

Terrestrial Orientation by the Eastern Long-necked Turtle, *Chelodina longicollis*, from Australia

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ABSTRACT. — Overland movements by the Australian chelid, *Chelodina longicollis*, have been documented extensively, and their relative straightness has led observers to conclude that these turtles must have a navigational sense. We observed terrestrial migration by adult *C. longicollis* between a permanent freshwater lake and an ephemeral swamp in Jervis Bay National Park, New South Wales, from January-March 1994. Migrating turtles used similar non-random paths to reach their goal; movements were exclusively diurnal and occurred only under sunny conditions. Experimental studies of the orientation mechanism showed that on sunny days turtles from 2.5 km away demonstrated highly significant directional orientation, but that this ability was disrupted on overcast days. Animals field-tested from a distant (23 km) population oriented randomly. Turtles acclimated to a 6 hr phase-advanced light regime demonstrated a clockwise shift in their angle of orientation which was not significantly different from the expected 90°, thus implicating a biological clock component in their sun-compass orientation. Open field vs. arena (no view of horizon) trials suggest the probable use of terrestrial landmarks in navigation. Olfactory cues may play an important role in terrestrial orientation because animals tested in a Y-tank showed highly significant directional preference when swamp mud and debris were used in one of the arms.

Terrestrial movements are an integral component of the natural history of most freshwater turtles. Mature females of all species (but see Kennett et al., 1993) must leave the water to nest, thereby necessitating overland movements of a few meters to more than 1 km. In addition, non-nesting terrestrial movements of immature and adult turtles of both sexes have been observed and attributed to such factors as habitat loss due to prolonged drought (Gibbons et al., 1983), food shortage (Goode, 1967; Parker, 1984), and rainfall (Goode, 1967; Parmenter, 1976; Wygoda, 1979). Gibbons (1970), using terrestrial pitfall traps, found that up to 30% of the turtles living in a freshwater Carolina bay traveled onto land (non-reproductive migration) during an eight month interval, and concluded that terrestrial activity may be very important in the population dynamics of aquatic turtles. Bennett et al. (1970) tagged turtles with radioactive pins as they emigrated from the same bay (Gibbons, 1970). They found that *Kinosternon subrubrum* burrowed 2-11 cm below the surface at distances up to 600 m from the bay for periods up to 142 days. Similarly, Teska (1976) noted that in response to receding water level in the dry season, *K. scorpioides* left a Costa Rican marsh and moved as much as 500 m into adjacent pastures and forests.

The ability of turtles to navigate unfamiliar terrain has been known for many years (Romanes, 1883). A variety of sensory modalities are used in animal orientation, e.g., visual, magnetic, chemical, aural, and electrical cues (reviewed by Able, 1991). Visual cues include such references as the sun, moon, stars, polarized light, and landmarks, while chemical cues include odors in air or water.

To orient using the sun as a compass, an animal needs a view of the sun and an internal biological clock in phase with local time to compensate for the movement of the sun across the sky (Ferguson, 1967). Several orientation studies of turtles have demonstrated compass orientation, i.e. the ability to move on a given compass heading in unfamiliar territory using a single external reference such as the sun's azimuth (Type II, Griffin, 1952). Box turtles, *Terrapene carolina*, and painted turtles, *Chrysemys picta*, demonstrated accurate homing under clear skies, but lost this ability when it was overcast (Gould, 1957, 1959). Gibbons and Smith (1968) noted that most *Gopherus polyphemus*, *Pseudemys floridana*, and *Chelydra serpentina* continued to move on the same heading after they were captured, displaced to a new area, and released. Murphy (1970) found that captured adult *Pseudemys* tested in a circular arena without reference to landmarks moved in a direction that would have taken them to deep water in their home pond (y-axis orientation). Lemkau (1970) reported that captured and displaced *T. carolina*

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exhibited compass responses toward home when released in unfamiliar territory. Displaced gopher tortoises, *G. polyphemus*, showed individual direction preferences which had no relation to their homeward direction, and when subjected to a six hour phase shift in photoperiod altered their preferred headings by about ninety degrees (Gourley, 1974). This response indicates that *G. polyphemus* is capable of sun-compass orientation. *Chrysemys picta*, trained for ten days on an E-W axis, showed a significant unipolar response when tested in a circular aquatic arena (DeRosa and Taylor, 1976). Following a photoperiod delay of six hours, orientation was shifted ninety degrees, indicating the possession of an internal biological clock. Subsequently, DeRosa and Taylor (1982) demonstrated that *C. picta*, *T. carolina*, and *A. spinifera* all possess a sun-compass.

Emlen (1969) observed that displaced *C. picta* were able to return home from release sites as far as 100 m from their home pond, even under overcast skies. Homeward orientation did not correlate with wind direction at the time of release, so he concluded that olfactory cues are probably not important guiding stimuli (Emlen, 1969). In contrast, Carroll and Ehrenfeld (1978) concluded that wood turtles, *Clemmys insculpta*, which were able to return to their home in a high percentage of instances after displacement, probably used olfactory cues or a combination of olfactory and magnetic inputs. Olfaction as a basis for turtle orientation has been circumstantially indicated by Manton et al. (1972) who discovered that *Chelonia mydas* has the ability to smell underwater. Their finding supports the theory that chemical cues may play a role in the open-sea reproductive migration of *C. mydas* (Manton, 1979). Ortleb and Sexton (1964) found that *C. picta* failed to orient to a water current bearing aromatics from aquatic plants in a Y-maze, but the significance of airborne olfactory cues to the orientation of turtles has not been examined.

In this paper, we investigate aspects of the terrestrial migration and orientation of the eastern long-necked turtle *Chelodina longicollis* from Australia. Our report presents experimental data on orientation and olfactory discrimination. Additionally, we summarize observations made on *C. longicollis* migrating overland in undisturbed eucalypt forest.

MATERIALS AND METHODS

Study Site.—Jervis Bay National Park consists of a roughly 7000 ha peninsula in coastal New South Wales, Australia (Fig. 1). It is a relatively undisturbed region, which provided a rare opportunity to study the movements and navigation of *C. longicollis* in a natural context. The

study area was generally characterized by Kennett and Georges (1990). One of two permanent lakes in the area, Lake McKenzie (roughly 9 ha), is a typical dystrophic dune lake isolated from the ocean and other freshwater bodies in the area. It has surface inflows but no outflows and is located about 2.5 km north of Ryan's Swamp. This swamp is an isolated shallow (1–2 m) ephemeral freshwater swamp with a dense cover of emergent vegetation dominated by jointed twig rush (*Baumea articulata*), tall spike rush (*Eleocharis sphacelata*), and water ribbon (*Triglochin procera*). Lake McKenzie generally lacks emergent plant life, except for a couple of very sparse stands of *E. sphacelata* along its eastern shore. In addition to the two permanent lakes and Ryan's Swamp, there are ephemeral waterbodies scattered about the territory, all of which contain *C. longicollis*.

Study Animal.—*Chelodina longicollis* is widespread and abundant in eastern and south eastern Australia where it occupies permanent waters, backwaters, swamps, farm dams, rain pools, and other ephemeral water bodies. The species makes overland migrations, particularly following rain (Anon, 1941; Goode, 1967; Cann, 1978; Stott, 1988), and is one of the most physiologically suited for such activity among the Australian chelids due to its high desiccation tolerance (Chessman, 1984). When the period of habitat loss is short (< three months), turtles may migrate overland to aestivate beneath logs or litter of the surrounding terrestrial habitat (Chessman, 1983), then return to water when it becomes available. Annual migrations to and from permanent water are typical of populations of the Armidale region (Parmenter, 1976). However, in the dune water bodies of the Jervis Bay region, forced emigration from ephemeral swamps to permanent lakes may occur only once in several years (Kennett and Georges, 1990). These authors demonstrated a complex metapopulation structure for *Chelodina longicollis* at Jervis Bay, where terrestrial migration is a key element in the persistence and abundance of this species in the region. Turtles used in this study for experimental orientation trials were captured in Lake McKenzie and a 10 ha farm dam at Falls Creek, about 23 km NW of Lake McKenzie, using baited hoop traps (after Legler, 1960), or by hand with the aid of mask and fins. On capture, all turtles were weighed with a 2.5 kg Pesola® precision spring balance accurate to 0.3%. Carapace lengths were measured with 280 mm Helios® dial calipers. Sex was determined by the criteria of Chessman (1978).

Field Observations of Migration.—The black butt (*Eucalyptus pilularis*) and southern mahogany (*E. botryoides*) forest extending about 2.5 km between Lake McKenzie and Ryan's Swamp was

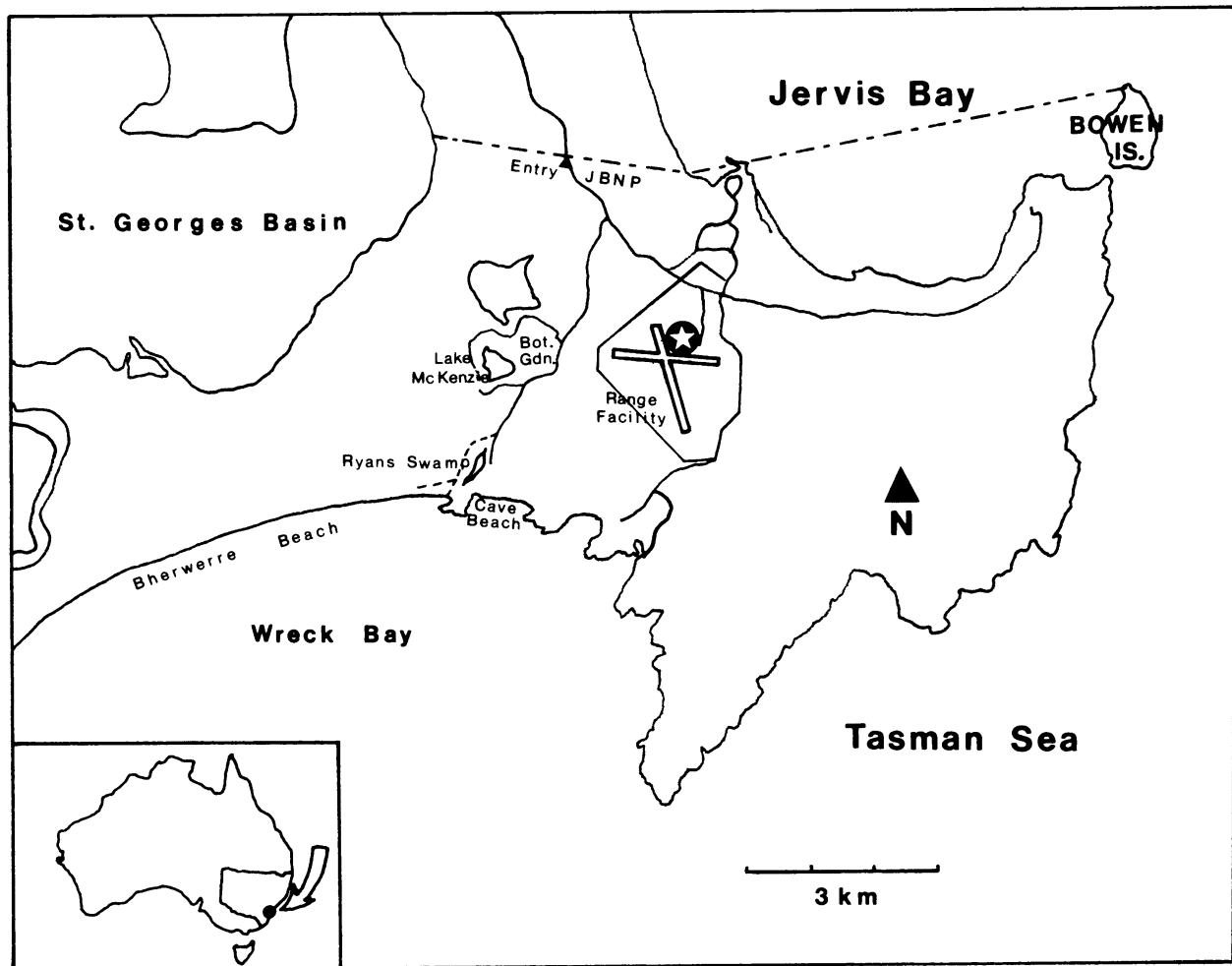


FIG. 1. A map of Jervis Bay National Park (JBNP) showing features and locations mentioned in this paper. The star indicates the site of field and arena orientation trials.

searched for migrating turtles during daylight hours as the opportunity arose between January and March of 1994. Seven of nine adults found moving on land were fitted with 1 km colored polyester thread spools taped to the dome of the carapace (after Breder, 1927). Turtle paths were observed indirectly from thread trails and in two instances turtles were observed directly with binoculars from a distance >50 m behind the animals so as not to disturb their behavior.

Air temperature was taken with a standard mercury thermometer about 30 cm above the ground adjacent to the turtles. The direction in which they faced when buried in leaf litter, or headed when on the move (from string trails), was determined with a sighting compass (Suunto Model KB-141360R). The slope of the ground traversed by each turtle was obtained with a hand-held clinometer (Suunto Model PM-5/PC66), and the actual distance each traveled was measured to the closest 0.1 m by running the spent thread through a hipchain (Topometric Products, Ltd.).

Orientation Experiments.—A large flat grassy area on the Jervis Bay Range Facility maintained by the Australian Department of Defense was

chosen for orientation experiments. The Range Facility was 2.5 km ENE from Lake McKenzie (straight line distance, Fig. 1). For each trial, eight turtles were transported from holding pens at Lake McKenzie in heavy black plastic bags to the Range Facility. We recorded weather conditions and air temperature (1.5 m from the ground) at the beginning of each experimental release.

After fitting turtles with 1 km thread spools (after Breder, 1927), we placed them on their backs at the release point, facing sequentially in N, E, S and W directions. We then left the site on a heading of approximately 150° to enable the turtles to move undisturbed for at least one hour. When we returned, we recorded (1) the compass bearing of the recapture point from the release point, (2) the straight line distance covered, and (3) the curvilinear (actual) path of travel as indicated by the discharged thread. The ratio of the thread path to the straight line distance covered was calculated as a "straightness index" (Emlen, 1969). On completion of each trial, the thread spools were removed and the turtles were returned in the black bags to the holding pens at Lake McKenzie. We re-

leased turtles under both sunny and overcast conditions.

The turtles were released far enough apart (10 m) to reduce the chance for social facilitation or interference during subsequent movement. Preliminary observation of a trial release group indicated the animals moved independently of one another and did not seem affected by the path of their neighbors.

Arena Trials.—Arena trials were conducted in a 15 m diameter circular enclosure constructed of a dark green woven fabric wall, 90 cm high. This arena was erected at the release site used in previous orientation trials. The fabric wall blocked the turtles' view of topography and vegetational landscape features. We placed turtles on their backs one at a time in the center of the arena facing N, E, S, and W on sequential trials. After they righted and moved, we recorded the compass direction between the centre of the arena and the point of first contact with the arena wall. On sunny days, arena trials were normally conducted around noon, when the sun was more or less directly overhead, so that the extent/effect of shadows within the arena was minimized.

Phase-Shifting.—Phase-shifted turtles were housed in an unheated room with all sources of external light eliminated. An artificial light regime (12L:12D) was introduced with the photophase beginning six hours in advance of natural sunrise. Since the apparent movement of the sun, due to the earth's rotation about the sun, is about 15° per hour, a photoperiod advanced by six hours should result in a 90° shift in orientation for species relying on solar cues for directional navigation. In the southern hemisphere, phase-advanced animals would be expected to shift their direction of orientation clockwise, not counterclockwise as in the northern hemisphere (Matthews, 1968). Phase-shifted turtles were used in both open field and arena experiments.

In a final experiment to test the possibility that knowledge of the local area was important to the navigational ability of *C. longicollis*, turtles from a farm dam at Falls Creek, about 23 km NW of Lake McKenzie, were obtained and used in field trials under sunny conditions. The experimental design was identical to that of field trials for Lake McKenzie turtles.

All orientation (open field) trials were conducted between 0800 and 1700 hr; arena trials were conducted between 1000 and 1200 hr. Statistical analysis of the data followed the procedures recommended by Batschelet (1972) and Zar (1984).

Olfactory Experiments.—We tested olfactory preference by turtles in a Y-shaped tank (two 120 cm arms, a 60 cm stem each with 25 cm high

walls, and a 25 cm wide base). The top of the tank was covered (stapled and taped) with heavy translucent polyethylene film. A plywood baffle was tacked 20 cm from the end of each arm, and extended inward at a 45° angle from the outside wall toward the fork in the tank. The baffles deflected air from a small, silent-running fan (Mistral M21) placed behind them, and concealed the fan and sample of distilled water or swamp mud placed immediately in front of the fan. We determined light levels in both arms and the stem of the apparatus to be equal using a Lunasix-F light meter (6.6 LW/EV at 100 ASA). Air temperature in the apparatus averaged 23 ± 2 C and in the surrounding room averaged 21 ± 3 C.

Twenty-nine turtles from Lake McKenzie (14M:15F) were first used in a control experiment to determine if the apparatus introduced any significant side bias. Distilled water only was placed before the fans in both arms. Turtles were placed singly at the base of the stem and given 15 to 20 mins to make their choice. A choice was recorded only when a turtle proceeded down one or the other of the two arms a distance of 60 cm. If 20 mins elapsed with no decision the turtle was removed and excluded.

The same turtles were then run in trials where distilled water was placed before the fan of one arm and a sample of swamp mud and organic debris was placed before the fan of the other arm. We determined the arm to receive distilled water by coin toss.

We used chi-squared contingency and goodness of fit tests, with Yates Correction for Continuity where appropriate (Zar, 1984) to compare olfactory choices.

RESULTS

Field Observations of Migration.—Mean carapace length (CL) of female turtles (N = 6) found moving in the bush was 200 mm (range = 176–219) and mean mass was 721 g (range = 565–795) while mean CL of males (N = 3) was 172 mm (range = 160–185) and mean mass was 473 g (range = 380–590).

All nine migrating individuals were adults, and the paths taken by the seven we tracked through the bush were all clearly in the direction of Ryan's Swamp (Fig. 2). Individual paths all differed significantly from random (Rayleigh test: $Z = 5.6$ to 29.4 ; $Z_{0.05} = 3.0$; $P < 0.05$). Turtles moved diurnally (0930 to 1830 h). We observed no movement at night; turtles were buried into leaf litter when observed after 1830 h. During their migrations, turtles travelled both uphill and downhill over terrain that varied in slope from +30 to -55%. Only when they got within 60 m of Ryan's Swamp did they all have

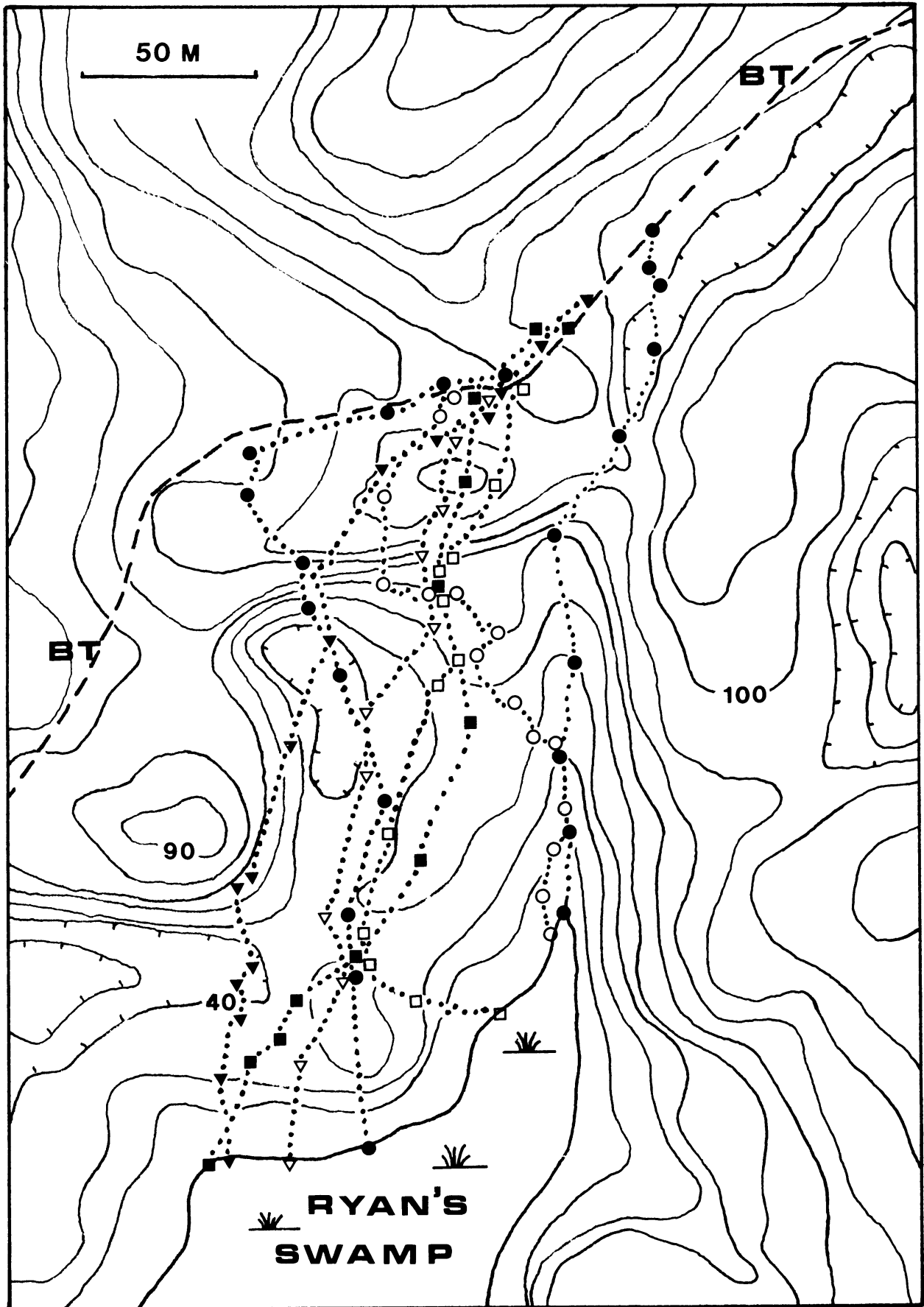


FIG. 2. Migratory paths taken by seven turtles from the Bherwerre Trail (BT) to their actual points of entry to Ryan's Swamp from 2-14 to 3-26-94.

TABLE 1. Observed behaviors of migrating turtles in relation to weather.

Behavior	Weather: Sunny— Dry	Sunny— Post rain	Overcast— Dry	Overcast— Post rain	Raining
Burying	4	0	2	0	0
Buried	28	0	11	9	14
Emerging	6	0	1	0	0
Moving	16	11	0	0	0

to travel downhill on slopes ranging from -2 to -35% .

The turtles typically moved under sunny conditions (Table 1). On only one occasion was an animal found moving under overcast-dry conditions. This animal had been on the move during sunny conditions and when it suddenly clouded over, it had not yet burrowed under leaf litter. All other turtles found during rain or under overcast conditions immediately following rain were buried under leaf litter, loose grass, or dead brush. Day time temperatures ($N = 19$) recorded in the bush when turtles ($N = 8$) were actively migrating during our study ranged from 17.5 – 32.8 C, and averaged 24.2 C.

Migrating turtles often engaged in episodes of gular pumping. With heads held high, they would lower and raise the gular apparatus of the head and throat, and periodically turn the head to look in different directions. These animals appeared to be "sniffing the air." The frequency of gular pumping episodes appeared to increase as the turtles got closer to the swamp and was especially obvious whenever they stopped in their travels. In a couple of instances, long pauses in travel were punctuated by lengthy (> 1 min) episodes of deep gular pumping. In the laboratory tests of olfactory discrimination, only a very few turtles were observed by the investigators during trials. However, all

of them evidenced gular pumping, especially when approaching and passing the fork in the tank. On two or three occasions thread trails left by turtles moving at different times in the bush near Ryan's Swamp were seen to be confluent for distances of 30 m or more. Whether these turtles were following the trail of a conspecific or orienting towards a cue is unclear.

The shoreline of Lake McKenzie was carefully checked for turtle tracks on several occasions. During the period just after the discovery of several animals migrating overland near the Bherwerre Beach Trail (Feb. 14), we found three sets of tracks coming out of the southwest corner of the lake. They headed towards a gully leading SW up to a firetower road. At the point where the gully and firetower road intersect, three turtles were seen moving between 1 and 28 February. On 18 February one of us (TG) hiked south through the bush from the firetower road for about 50 min and came out on the Bherwerre Beach Trail at the same spot where most of our thread-trailed turtles were first seen. The path they must have followed would have taken them through wet depressions which Kennett (1987) felt might lie along the migration route of this species between Lake McKenzie and Ryan's Swamp.

Orientation Experiments.—When conditions were sunny, turtles oriented non-randomly in the open field (Rayleigh test: $Z = 30.8$, $N = 42$, $P < 0.001$; Table 2; Fig. 3A). When conditions were overcast orientation was random ($Z = 0.4$, $N = 42$, $P > 0.05$; Table 2; Fig. 3B). In contrast, turtles transported 23 km from Falls Creek failed to show significant directionality under sunny conditions ($Z = 1.6$, $N = 45$, $P > 0.05$; Table 2; Fig. 3D), and also had a significantly higher straightness index (1.89 ± 0.17 , $N = 43$) compared to those of Lake McKenzie animals under both overcast (1.43 ± 0.07 , $N = 42$) and sunny conditions (1.26 ± 0.03 , $N = 42$) (ANOVA $F = 11.7$; $df = 3,171$; $P < 0.0001$; Tukey Test, $P < 0.05$). The difference in straightness index of Lake McKenzie turtles moving under sunny compared to overcast conditions was not significant.

Our experiments were not designed to test for homing ability. However, Lake McKenzie turtles moving in the open field under sunny

TABLE 2. Results of arena and field orientation trials of *Chelodina longicollis*. LMS = Lake McKenzie sunny trial; LMO = Lake McKenzie overcast trial; FCS = Falls Creek sunny trial; LMPA = Lake McKenzie phase-advanced sunny trial; LMAS = Lake McKenzie arena sunny trial; LMAPA = Lake McKenzie arena phase-advanced sunny trial.

Trial	N tur- tles	Z value	Z value for		95% Conf. Int.
			$P <$ 0.001	Mean direction	
LMS	42	30.7689	6.703	233.707	$\pm 7.5^\circ$
LMO	42	0.43797*	6.703	(160.795)	
FCS	45	1.61350*	6.717	(51.8938)	
LMPA	48	28.0664	6.729	264.751	$\pm 13.4^\circ$
LMAS	47	23.9171	6.725	191.639	$\pm 14.9^\circ$
LMAPA	44	22.5050	6.712	296.406	$\pm 14.4^\circ$

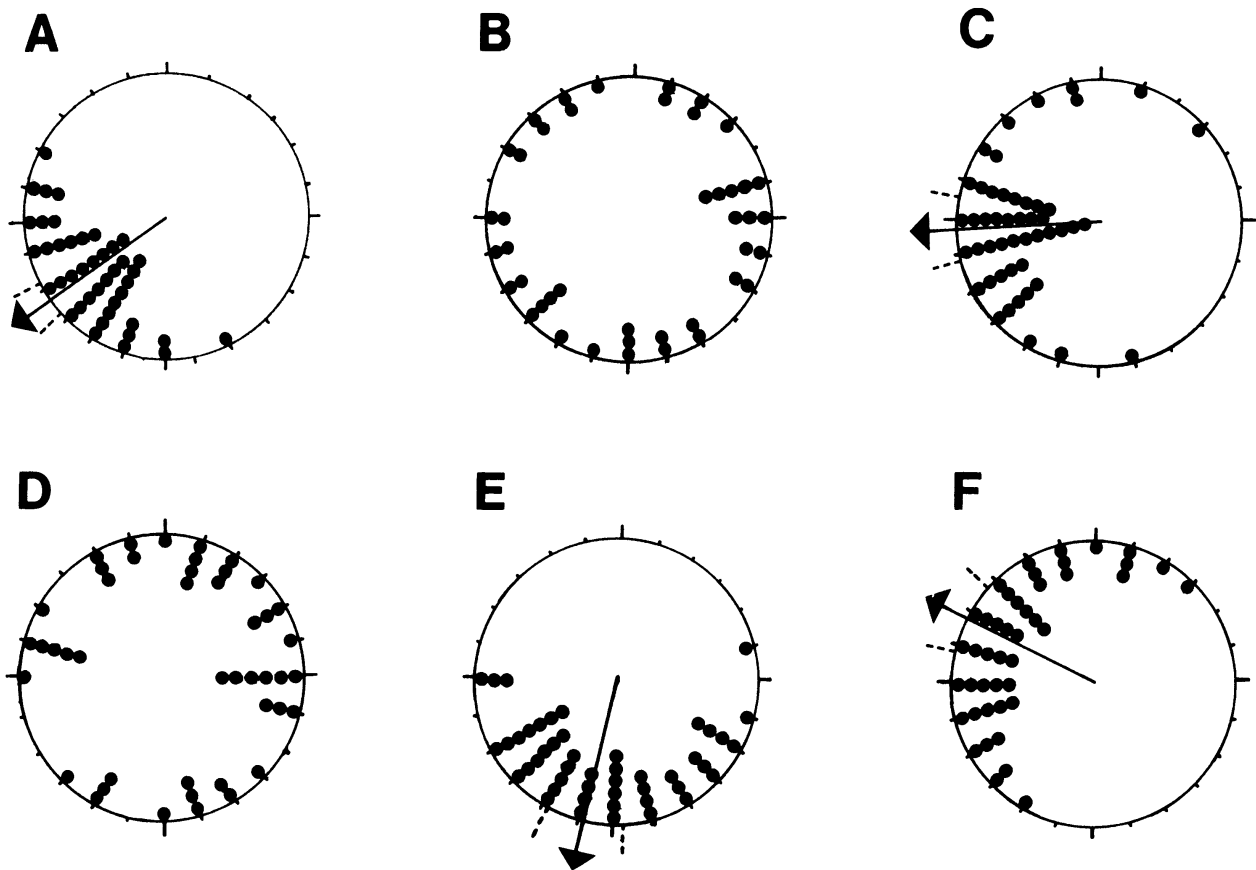


FIG. 3. Orientation trials of eastern long-necked turtles released in the open field (A-D) and in a test arena (E-F). A = Lake McKenzie sunny; B = Lake McKenzie overcast; C = Lake McKenzie phase-advanced sunny; D = Falls Creek sunny; E = Lake McKenzie arena sunny; F = Lake McKenzie arena phase-advanced sunny.

conditions showed distinct directionality (234° , V-test, $u = 7.72$, $df = 42$, $P < 0.00005$), but not to Lake McKenzie ($247-258^\circ$).

Arena Trials.—In the arena, turtles oriented non-randomly under sunny conditions ($Z = 23.9$, $N = 47$, $P < 0.001$; Fig. 3E). A possible influence of variation in the visual horizon on orientation was suggested by the significant difference in orientation of turtles released under sunny conditions in the open field compared to the arena (on comparison of confidence limits in Figs. 3A,E).

Phase-Shifting.—Turtles phase-shifted 6 h moved in directions that were significantly different from those of non-shifted controls, both in the open and in the arena. In both of the phase-shift experiments, the effect of advancing the phase of the light regime was to shift orientation in a clockwise direction, in line with expectation for the southern hemisphere. A phase advance of 6 h should theoretically produce a clockwise shift in orientation of 90° , but this was consistent with observations only in arena trials where the horizon was obscured (Fig. 3E,F). There the phase-advanced animals' mean heading was 296° ($CL = \pm 14.4^\circ$, $N = 44$; Table 2) which was not significantly different

from their expected direction of 282° ($CL \pm 14.9^\circ$, $N = 47$).

In the open field, the directional shift of the phase-advanced turtles was 31° , much less than the expected 90° . We attribute this to the confounding effects of topography and vegetation on the visual horizon, which may act to shift the direction of maximal illumination. Such effects were also strongly suggested by the significant difference in directionality of turtles from Lake McKenzie released in open field vs. arena trials in the absence of phase-shift (on comparison of confidence limits in Figs. 3A,E).

Olfactory Experiments.—Differences in response between males and females ($\chi^2 = 0.85$, $df = 1$, $P = 0.36$) were not significant; the data were therefore pooled for the two sexes. Turtles showed no significant preference for the right fork (32 turtles) over the left fork (36 turtles) ($\chi^2 = 0.13$, $df = 1$, $P = 0.72$) when presented with distilled water in both arms of the Y-tank.

When presented with a choice between distilled water and swamp mud and organic debris, there was no significant difference in choices made by males and females ($\chi^2 = 0.0$, $df = 1$, $P = 0.99$). There was, however, a very pronounced preference by both sexes (61 of 76

trials) for the arm containing swamp mud and debris ($\chi^2 = 26.6$, $df = 1$, $P < 0.00001$).

DISCUSSION

Field Observations of Migration.—Stott (1988) found that emergence of *C. longicollis* from four man-made study ponds was significantly directional (Rayleigh Test, $P < 0.001$), and toward other nearby ponds. Our discovery of turtle tracks leading out of Lake McKenzie at only one specific SW point on its perimeter, suggests that emergence from natural lakes may also be non-random, and oriented in the direction of intended terrestrial travel.

Our report of strictly diurnal movements by *C. longicollis* contradicts reports by Chessman (1978) and Stott (1988). Stott (pers. comm.) has indicated that the high level of human activity, availability of artificial lighting, and man-altered habitat on the college campus where he conducted his study may have produced what he considered to be predominantly nocturnal movement in this species. In addition, he felt that very high diurnal air temperatures (40 + C) recorded near turtle refugia during his study may have caused the turtles to become nocturnal in habit (Stott, pers. comm.). This is considerably higher than ambient diurnal temperatures we recorded, so we agree that daytime movements of *C. longicollis* in the Adelaide region may have been thermally inhibited.

Our observations of gular pumping and confluence of thread trails in the eucalypt woodland near Ryan's Swamp suggest an olfactory component in the orientation of *C. longicollis*. Since these turtles are locally known as "stinkers," trails left by previous turtles may have borne their pungent scent and thus enabled other individuals to follow their path precisely. Chemical odors on the substrate, as well as airborne odors, may be useful to terrestrial navigation. Scent-trailing has been documented for snakes and lizards, but among the turtles little is known about this phenomenon. Butler and Graham (1995) concluded that emerged hatchling Blanding's turtles, *Emydoidea blandingii*, used conspecific scent trailing, based on confluence of their paths.

Orientation Experiments.—Our observation of highly directional orientation in *C. longicollis* on sunny days, but not on overcast days, is consistent with previous data for turtles in the northern hemisphere (Gould, 1957, 1959; Gourley, 1974; DeRosa and Taylor, 1976, 1982). Any concerns about the possible role of social facilitation were allayed upon comparison of the experimental results obtained under overcast vs. sunny conditions. If social facilitation were operating to cause the significant orientation observed under sunny circumstances, it should have similarly resulted in non-random orien-

tation in the overcast (control) group. This clearly did not happen, so we consider our group releases to be independent releases.

The ratio of the actual (curvilinear) distance traveled to the straight line distance was used by Emlen (1969) as an index of the straightness of path for painted turtles (*Chrysemys picta*) traveling overland. A value of 1.0 indicated perfect linearity of travel, while the value grew larger the more sinuous the path taken. He found that the mean straightness of path index for turtles released one mile from their home pond was significantly greater than for turtles let out 100 m from the pond. Our findings with *Chelodina* were similar in that the Lake McKenzie turtles (released 2.5 km from the lake) took significantly straighter routes than the Falls Creek turtles released 23 km from home.

Mean straightness indices were greater for Lake McKenzie turtles released on overcast than on sunny days. They wandered a bit more when the sun was not visible, but these differences were not statistically significant. Yeomans, however, (1995) found that path straightness was significantly greater for yellow-bellied pond sliders (*Trachemys scripta*) released on sunny/mixed days than on rainy/overcast days.

The finding that our Falls Creek turtles (transported 23 km) had no significant directionality when released, is consistent with the report of Carroll and Ehrenfeld (1978). They found that a high percentage of wood turtles, *Clemmys insculpta*, were able to return home after displacement to unfamiliar territory. Homing was independent of the direction of displacement, but success fell off sharply when displacement distance exceeded 2 km. Carroll and Ehrenfeld speculated that wood turtle orientation was probably based on olfactory cues or on a combination of olfactory and magnetic inputs, but presented no evidence to support this.

Although the random orientation of our Falls Creek turtles following long distance displacement suggests a strong dependence on local landmarks for effective navigation, the idea is inconclusive. This is because we were subsequently unable to conduct the necessary control experiment (closer to home) on this population due to the onset of colder weather in mid-May; thereafter turtles refused to move when released in the open field.

When Stott (1988) found terrestrial movements of *C. longicollis* to be remarkably straight, he concluded that they must have navigational sense, and probably make use of terrestrial landmarks. He further indicated that his limited data on wind direction prevailing when adults were migrating suggested that it was not olfaction they were using to attain their goal. Instead, because several animals changed course abruptly when they came into view of local

landmarks, he suggested that visual piloting may have been their principal method of navigation in open terrain. Other investigators (Auffenberg and Weaver, 1969; Emlen, 1969; DeRosa and Taylor, 1982; Yeomans, 1995) have reported orientational response to visual landmarks by other species of turtles.

Chelodina longicollis released under sunny conditions in both open field and arena trials (Fig. 3) showed significantly nonrandom movement, but mean compass headings of the two experimental groups differed by about 42°. We suggest that this difference occurred due to the influence of local landmarks visible to our turtles in the open field, and not in the arena. Turtles tracked in the bush all turned south to follow the Bherwerre Trail when they first contacted it after emerging from the forest (Fig. 2). Linear landmarks, such as a road, or forest edge have been shown to compete with celestial cues in bee orientation. When bees were trained to find a food table along a north-south edge, and later tested along an east-west edge, most flew along the edge to a food table instead of taking a southerly course from the edge (Lindauer, 1961). Other bee orientation experiments by von Frisch and Lindauer (1954) showed that landmarks have the greatest orientational effect if they are linear and lead directly to food. Perhaps where the goal is not food, but is instead a particular destination like Ryan's Swamp, turtle reliance on useful linear landmarks is strong. In our case, maybe the most influential linear landmark, the Bherwerre Trail, was followed for a ways by migrating turtles because it led in the general direction they were headed before they saw it. Yeomans (1995) noticed that slider turtles moving through the woods would change direction to follow an existing trail, and that they turned as often uphill as downhill onto these paths. Although this action caused them to take a less direct route to achieve their goal, it may have been energetically less costly to travel the cleared pathway. Alternatively, turtles may have mistaken cleared trails for dry watercourses, but this seems unlikely because they turned uphill as often as downhill onto them (Yeomans, 1995).

Olfactory Discrimination.—Stott (1988, pers. comm.) tested hatchling *C. longicollis* from natural nests for the ability to use olfaction to find water. Controls (nasal irrigation with distilled water) all moved in the direction of a nearby pond when released downwind from that pond at night, whereas experimentals (nasal irrigation with the local anaesthetic amethocaine) did not show any orientation. It is likely that Stott's preliminary observations were confounded by the fact that amethocaine probably affects other functions besides olfaction.

Contrary to popular belief, throat movements

in turtles do not take place during periods of lung ventilation, but their frequency increases significantly when food extracts are presented (McCutcheon, 1943). McCutcheon (1943) concluded from these observations that the main function of throat movements is olfaction. Intrapulmonic pressure changes responsible for lung ventilation are caused by muscles that expand or contract the limb pockets (Gans and Hughes, 1967; Jackson, 1979).

Ortleb and Sexton (1964) reported that submerged female painted turtles tested in a laboratory Y-maze failed to orient towards water current bearing aromatics from aquatic plants. Boycott and Guillery (1962) used *Trachemys scripta elegans* to demonstrate that freshwater turtles can be trained to make discriminations based on chemical cues. To date apparently no one has tested the ability of highly migratory species, like *Chelodina*, to use olfaction as a navigational aid. Our observation of gular (throat) pumping by migrating *Chelodina* suggested that olfaction might be important to terrestrial navigation. The lab experiments confirm that these animals can distinguish and orient toward the odor of swamp muck. How far away turtles can distinguish odors is unknown, but olfaction may become more important to them the closer they get to the odor source.

The ability of freshwater turtles to orient towards airborne odors has previously not been tested. The fact that wind direction did not seem to influence turtle orientation during our open field trials does not rule out the possibility that *C. longicollis* uses an olfactory orientation mechanism relying on airborne cues. Papi et al. (1974) proposed an elegantly simple intermediate-range olfactory orientation mechanism for pigeons that is independent of wind direction. It relies on an olfactory map established at the bird's home loft as a result of the learned direction of various odors. The closer the turtles are to their goal when the wind is from that direction, the greater the chance that they may detect airborne odors and use them to orient. Our observations of turtles moving very deliberately in the bush when the wind was blowing directly towards them from Ryan's Swamp suggests that olfactory orientation is a useful strategy when employed under the right conditions, but that it is only one in a suite of mechanisms which *Chelodina* can employ. A combined olfaction and sun-compass orientation mechanism which relies on more than one sensory input has definite advantages for complex navigation (Keeton, 1974).

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