

zwar höchstens zwei verschiedenartige, zufällig vorher bestimmte Beutetiere je Tag. Eines galt als abgelehnt, wenn es während der Darbietungsdauer nicht geschnappt war; auch wenn es ablehnende andere Individuen beträchtlich länger reizte, stiessen sie ihre Entscheidung nicht um. Die selektive Ablehnung eines bestimmten Beutetieres liess sich meist von einer allgemeinen durch mangelnden Hunger unterscheiden, wenn ein sofort danach gebotenes anderes Beutetier gefressen wurde. Bei der ersten Darbietung der 5 Beutetierarten lehnten weit mehr *Anolis* Heimchen und Asseln ab als Mehlwürmer und Getreideschimmelkäferlarven. Hingegen nahmen alle Individuen Wachsaupen an (Figur a). Von 32 möglichen Kombinationen der Annahme und Ablehnung sind nur 7 verwirklicht. Das selektive Verschmähen von Heimchen bleibt bei 19% der *Anolis* über wenigstens 9 Heimchendarbietungen bestehen, d.h. in der Regel 5 Wochen lang. Dagegen werden Asseln, bis auf eine Ausnahme, und die übrigen Beutetiere schon nach wenigen Darbietungen nicht mehr abgelehnt; nach 5 Wochen sind von den sieben Verhaltenstypen nur mehr 3 übrig geblieben, die *Anolis* also einander ähnlicher geworden (Figur b). Die raschere Annahme der Asseln und die Tatsache, dass Heimchen- und Asselablehner verschiedene Tiere sind, legt die Annahme nahe, dass zumindest

Heimchen und Asseln aus verschiedenen Gründen verschmäht werden. Die *Anolis* erweisen sich als «Generalisten» nach Modell (b), deren Gemeinsamkeit, Wachsaupen zu fressen, zunächst zwar gering ist, später aber die ursprüngliche angeborene Spezialisierung (Figur a) weit übertrifft.

Die Ergebnisse lassen vermuten, dass die *Anolis* in bestimmten Eigenschaften ihrer Wahrnehmung polymorph sind, ähnlich wie es BURGHARDT³ bei Strumpfbandnattern (*Tamnophis s. sirtalis*) gegenüber zwei Beutesorten gefunden hat. Einzeltiere bevorzugen entweder Wurm oder Fisch, sind hierin aber flexibler als unsere bei Geburt beutestarr festgelegten *Anolis*. Die individuelle Spezialisierung könnte im Freileben innerartliche Nahrungskonkurrenz mildern. Die Untersuchungen werden fortgesetzt.

Summary. Newborn lizard (*Anolis lineatopus*) individuals differ clearly by their acceptance of 5 different prey items; there are 7 'etho-types' of differential acceptance which after 5 weeks of feeding have become reduced to only 3.

FRIEDERIKE VON BROCKHUSEN und E. CURIO

Ruhr-Universität Bochum, Abteilung für Biologie,
Arbeitsgruppe für Verhaltensforschung, Postfach 2148,
D-463 Bochum-Querenburg
(Bundesrepublik Deutschland, BRD), 6. August 1974.

³ G. M. BURGHARDT, Behaviour, im Druck.

Moth Mating Periodicity: Temperature Regulates the Circadian Gate

In moths, the periodicities of female pheromone emission and male responsiveness have been accepted to be temporally synchronous, rigidly programmed, and to serve as isolating mechanisms among species utilizing a common chemical communication system¹⁻³. Recent findings in an arctiid⁴, a noctuid^{5,6} and numerous tortricids⁷⁻⁹ have revealed that rhythms of female calling behavior, or male response, or both, appear to be greatly modified by fluctuations in temperature regimes: lower ambient temperatures cause the mating response intervals to be shifted to warmer periods of the day or night. Such temperature-related rhythm modifications of female calling behavior and male flight have also been reported¹⁰ in the semi-domesticated saturniid, *Antheraea pernyi*. One previous study¹¹ with this silkworm moth indicated a discrete mating interval, whereas others^{12,13} on the contrary reported that this species lacks overt calling behavior and mating periodicity. TRUMAN¹⁰ found that the temperature regime during the 20 days of adult maturation in the pupa programmed the periodicities of female calling behavior and male flight. Cool developmental temperatures such as 12°C result in adult rhythms of female calling behavior and male flight occurring several hours prior to these rhythms in moths from pupae maintained at 25°C. These fixed intervals persisted throughout adult life regardless of ambient temperature.

In Lepidoptera the temperature modulation of circadian mating rhythms appears to be prevalent. In at least several lepidopterous species this modification is under regulation of a quite different mechanism: in *Argyrotaenia velutinana* (Walker), a tortricid, and *Holomelina immaculata* (Reakirt), and arctiid, adjustments of periodicity are coordinated to daily rather than seasonal temperature fluctuations.

The *A. velutinana* laboratory colony originated from material collected in Geneva, N. Y. and the *H. immaculata* culture was obtained from Dryden, N. Y. All insects were reared on an artificial medium⁴ at 24°C under a 16:8 LD (light-dark) cycle, with photophase at 2800 lux.

For determination of female calling periodicities, 0-1-day-old females were confined individually in airtight plastic vials 5 cm in diameter and 8.5 cm in height. Viewing of behavior during scotophase was accomplished with a low intensity light filtered with a Kodak Wratten Filter 29, eliminating light below 6100 Å.

¹ E. O. WILSON and W. K. BOSSERT, Recent Progr. Horm. Res. 14, 673 (1963).

² K. HOFFMAN, Proc. int. Symp. Circadian Rhythmicity (Purdue, Wageningen, Holland 1972), p. 175-205.

³ W. L. ROELOFS and R. T. CARDÉ, in Pheromones (Ed. M. C. BIRCH; North Holland Publ., Amsterdam 1974), p. 96-114.

⁴ R. T. CARDÉ and W. L. ROELOFS, Canad. Entom. 105, 1505 (1973).

⁵ C. A. SAARIO, H. H. SHOREY and L. K. GASTON, Ann. ent. Soc. Am. 63, 667 (1970).

⁶ L. L. SOWER, H. H. SHOREY and L. K. GASTON, Ann. ent. Soc. Am. 63, 1090 (1970).

⁷ W. C. BATISTE, J. econ. Entom. 63, 915 (1970).

⁸ C. J. SANDERS and G. S. LUCIUK, Canad. Entom. 104, 1751 (1972).

⁹ W. C. BATISTE, W. H. OLSON and A. BERLOWITZ, Envir. Entom. 2, 673 (1973).

¹⁰ J. W. TRUMAN, Science 182, 727 (1973).

¹¹ R. H. BARTH JR., Science 149, 882 (1965).

¹² L. M. RIDDIFORD, J. Insect Physiol. 16, 653 (1970).

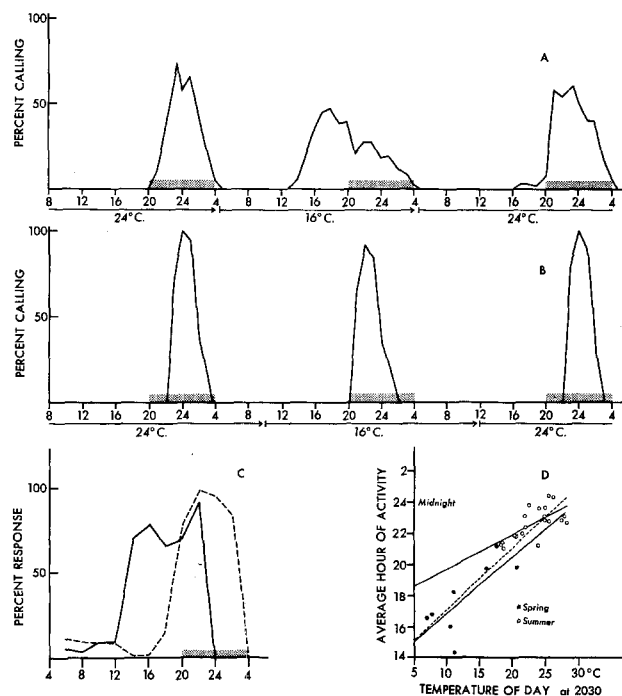
¹³ L. M. RIDDIFORD and C. M. WILLIAMS, Biol. Bull. 140, 1 (1971).

Laboratory *A. velutinana* male response tests were conducted under a simulated scotophase of 0.35 lux and a photophase of 2800 lux. The bioassay chambers consisted of $6 \times 8 \times 12$ cm plastic boxes holding 10 males. Through-out, 10^{-3} equivalents of methylene chloride female abdominal tip extract on 1×2 cm of filter paper were used as a stimulus for 1 min and wing fanning and flight were selected as the key behavioral responses. Males were assayed at hourly intervals and were not re-used. Field trials were conducted with an automated trap which

indicated the hour of attraction and 25 mg *cis*- and *trans*-11-tetradecenyl and dodecyl acetates (9:1:15) as a lure.

Results. At a constant temperature (24°C) these species differ in their responses to the photoperiodic cues affecting entrainment of their endogenous female calling rhythms. The rhythm of *A. velutinana* is entrained by the lights-on signal and the endogenous rhythm persists in either constant photophase or scotophase (LD); in *H. immaculata* lights-off serves as the critical photoperiodic cue and the rhythm is maintained only in continual scotophase⁴. *A. velutinana* females reared and observed at 24°C under a 16:8 LD call from the 1st h of darkness to its termination, whereas females held at 16°C initiate this interval some 6 h prior to scotophase (Figure a). Females of *H. immaculata* exhibit the same sort of temperature sensitive shift when contrasted at 16° and 24°C (Figure b). In both species females alternated through 24°, 16° and 24°C regimes modify their calling intervals in accordance with daily temperature. *A. velutinana* overwinters as a pupa¹⁴ and females from pupae chilled at 16°C from pupation until emergence, similar to the testing of *A. pernyi*¹⁰, exhibit the same adjustment of their calling rhythms as those maintained at 24°C. Thus, in some Lepidoptera, the female modifies its calling periodicity in response to daily temperature fluctuations rather than possessing a fixed interval programmed during adult development, as previously reported¹⁰.

A. velutinana males exhibit a similar temperature sensitivity of their periodicity of pheromone response. In laboratory bioassays at 24°C males were stimulated by natural pheromone extracts only during scotophase, whereas at 16°C male response occurred as much as 6 h prior to scotophase (Figure c). Under natural conditions the timing of attraction of wild males to the synthetic pheromone blend¹⁵ was correlated with temperature. In central New York in late April and early May during the spring flight, attraction occurred in the afternoon, whereas in the July summer flight, attraction took place after sunset (Figure d). Regression analyses comparing the average h of attraction and the temperature



A) *A. velutinana* (N = 60) and B) *H. immaculata* (N = 100) female calling periodicities in a laboratory 16:8 LD cycle alternated through daily temperature regimes of 24°, 16° and 24°C. Scotophase indicated by shaded areas. C) Laboratory flight response of *A. velutinana* males (N = 60) to female pheromone gland extract in 16:8 LD cycles at 24°C (broken line) and 16°C (solid line). Scotophase indicated by shaded area. D) Effect of ambient temperature on the mean time of wild male attraction in the field. Regression lines for the summer (top) and spring (bottom) are in solid line. The broken line is for the pooled flights.

¹⁴ P. J. CHAPMAN and S. E. LIENK, *Tortricid Fauna of Apple in New York* (Special publ. New York State Agric. Exp. Station, Geneva 1971), 122 p.

¹⁵ W. ROELOFS, A. HILL and R. CARDÉ, *J. chem. Ecol.* 7, 83 (1975).

Effects of a decrease in temperature of 24° to 16°C on the initiation of female calling behavior and male pheromone responsiveness in the laboratory under a 16:8 LD

Hours relative to scotophase	Percent females calling (N = 50)				Percent male pheromone response (N = 60)	
	min at 16°C			Constant 24°C	15 min at 16°C	Constant 24°C
	10	30	60			
-8	0	0	0	0	40	20
-7	2	2	4	0	62	20
-6	2	2	4	0	80	3
-5	5	8	13	0	73	0
-4	6	17	22	0	77	0
-3	13	25	31	0	75	1
-2	13	27	31	0	98	0
-1	11	20	25	0	97	7
0	12	30	35	0		
+1	36	36	36	17		

at 20.30 h (E.D.S.T.) shows $r = 0.768$ ($p < 0.05$) for the spring flight, $r = 0.664$ ($p < 0.01$) for the summer flight and $r = 0.908$ ($p < 0.001$) for the pooled data. Similarly, wild *H. immaculata* males were lured to synthetic 2-methylheptadecane, the female sex pheromone¹⁶, for the 2 h prior to sunset on a cool day (a high of 24°C) and for 2 h after sunset on a warm day (a high of 30°C)⁴.

In the oscillating daily temperatures found in nature these rhythmic modifications of the mating clock could be a function of the daily thermoperiod or they could be initiated by ambient temperature fluctuations occurring during a specific daily interval or selective circadian gate. The interactions of temperature and light cycles in affecting the initiation and duration of female calling behavior and male responsiveness are complex. Notwithstanding, in *A. velutinana* a decrease in temperature occurring within a specific daily gate can induce both female calling and male responsiveness within a few minutes (Table). Even if this decrease in temperature is as little as 1°C, a significant number initiate mating behavior. In the laboratory, 14.3% of the females ($N = 210$) experiencing a decrease from 24° to 23°C 1 h prior to lights-off in a 16:8 LD commenced calling behavior within 10 min [where the 95% confidence interval (CI) extends from 9.5 to 19.3%]. In the control group 0.5% of the females were calling (a CI to 2.6%). In male pheromone bioassays ($N = 200$) 54.3% experiencing an identical decrease in temperature were responsive to

female pheromone extract (CI 47.4 to 61.3%), whereas only 24.5% control males were responsive (CI 18.9 to 31.0%).

These findings indicate that the control centers for female calling behavior and male pheromone responsiveness have inputs from the circadian clock as well as external stimuli, apparently unlike the periodicities of female calling behavior and male flight in *A. pernyi* which are tightly coupled to the output of the clock¹⁰. This is the first report of current conditions modifying the timing of a circadian rhythm without appearing to affect its entrainment.

The adaptive significance of this intricate, daily temporal coordination of mating rhythm with temperature is obvious: cool temperatures are undesirable because they increase the demand for metabolic energy necessary to sustain mating flight¹⁷. This consideration is most crucial in small insects (such as *A. velutinana*) that possess a high surface area to volume ratio. Operating against this factor are possible evolutionary disadvantages such as increased difficulty in maintenance of temporal partitioning of closely-related species that utilize a common chemical communication system¹⁻³ and exposure to additional predator pressure during diurnal activity.

Résumé. Les lépidoptères modifient leur rythme endogène d'activité sexuelle selon le régime de température du jour. Les fluctuations de température dans certaines parties du cycle photopériodique servent de signal pour déterminer l'heure de l'accouplement.

R. T. CARDÉ, A. COMEAU¹⁸, T. C. BAKER and W. L. ROELOFS¹⁹

New York State Agricultural Experiment Station,
Department of Entomology, Geneva
(New York 14456, USA), 6 August 1974.

¹⁶ W. L. ROELOFS and R. T. CARDÉ, *Science* 171, 684 (1971).

¹⁷ J. L. HENEGAN and J. E. HEATH, *J. exp. Biol.* 53, 349 (1970).

¹⁸ Present address: Station de Recherches, Canada Department of Agriculture, Ste. Foy, Quebec, Canada.

¹⁹ This research supported by the Rockefeller Foundation and NSF Grant No. GB-38020. We thank Dr. R. Hoy for his comments.

The Rate of Testicular Development in Japanese Quail (*Coturnix coturnix-japonica*) Following Stimulation of the Extra Retinal Photoreceptor

Seasonal reproduction in many birds is regulated by the annual change in daylength, with the longer photoperiods of spring and summer causing increased gonadotrophin secretion. Knowledge about the neuroendocrine basis of this photoperiodic response is quite extensive^{1,2} but our understanding of the sensory structure(s) involved in light detection, and of the mechanisms used for measuring its daily duration³ is much more limited. The issue of light perception has been especially intriguing ever since Benoit suggested in the thirties that an extra-retinal photoreceptor existed in the duck. His many experiments led him to conclude⁴ that the eye played little or no role in the photoinduction of testicular growth and that another photoreceptor must exist elsewhere in the brain, probably within the hypothalamus. More recent studies in the house sparrow by MENAKER et al.⁵⁻⁸ confirm these findings and they have concluded that the eyes do not participate at all in the reception of light for the photoperiodic response. This is possibly true in other species also⁹⁻¹¹.

In the Japanese quail (*Coturnix coturnix-japonica*) there is clearcut evidence that enucleation does not block photoinduced gonadal growth^{12,13} or lead to regression in sexually mature birds maintained on long daylengths¹⁴⁻¹⁶.

¹ I. ASSENMACHER, in *Breeding Biology of Birds* (Ed. D. S. FARNER; National Academy of Sciences, Washington D.C. 1973), p. 158.

² B. K. FOLLETT, in *Breeding Biology of Birds* (Ed. D. S. FARNER; National Academy of Sciences, Washington D.C. 1973), p. 209.

³ B. K. FOLLETT, *J. Reprod. Fertil. suppl.* 19, 5 (1973).

⁴ J. BENOIT, in *La Photoregulation de la Reproduction chez les Oiseaux et les Mammifères* (Eds. I. ASSENMACHER and J. BENOIT; CNRS, Paris 1970), p. 121.

⁵ M. MENAKER, *Biol. Reprod.* 4, 295 (1971).

⁶ M. MENAKER, *Proc. natn. Acad. Sci., USA* 59, 414 (1968).

⁷ M. MENAKER and H. KEATTS, *Proc. natn. Acad. Sci., USA* 60, 146 (1968).

⁸ M. MENAKER, R. ROBERTS, J. ELLIOTT and H. UNDERWOOD, *Proc. natn. Acad. Sci., USA* 67, 320 (1970).

⁹ T. W. MUNNS, *Anat. Rec.* 166, 352 (1970).

¹⁰ E. GWINNER, F. W. TUREK and S. D. SMITH, *J. comp. Physiol.* 75, 323 (1971).

¹¹ P. C. HARRISON and W. C. BECKER, *Proc. Soc. exp. Biol. Med.* 132, 161 (1969).

¹² A. SAYLER and A. WOLFSON, *Arch. Anat. Histol. Embryol.* 51, 615 (1968).

¹³ K. HOMMA, W. O. WILSON and T. D. STOPES, *Science* 178, 421 (1972).

¹⁴ T. OISHI, T. KONISHI and M. KATO, *Envir. Cont. Biol.* 3, 87 (1966).

¹⁵ T. OISHI and J. K. LAUBER, *Am. J. Physiol.* 225, 155 (1973).

¹⁶ T. OISHI and J. K. LAUBER, *Am. J. Physiol.* 225, 880 (1973).