</td>
<td>38.1 ± 1.5</td>
<td>38.1 ± 1.5</td>
</tr>
<tr>
<td>9</td>
<td>38.2 ± 1.3</td>
<td>38.3 ± 1.3</td>
<td>38.3 ± 1.4</td>
<td>38.3 ± 1.4</td>
</tr>
<tr>
<td>10</td>
<td>38.5 ± 1.2</td>
<td>38.4 ± 1.5</td>
<td>38.5 ± 1.4</td>
<td>38.5 ± 1.4</td>
</tr>
</tbody>
</table>
TABLE 3.—Data from eggs and hatchlings from 10 clutches of Caretta caretta incubated in sand containing different percentages of moisture. The number of hatchlings measured in the 25% moisture treatment was 185 (a maximum of 20 live hatchlings from each subsample). All live hatchlings were measured in the other treatments.

<table>
<thead>
<tr>
<th>Treatment (% moisture of sand)</th>
<th>0</th>
<th>25</th>
<th>50</th>
<th>75</th>
<th>100</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. eggs</td>
<td>200</td>
<td>376</td>
<td>200</td>
<td>200</td>
<td>200</td>
</tr>
<tr>
<td>No. live hatchlings</td>
<td>127</td>
<td>321</td>
<td>140</td>
<td>64</td>
<td>38</td>
</tr>
<tr>
<td>% hatch</td>
<td>65.5</td>
<td>85.6</td>
<td>70.0</td>
<td>32.0</td>
<td>19.0</td>
</tr>
<tr>
<td>No. dead hatchlings</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>± incubation time ± SD (days)</td>
<td>62.4±2.1</td>
<td>62.1±1.6</td>
<td>63.1±1.5</td>
<td>66.5±3.3</td>
<td>66.7±3.3</td>
</tr>
<tr>
<td>± hatchling mass ± SD (g)</td>
<td>22.3±1.8</td>
<td>21.9±1.5</td>
<td>22.3±1.9</td>
<td>22.3±2.1</td>
<td>21.9±1.7</td>
</tr>
<tr>
<td>± hatchling carapace length ± SD (mm)</td>
<td>46.2±1.7</td>
<td>46.1±1.4</td>
<td>45.9±1.8</td>
<td>45.6±1.8</td>
<td>45.2±1.8</td>
</tr>
<tr>
<td>± hatchling carapace width ± SD (mm)</td>
<td>33.8±1.1</td>
<td>33.7±1.2</td>
<td>33.7±1.6</td>
<td>33.9±1.4</td>
<td>33.9±1.5</td>
</tr>
<tr>
<td>± hatchling plastron length ± SD (mm)</td>
<td>32.3±1.9</td>
<td>33.6±1.8</td>
<td>33.2±1.9</td>
<td>32.5±2.0</td>
<td>32.5±1.8</td>
</tr>
</tbody>
</table>

clutches with larger eggs produced larger hatchlings), the moisture content of the sand during incubation also had a significant effect on hatching. Sand moisture affected hatching success whereas egg size and interclutch variation did not in this experiment. Eggs incubated at 25% moisture produced the highest percent hatch; therefore, of the moisture levels tested, 25% moisture was the optimum for successful hatching. Hatching success at 0% moisture was significantly lower than optimum, indicating harmful effects of desiccation. Packard et al. (1981a, 1987) described a similar result for eggs of nonmarine turtles; hatching success was lower in eggs exposed to dry substrates than in eggs incubated in wetter conditions. Sand moisture therefore is critical for successful hatching of loggerhead turtle eggs.

Hatching success was lowest for eggs kept at the wettest conditions (75 and 100% moisture levels). These findings indicate that incubation in the presence of moisture levels much higher than optimum may be more harmful to the developing eggs than desiccation. Previous studies have shown that high moisture levels caused by heavy rains and high tides can destroy entire turtle clutches (Caldwell, 1959; Kraemer and Bell, 1980; Plummer, 1976; Ragotzkie, 1959). Gas exchange is impeded when the eggs are in a moisture saturated environment (Packard et al., 1977; Plummer, 1976), and oxygen diffusion between the atmosphere and the eggs in a turtle clutch may affect the rate and success of embryonic development (Ackerman, 1980; Ackerman and Prange, 1972; Ackerman et al., 1985; Prange and Ackerman, 1974).

Incubation time increased as moisture level increased such that eggs kept at the wettest levels required the longest incubation times. Similar findings have been reported for eggs of the green sea turtle, Chelonia mydas (Hendrickson, 1958; Schulz, 1975). Turtle eggs of several nonmarine species have been shown to absorb more moisture when incubated in wet substrates than when kept in dry environments (Gettinger et al., 1984; Morris et al., 1983; Packard et al., 1980, 1981a,b, 1983, 1985, 1987; Tracy et al., 1978). These studies indicated that embryonic turtles exposed to wet conditions during development had longer incubation periods and grew larger than embryos incubated in drier settings. Morris et al. (1983), Packard

TABLE 4.—Results of comparisons of moisture treatments (given as percent moisture) by 95% confidence intervals, multiple range tests. Treatment connected by the same line are not significantly different (α = 0.05).

<table>
<thead>
<tr>
<th>Hatching success</th>
<th>25%</th>
<th>50%</th>
<th>0%</th>
<th>75%</th>
<th>100%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incubation time</td>
<td>25%</td>
<td>0%</td>
<td>50%</td>
<td>75%</td>
<td>100%</td>
</tr>
<tr>
<td>Carapace length</td>
<td>0%</td>
<td>25%</td>
<td>50%</td>
<td>75%</td>
<td>100%</td>
</tr>
<tr>
<td>Plastron length</td>
<td>25%</td>
<td>50%</td>
<td>100%</td>
<td>75%</td>
<td>0%</td>
</tr>
</tbody>
</table>
and Packard (1988), and Packard et al. (1985) suggested that there was differential inhibition of metabolism in embryos developing in dry versus moist conditions which may have caused variations in growth rates leading to differences in hatching sizes. A favorable hydric environment may allow incubating embryos to delay hatching, giving them more time to grow and giving rise to larger hatchlings than those incubated in drier conditions (Packard and Packard, 1985; Packard et al., 1983). Thus, if the moisture content of a turtle nest affects hatching size, hatching survival may subsequently be affected; i.e., larger hatchlings have increased survival capabilities (Morris et al., 1983; Packard et al., 1986, 1983, 1985, 1987; Swingland and Coe, 1979).

In the present study, there were no differences among treatments in hatching masses and carapace widths, but differences in carapace lengths and plastron lengths suggested trends in hatching size which did not follow those seen in the studies previously discussed (i.e., high sand moisture levels generally resulted in longer incubation periods, consequently producing larger hatchlings). In the present experiment, incubation time was longer for eggs of Caretta in wetter sand, but the hatchlings were not larger. In fact, hatchlings from sand with the highest moisture contents (75% and 100% moisture) were in the groups with the smallest carapace lengths and plastron measurements. Turtles in the categories of largest carapace and plastron lengths were produced from eggs incubated at the optimum moisture level for percent hatch (25% moisture). Turtles from sand with moisture content of 50% were in a relatively central category significantly different from the largest and smallest carapace and plastron lengths. It is difficult to interpret the result that eggs in the 0% moisture treatment yielded hatchlings with the largest carapace lengths and the smallest plastron measurements. The value of these findings is open to speculation as to whether carapace and plastron sizes are any indications of hatching fitness; but if they are, incubation in sand with 25% moisture would appear to produce more fit hatchlings than other moisture treatments. The results of the present study suggest that the sand moisture level for optimum hatching success (resulting in the maximum production of Caretta) required shorter incubation periods (thus requiring less time for hatchery maintenance) and produced larger hatchlings (potentially maximizing hatching fitness). Therefore, it appears best to incubate eggs of Caretta in sand kept at or near the 25% moisture level. The differences in findings between this study and those cited previously could be due to differences in experimental design, subject species or egg mass.

The treatment × clutch interaction seen in analyses of hatching measurement data suggests that the effects of sand moisture vary with the size of the eggs. Due to differences in volume, surface area, and degree of exposure to the substrate, small eggs may be inclined to lose or exchange moisture with the surrounding medium more readily than larger ones. The possibility that large eggs can retain more moisture than smaller ones may contribute to the result that larger eggs generally give rise to larger hatchlings.

In subsamples kept at 0% moisture, eggs near the tops of the buckets became desiccated and collapsed whereas those underneath did not, a phenomenon not observed in buckets maintained at higher moisture levels. This pattern of desiccation has been observed in natural nests of Chelonia mydas (Bustard, 1971). The layer of eggs on top of a clutch is in closer contact with the overlying atmosphere than eggs below it and so is more inclined to lose moisture by evaporation (Packard et al., 1977). Eggs absorb moisture from the water in the gas volume and substrate surrounding the clutch; water availability is different for eggs in the center of clutches than for eggs at the periphery (Ackerman et al., 1985; Packard et al., 1980). Similarly in this study, eggs at the surface of a clutch appeared to lose viability due to desiccation whereas those toward the center retained moisture. The sand packing and plastic walls of each incubation container, along with the layer of eggs on top of the egg mass, probably acted as a buffer to retard dehydration of eggs within the nest.
This limited loss of moisture from centrally located eggs apparently allowed them to retain sufficient water to develop normally and yield a relatively high percent hatch in subsamples incubated at 0% moisture. However, the hatching success at 0% moisture was significantly lower than maximum, indicating that moisture must be maintained at higher levels to promote a high percent hatch from incubating turtle eggs. The studies discussed here suggest that the size of a clutch, type of egg container, type of substrate, and depth of burial may affect moisture availability to eggs during incubation and subsequently affect hatching success. Additionally, the hydric environment of the nest may influence temperature and subsequent sex determination of the embryos (Gutzke and Paukstis, 1983). These factors should be taken into consideration when establishing a turtle egg hatchery.

Under excessively wet conditions (e.g., 75 and 100% moisture), mold grew on some of the nonviable eggs. This growth also was observed on eggs near the bottom of nonexperimental hatchery clutches where moisture accumulated in the sand. The mold typically was black and discolored the exteriors of the eggshells and sand around them. Similar observations on sea turtle eggs were reported by Bustard and Greenham (1968) and Ragotzkie (1959). Clark (1946) claimed that mold did not cause embryonic death in reptile eggs but appeared as a sequel to it. However, Fitch and Fitch (1967) believed that mold contributed to mortality of reptile eggs. Solomon and Baird (1950) studied fungal penetration of green turtle eggs and concluded that a heavy infiltration of fungus may impair gas exchange across the eggshell, posing a hazard to the development of the embryo. Thus, high moisture levels in the sand around incubating eggs should be avoided, as these conditions are favorable for fungal growth which may cause egg mortality.

Of all the experimental values investigated, the one that produced the highest percent hatch (25% moisture) most closely approached the mean moisture content (18%) found in natural marine turtle nests. The moisture conditions in areas frequent-
can aid in establishing the proper moisture conditions required in the maintenance of a successful hatchery.

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