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Thermal ecology and spatio-temporal distribution of the Mediterranean lizard Psammodromus algirus

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We studied summer activity patterns and thermoregulation in the Mediterranean lizard *Psammodromus algirus* in a holm oak wood in Central Spain. The circadian rhythm curve was bimodal, with a pronounced peak after sunrise, a minimum at noon and a second lower peak in the afternoon. Increased activity in the morning could be explained by insolation levels, whereas the midday low was caused by the rise in temperature.

There was a strong positive correlation between body temperature and both air and ground temperatures. Nevertheless, there was no significant correlation between body and air temperatures when the effect of radiation was removed, which was done by considering only individuals in the shade at high temperatures.

Activity showed a bell-shaped relationship with body and air temperatures, with maximum activity at 24.5°C (air temperature) and 31.4°C (body temperature). The spatial distribution pattern of *P. algirus* (selection of sunny areas and distance to the vegetation edge) reflects the environmental temperatures that are optimal for activity; the lizards show a strong preference for sunny patches when air temperature is lower than the optimum. We conclude that heliothermy is the only viable thermoregulation pattern in Mediterranean forest environments, with heat conduction playing a negligible role.

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Introduction

Endothermic birds and mammals manage to control their body temperatures in a changing thermal environment by means of physiological regulation, whereas in reptiles, thermoregulation is basically a behavioural process (e.g. Avery 1982 and Spellerberg 1982). The amount of energy produced by the reptilian metabolic pathways is insignificant when compared with external sources of heat (mainly conduction and radiation; Tracy 1982), thus defining reptiles as ectothermic organisms whose low oxygen consumption rate and high thermal conductivity play an essential role in their energy balances (Avery 1982). Therefore, their spatial and temporal distribution are strongly determined by the thermal environment, which, affecting their physiological conditions, allows them to reach maximal performance levels (Tracy 1982, Hertz et al. 1988). This leads to the point of view that the thermal environment is a resource that can be exploited, and thus provides a bridge between physiological and population ecology (Tracy and Christian 1986).

Although there is a great number of lacertid species in southern Europe (see e.g. Spellerberg 1982 and Arnold 1987), works dealing with their thermoregulation in a Mediterranean climatic environment are still very scarce, and most of them merely consist of a collection of data concerning body temperatures (see Avery 1982 for references and review by Arnold 1987 on southwestern European lacertids). In addition, thermal restric-

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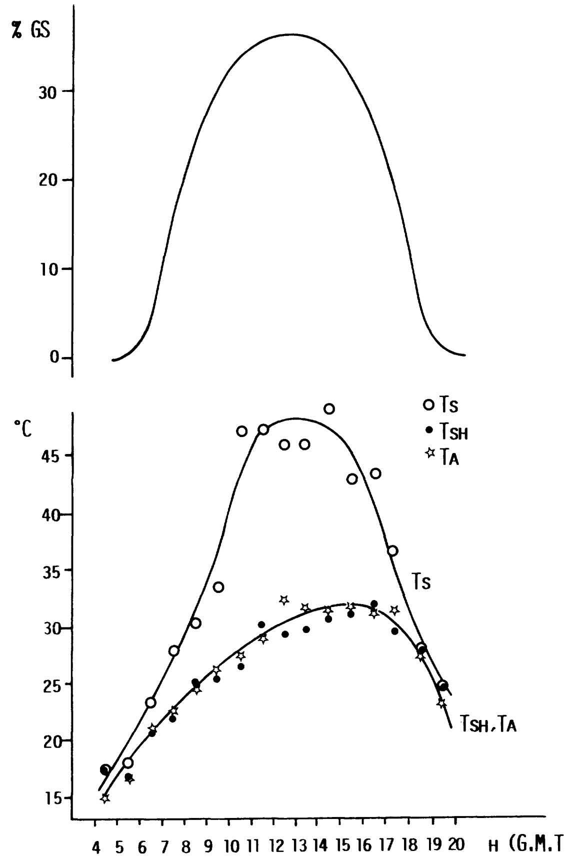

Fig. 1. Percentage of ground exposed to sun (%GS; top) and diel variations of air (Ta) and ground (Ts: areas exposed to sun; Tsh: areas in the shade) temperatures (bottom). Latter curves fitted by eye.

tions and requirements are especially important for small lizards, whose low thermal inertia makes thermoregulation mechanisms to be of crucial adaptive significance (Grant and Dunham 1988). This lack of knowledge is even more evident if we consider species of broad geographic distribution within a varied range of habitats, such as *Psammodromus algirus* in the Iberian Peninsula, where it occupies a remarkable diversity of environments (Arnold and Burton 1978, Salvador 1985). For this species, the data are scarce (Busack 1978), and do not explain the width of the species' habitat selection pattern according to the thermal environment and the optimal values for its ecological performance (see e.g. Roughgarden et al. 1981 for discussion).

In this context we have analyzed the temporal (circadian rhythm) and spatial distribution of *P. algirus* in a Mediterranean holm oak forest located in Central Spain; samples were taken during June and July, which are the months with the most contrasting temperatures on an annual basis. We have considered the role of heliothermy and thigmothermy in thermoregulation, and the influence of the thermal environment on the within-habitat distribution pattern.

Materials and methods

Study area

The study area (100 ha) was located in the middle of the Iberian Peninsula, in Soto de Viñuelas, Madrid (40°35'N, 03°34'W). The vegetation of the study area consists of a characteristic Mediterranean forest of *Quercus rotundifolia* with an undergrowth of *Cystus ladanifer* and *Lavandula pedunculata* shrubs. Canopy height averages from two to four metres and bush coverture is about 65%. Summer mean temperature (June and July) is 22°C, and the mean value for precipitation is 23 mm (Elías and Ruiz 1977). The study was conducted between 24 June and 23 July 1987. For more details on the study area see Díaz (1988).

Sampling methods

Activity rates were determined by the number of detected individual lizards; during the study period only subadult and adult individuals were present. The contacts were made by hearing and sighting the animals when they started fleeing. The time employed in searching for lizards was controlled by two persons with a chronometer; activity rates are given as number of individuals per ten minutes of search. Only observation periods of more than 20 minutes were analyzed.

For each period the following data were recorded: hour (G.M.T.), air temperature near the ground (measured to the nearest 0.5°C with mercury thermometer) and ground temperature (at a soil depth of 0–0.5 cm) both in sunny and shady areas (see Fig. 1).

The circadian activity pattern was obtained by pooling the data (1592 min of search and 162 individuals observed) of each of the 16 one-hour observation periods (betweeen 0400 and 2000 h G.M.T.) from the different sampling days. For each observed individual the distance to the edge of the nearest vegetation patch was noted, as well as whether or not it was basking. In addition, 57 lizards were captured at different times of the day. The body temperature of the lizards was recorded to the nearest 0.5°C by inserting a thermometer in the lizard's cloaca, and the air and ground temperatures were also recorded at the place and time of capture. Finally, the distance to the edge of the nearest shrub was measured at 43 randomly-selected spots.

Data handling

The percentage of ground exposed to sun was estimated by the angle formed by the sun upon the horizon, taking into account the tree height and bush cover of the study area (obtained by a simulation program model; Fig. 1).

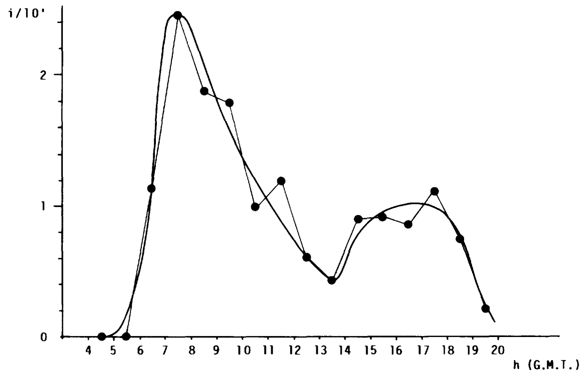

Fig. 2. Diel variations of activity (number of individuals per 10 minutes of search). Curve fitted by eye.

As we found no differences in circadian activity rhythm, basking frequencies or body temperatures between subadults and adults (Díaz 1988), calculations are based upon the combined sample. In the statistical analysis of the data the following techniques were used: t-test for means, F-test for variances, Mann-Whitney's U-test and correlation and regression analysis. The data on the distances to the nearest shrub edge were normalized by square root transformation (Sokal and Rohlf 1969).

Results

Circadian activity rhythm

The diurnal activity curve was clearly bimodal. There was a pronounced peak after sunrise (0800–0900 h G.M.T.) and a second lower peak in the afternoon (1600–1700 h G.M.T.; Fig. 2) There was not a linear relationship between activity and air temperature or ground temperature (Ta: air temperature; Ts: temperature of ground exposed to sun; Tsh: temperature of ground in the shade; $|r| < 0.2$ and $p > 0.1$ for the three correlations).

Thermoregulation: Relationship between body temperatures and environmental temperatures

There was a strong positive correlation betwen body temperature (Tb) and both Ta and ground (Tg) temperature (Ta: $r = 0.847$; Tg: $r = 0.654$; $n = 57$, $p < 0.001$ in both cases). Ta was the variable responsible for this association (Fig. 3), as it showed a significant partial correlation with Tb (Ta: $r = 0.722$, $p < 0.001$; Tg: $r = 0.183$, $p > 0.1$). Nevertheless, there was no significant correlation between Tb and Ta when the effect of radiation was removed. This was done by considering only the individuals that were found in the shade at ambient temperatures of 28°C or higher ($r = 0.394$, $n = 15$, $p > 0.1$), when a very low percentage of animals were basking (8.4%; see below).

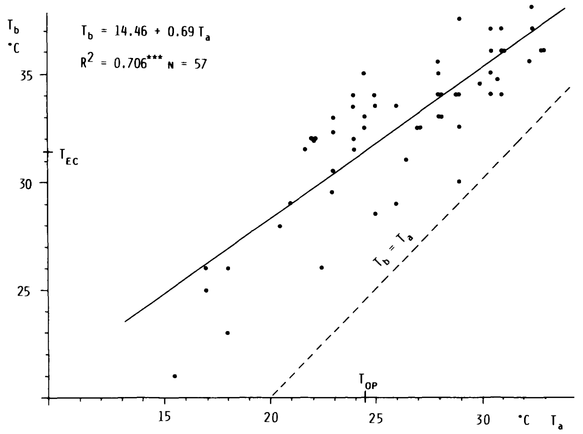

Fig. 3. Linear regression between body (Tb) and air temperatures (Ta). Top: optimal temperature (the temperature corresponding to maximum levels of activity); Tec: eccritic body temperature.

Although there was a clear association between Tb and Ta, some thermoregulation took place, as the variation in Tb was less than the variation in Ta (Tb: $SD = 3.62$, $n = 57$; Ta: $SD = 5.17$, $n = 199$; $p < 0.01$ in the F-test). In addition, there was a significant inverse correlation between Ta and the difference Tb-Ta ($r = -0.582$, $n = 57$, $p < 0.001$), showing that heat absorption is greater at low temperatures.

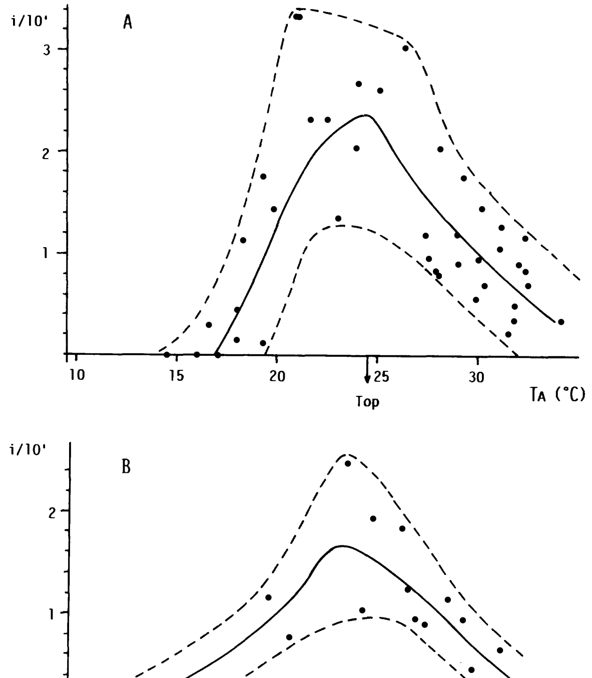

Fig. 4. Relationship between activity and air temperature (Ta). The arrow indicates the optimal value of Ta (Top). B: Relationship between activity and body temperature (Tb). The arrow indicates the eccritic value of Tb. See text for more details.

Tab. 1. Correlation coefficients (r: simple correlation; r': partial correlation) between activity values and thermal variables of the environment. Ta: air temperature; %GS: percentage of ground exposed to sun. Underlined signs: data agreed with predictions. See Fig. 2 and text for more details.

h (G.M.T.)	n	r		r'		PREDICTIONS	
		Ta	%GS	Ta	%GS	Ta	%GS
4–8	4	0.965*	0.999***	–0.003	0.985**	+	$\underline{+}$
7–14	7	–0.955***	–0.982***	–0.794*	–0.377	$\underline{-}$	–
13–18	5	–0.726(*)	–0.737(*)	–0.129	–0.224	–	–

(*): $p<0.1$ *: $p<0.05$ **: $p<0.01$ ***: $p<0.001$

Variations of activity related to the thermal environment

Fig. 4a shows that there was a bell-shaped relationship between activity and Ta (polynomial regression of order three; $r = 0.664$, $n = 43$, $p < 0.001$). The optimal value for Ta (Top), which was related to maximal activity, was 24.5°C. The influence of Ta on activity levels was mediated by its effects on Tb, as shown in Fig. 4b, which was obtained by plotting the mean value of activity against the mean body temperature for each of the 1-h observation periods (15 h; polynomial regression of order three: $r = 0.772$, $p < 0.001$). According to the regression line in Fig. 3, maximal activity was attained at a body temperature of 31.4°C; a similar result is shown in Fig. 4b.

To study the relationship between circadian activity rhythm and variations in the thermal environment, we divided activity time into three shorter time periods. The lengths of the different periods were established based on the maximums and minimums of Fig. 2. The drop in activity prior to sunset was not studied due to the lack of data (only three hours available). Tab. 1 shows the predictions derived from the hypotheses which are described below; the environmental variables and activity values used are shown in Fig. 1 and 2. The data were tested using one-tailed tests in all cases.

Activity should increase when Ta is less than Top (i.e. the temperature corresponding to maximal activity), and should decrease when Ta is greater than Top (Fig. 4a). The predictions were corroborated by the data (Tab. 1), although the data were marginally significant ($p < 0.1$) in the third period. In other words, activity increases significantly with Ta from sunrise to 0800 h G.M.T. ($Ta < 24.5$°C), and then falls significantly from 0800 h to noon ($Ta > 24.5$°C; Tab. 1).

When Ta is less than Top, the lizards should move to sunny areas because, by basking, they should be able to absorb heat from direct radiation, thereby increasing their body temperature and hence their activity. Conversely, under $Ta > Top$ conditions they should remain out of the sunny areas to avoid overheating (caused by radiation), which in turn would lower their activity even more. It follows that activity should be positively correlated to "sun availability" (percentage of ground exposed to sun; Fig. 1) with air temperatures lower than Top, and that this correlation should be negative with air temperatures higher than Top. Tab. 1 shows that all predictions were corroborated for the three analyzed periods, though significance in the third period was marginal ($p < 0.1$).

When the preceding analysis was performed by means of partial correlations, it became clear that the increasing percentage of ground exposed to sun (absorbed radiation heat transfer) was responsible for the morning increase in activity ($p < 0.01$), whereas Ta appeared to be the factor responsible for the midday fall in activity ($p < 0.05$; see r' in Tab. 1). The lack of significance in the third period can be attributed to the combined effect of both variables (R^2 for %GS on Ta = 90% vs the above mentioned low correlations with activity rates) and especially to the lack of variation in Ta during this period.

There is another fact that reinforces the role played

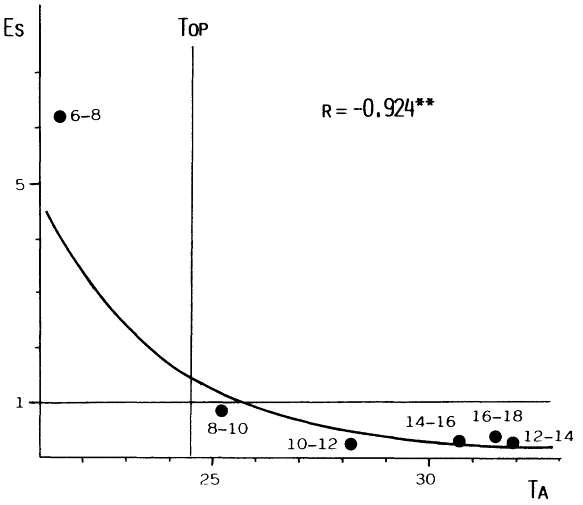

Fig. 5. Regression model showing the relationship between electivity of the lizards for sunny areas (Es; see text) and air temperature. Each point was obtained by considering the quotient between basking frequency and percentage of ground exposed to sun for the six two-hour periods between 0600 and 1800 h G.M.T. Air temperatures were averaged over the same periods.

by radiation in the rapid increse in morning activity. Activity levels observed after sunrise were compared between sunny days and days that were extremely overcast, at the same Ta (18–20°C). On sunny days activity (1.44 individuals per 10 min) was greater than on cloudy days (0.25 individuals per 10 min; $U = 0$, $p = 0.05$).

Influence of the thermal environment on the within-habitat distribution pattern

The mean distance to the nearest vegetation edge, as determined from random sampling, was 0.75 m ($SD = 0.64$, $n = 43$), showing that the vegetation patches were very close to one another. Nevertheless, the mean distance observed for the lizards was significantly smaller ($x = 0.19$, $SD = 0.18$, $n = 164$, $p < 0.001$, t-test), showing that *P. algirus* occupied areas covered by shrubs and the immediate surroundings.

Fig. 5 shows that the electivity of lizards for the sunny areas within their home ranges was inversely related to air temperature (polynomial regression of order two, $r = -0.924$, $n = 6$, $p < 0.01$). The proportion of basking individuals vs the percentage of ground exposed to the sun was greater than one when the air was cooler than Top; this relationship became less than one when Ta was greater than Top. In addition, the electivity at $Ta = Top$ predicted by this regression model did not differ significantly ($p > 0.2$) from one (random use of sunshade patches). This means that under thermal conditions optimal for activity, the animals were not constrained to select their position within the thermal mosaic of sunshade patches. Conversely, at low temperatures the lizards moved to the few available areas which were exposed to sun, whereas at high temperatures, and despite the high percentage of ground exposed to sun, almost all the individuals remained in the shade within the shrubs.

Consequently, we postulated that the lower the value of Ta, the further the lizards should move away from the vegetation edge, allowing themselves to warm up by basking. Conversely, at high temperatures they should remain out of the sunny areas, protecting themselves from radiation inside the vegetation patches. If this was true, it would show that the thermal environment is at least partially responsible for the observed within-habitat distributional pattern. The average distance from the edge of the vegetation was compared at extreme temperatures at both sides of the central optimum ($Ta < 21°C$ and $Ta > 28°C$). The mean distance was greater at low temperatures than at high temperatures ($p < 0.05$, t-test; 0.32 m at $Ta < 21°C$ vs 0.10 m at $Ta > 28°C$), confirming the effects of the thermal environment on the within-habitat distribution of *P. algirus*.

Discussion

Variations in the body temperature of *P. algirus* were strongly determined by radiation, according to the general pattern of heliothermy (Pough and Gans 1982) which characterizes lacertid species (Avery 1982). *Psammodromus algirus* exhibited a thermoregulation pattern which, through basking, exploited the within-habitat thermal patchiness of the cleared forest, hence resulting in a broad range of environmental temperatures available for activity (Ruibal and Philibosian 1970, Porter and Tracy 1983). The same thermoregulation pattern has been described for other non-forestal Mediterranean lizards (*Podarcis pityusensis*; Perez-Mellado and Salvador 1981) and for certain tropical iguanids inhabiting open forests (*Anolis* spp.; Avery 1982 and references therein).

Thermoregulation based upon heliothermy was accomplished behaviourally. The animals carefully selected the available patches within their home ranges, searching for sunny open areas (without vegetation) on the ground at low ambient temperatures and, conversely, hiding in the shady areas within the vegetation when ambient temperatures were high. Heliothermy provides a basis upon which the thermal environment, heterogeneous over space (according to shrub and tree cover) and variable over time (according to circadian rhythm), can be regarded as an exploitable resource (Magnuson et al. 1979, Spotila and Standora 1985, Tracy and Christian 1986). Thermal constraints resulted in a differential use of the home-range (Christian et al. 1983, Waldschmidt and Tracy 1983), with a majority of individuals facing the southeast in the early morning and a more uniform distribution in the middle of the day (pers. observ.). All of this evidence suggests that movements between sun and shade in *P. algirus* are "predictive" rather than "reactive" (Neill 1979), as lizards were trying to maintain body temperatures within a range of values optimal for activity. This conclusion is reinforced by the significant inverse correlation between air temperature and heat absorption (see Results), with increased heat gain at low temperatures, when a majority of individuals were basking in sunny areas (Fig. 5).

Thigmothermy (Pough and Gans 1982) seemed to play no role in the thermoregulation pattern of *P. algirus* as there was no significant partial correlation between body temperature and ground temperature. This lack of heat conduction from the substrate contrasts with the pattern observed in Mediterranean lacertid species inhabiting subalpine environments, where ambient temperature is always very low and lizards attain optimal body temperatures absorbing heat from the warm surface of the rocks (e.g. *Lacerta monticola*, an endemic species from the Iberian mountains; Martinez-Rica 1977).

Thigmothermy is probably not a suitable thermoregulation strategy in Mediterranean forest environments where ground temperatures, due to the sun-shade effect, are extremely variable (see Tsh and Ts in Fig. 1). During their daily movements within their home-ranges (foraging, predator avoidance, territorial displays, etc), individual lizards did not spend a sufficient amount of time in either the sun or the shade patches of the thermal mosaic so that body temperatures could equal ground temperatures (Bartholomew 1982).

On the other hand, the lack of significant correlation between body temperature and air temperature when the effect of radiation was removed (animals in the shade; see Results), revealed the negligible role of heat conduction from the air as a general feature in the thermoregulation pattern of *P. algirus* (see Tracy 1982 and references therein for a similar conclusion; but see Spotila and Standora 1985). The above-mentioned significant correlation between air and body temperatures should therefore be regarded as a loose association as air temperature is a summary variable for the thermal state of the environment.

The behavioural adjustments of *P. algirus* in the utilization of the thermal mosaic of sun-shade patches within its habitat, can be explained by considering that there is an optimal value for the physiology, and hence activity, of the species (see Huey 1982). Activity is an index of performance whose biological significance has been demonstrated (Huey and Stevenson 1979); in lizards, maximal activity is directly related to foraging efficiency and vulnerability to predation as well as other ecological traits (Huey and Slatkin 1976, Christian and Tracy 1981, Bauwens and Thoen 1981, Huey 1982).

The thermoregulatory behaviour of the *P. algirus* varies with ambient temperature (as it relates to Top) as was shown in its temperature-dependent fluctuations in electivity for sunny areas. The rise of air temperature over the optimal value in the middle of the day, explains the bimodality observed in the circadian activity pattern of *P. algirus* and, presumably, of other Mediterranean lacertid species with similar bimodal patterns (e.g. *Acanthodactylus erythrurus*, Busack 1976, *Podarcis pityusensis*, Pérez-Mellado and Salvador 1981, and *Lacerta scheriberi*, Salvador and Argüello 1987). It can therefore be concluded that the spatio-temporal distribution of *P. algirus* is dependent upon the thermal environment according to the environmental temperatures that are optimal for activity (Grant and Dunham 1988).

The strategy of heliothermic ectothermy allows the lizards to have relative densities (260 active individuals per 10 ha, estimated by the line-transect method; Telleria 1986) that exceed those of endothermic vertebrates of a similar body size. Density of birds weighing less than 11 g, for instance, has been estimated as 3.9 individual birds per 10 ha in a structurally similar forest located nearby the study area (*Sylvia undata, S. melanocephala, Parus caeruleus* and *Aegithalos caudatus*; Tellería and Garza 1981), with an average density of one individual bird per 10 ha per species. Therefore, heliothermy allows *P. algirus* to prosper in the hot, dry Mediterranean environments with considerably lower energy expenditures than that of similar sized homeothermic-endotherms (Pough 1980 and Nagy 1983).

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