embryo was 12 h older when the nighttime measurement was made, the effect of aging is to reduce the size of the diurnal modulation as measured.

When the difference is found, instead, by subtracting the nighttime value from the daytime value that would be expected for an embryo of the same age, the amplitude of the diurnal modulation very nearly coincides with that found for adult birds [2]. That is, these data provide strong evidence that even under constant external conditions a diurnal rhythm of energy metabolism is already present in the early days of embryonic development. Similar results were obtained by Barnwell [3], who found that the metabolic rate of chicken embryos was lower at night than during day. The opposing view, that circadian rhythms are not (yet) present in vertebrate embryos, has been supported by Rensing [4]. A diurnal rhythm has also been demonstrated in the herring gull (*Larus argentatus*) by Drent [5], though his experiments were indirect: he measured the egg temperature, keeping the incubation temperature constant, and found lower values at night, which could be explained only by reduced metabolism in this phase. Although no other relevant studies on birds have been published [6], the available data show quite clearly that phenomena with a circadian rhythm, perhaps already under endogenous control, cannot be ruled out in the embryo.

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Equatorial Sandhoppers Do Not Have a Good Clock

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In equatorial regions, animals which use the sun compass for their orientation come across a number of difficulties [1]. The first is that every 6 months the sun changes its path from clockwise to anticlockwise, and vice versa. Secondly, as it moves from one hemisphere to the other, the sun passes over the zenith, and during this period it does not supply any azimuthal information. Finally, at the solstices the sun's speed on the horizontal plane during the day is far from constant: until approximately 10 a.m. and again after about 2 h in the afternoon there is little change in the solar azimuth, but during the middle of the day the azimuthal variation per hour is considerable. Consequently, [2] a constant change in the angle of orientation is not always sufficient to guarantee a constant direction within tolerable limits. Recently, we demonstrated [3] that *Talorchestia martensii* Weber uses a magnetic compass which gives the sea-land axis of the sandhoppers' home beach and works in conjunction with the sun compass. The existence of the sun compass in equatorial sandhoppers was first demonstrated in [2, 4].

Our experiments aimed to determine the sun's role as an orienting cue in relation to the magnetic compass. We used for this purpose an apparatus which consists basically of a transparent Plexiglas bowl (diameter 20 cm) with a white Plexiglas screen to hide the surrounding landscape from view. Two horizontal Helmholtz coils were set on each side of the apparatus. The coils were connected to a car battery, and the intensity of the artificial magnetic field was regulated with a stabilized rheostat. For the experiments, adult individuals of *T. martensii* were used which had been collected no more than 10 days before from a sandy beach at Temple Point (Malindi, Kenya). The theoretical escape direction (TED = direction toward the sea perpendicular to the coastline) was 192°. The individuals were released in the bowl one at the time, and the directions they assumed at the edge of the bowl were read every 3 to 5 s from a goniometer underneath. The behavior of each individual was noted as well as the direction and position of the long body axis with respect to the radius of the bowl to obtain a total of 30 radial readings for each individual. A reading was considered radial if the long body axis of the sandhopper fell between ± 45° with respect to the radius of the bowl.

Both field and laboratory experiments were held at Malindi (3°13' S, 40°07' E) from November to December 1989. Laboratory experiments were conducted in a darkroom with an artificial zenithal light (electric torch) over the bowl. In the field, the sandhoppers were tested at different times of the day under the sun. In both the laboratory and field experiments the sandhoppers were tested with the natural magnetic field and in absence of its horizontal component. In some releases under the sun we deflected the magnetic north to the east.

Because of the bidirectional tendency in the orientation of *T. martensii* along the *Y*-axis [4], it was not possible to use second-order statistical analysis. For first-order analysis we employed the methods for circular statistics [5].

In the dark room, with only the magnetic field, the sandhoppers were well able to orient along the *Y*-axis of their home beach (Fig. 1 A). When the horizontal component was zeroed (Fig. 1 B), however, they clearly lost this capacity and most of the individual distributions (10 out of 15) are dispersed. In the experiments held under the sun with the natural magnetic field deflected to the east (Fig. 1 C, D) the controls (C) are well clustered along the sea-land axis, but the experimentals (D) tend to be tetramodal. We had already obtained similar results in previous tests under the sun with clock-shifted individuals [3]. This tetramodal tendency probably depends on the alternate use of the two compasses, which are not synergic under these experimental conditions.

In the releases under the sun, the effect of the zeroed magnetic field is most evident when the individual distributions are grouped into time intervals (Fig. 2). The controls are well clustered along the *Y*-axis, more or less regardless of the time of day. In the middle of the day (when the sun appears to cross the sky more rapidly) the experimentals tend to be dispersed. However, it should be emphasized that the experimentals show a similar orientation to the controls in the morning and afternoon (times of the day when the sun's azimuth varies little around east and west).

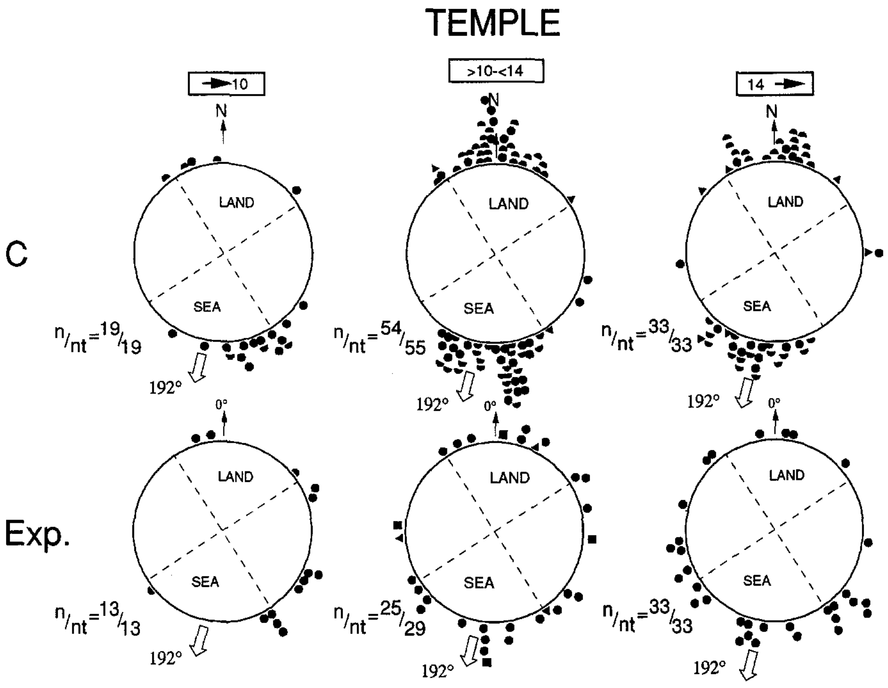

Fig. 2. Releases under the sun with natural (controls) and zeroed magnetic field (experimentals) grouped under different times of the day. → 10: releases made up to 10 a.m.; > 10 – < 14: releases made between 10 a.m. and 2 p.m. (period in which the apparent movement of the sun is very rapid); 14→: release made after 2 p.m. For further explanations, see Fig. 1

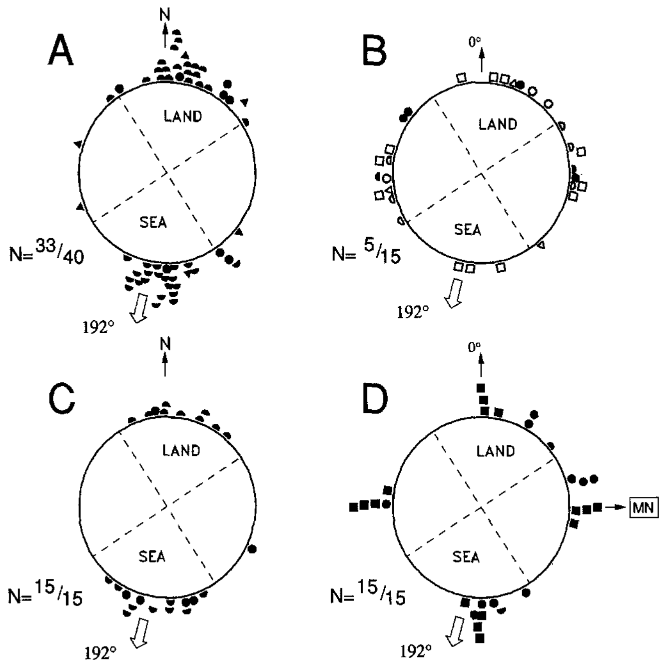

Fig. 1. Darkroom releases with the natural magnetic field (A) and without horizontal component of the magnetic field (B). C, D) Experiments under the sun with natural (C) and deflected (D) magnetic field. *Dots*, *half dots*, *triangles*, and *squares* represent the mean angles for uni-, bi-, tri-, and tetramodal individual distributions differing from uniformity (black symbols, $P < 0.05$ at least, Rayleigh test). *Open arrows* represent the TED; *N* number of significant individual distributions, *NT* total number of individuals tested. In B) the mean angles of non-significant distributions are included for graphic reasons

Considering the frequency of multimodal distributions (Table 1), it can be seen that they mostly occur when only the magnetic field is available to the sandhoppers, and decrease when the sun (perhaps together with other sky factors) takes over as the most important orienting cue.

From the above results, we can conclude that (1) both the sun compass and magnetic compass are confirmed to exist in equatorial sandhoppers; (2) the sun compass seems to be based on an imperfect internal clock, which only gives (or is only sufficiently precise for) the first hours in the morning and in the late afternoon, thus at these times of the day sandhoppers can orientate by the sun the whole year-round; (3) it seems that the sun informs the sandhoppers in which direction they should head along the *Y*-axis, and therefore reduces any bimodality resulting from magnetic orientation [6].

Our results point to a particular use of the solar reference, which is secondary to the magnetic compass. This type of mechanism could be a general rule for

Table 1. Distributions of the frequency of individual unimodal and multimodal distributions, with the magnetic field only (darkroom experiments), sun plus natural magnetic field, and sun only (magnetic field without horizontal component)

	n	Unimodal [%]	Multimodal [%]	G test
Magnetic field	33	24	76	9.056 $P < 0.01$
Sun + magnetic field	121	56	44	1.857 NS
Sun	71	94	6	67.172 $P < 0.001$

orientation in intertropical regions and in those cases when the sun's azimuth can only be utilized in the morning and afternoon [7].

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Invasive Dynamics of Africanized Honeybees in North America

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There have been many *a posteriori* ecological interpretations of newly introduced species in Europe and elsewhere, yet few studies have rigorously tested predictions about the dynamics of such invasions [1]. In this study, we examine the range expansion of an exotic insect, the Africanized honeybee in North America, and demonstrate how one can predict the dynamics of its spread using recent past events. African honeybees were introduced into Brazil in 1956 for the purpose of improving honey production among managed colonies in that country [2]. The subsequent range expansion of African-derived or "Africanized" honeybees has been intercontinental in scope, ranging from Uruguay and northern Argentina [3, 4] to southern Texas [5]. While the bees appear to have reached their southernmost distributional limits, to the north they continue to expand their distribution in Mexico and the United States. Climatic factors are expected to limit the northern distribution of these insects to southern or central United States [4, 6 – 8]. Initial northward movement of Africanized honeybees through subtropical South American latitudes was relatively slow (80 km/year in 1957 – 1963) [7]. However, as the bees reached more tropical latitudes in nothern South America, their rate of invasion increased (258 km/year in 1963 – 1976) [7]. Subsequently, range expansion from Panama to southern Mexico reached an average speed of 360 km/year [9]. Long-distance movement associated with range expansion is thought to result from reproductive and absconding swarm processes (natural range expansion) rather than human-assisted dispersal [7]. The rapid spread is partly due to accelerated colony growth and frequent issuing of reproductive swarms [10].

The arrival of Africanized honeybees at various locations in Mexico was established from swarms captured in bait hives consisting of 25-l cardboard boxes covered with plastic bags. Bait hives contained mixtures of citral, cit-