

## STRIDULATORY MOVEMENTS IN EIGHT SPECIES OF *NEOCONOCEPHALUS* (TETTIGONIIDAE)\*

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**Abstract**—High-speed sound-synchronized photography showed details of stridulatory movements and their relation to the sounds produced. Closing movements were more prolonged than opening movements and generally produced more intense sounds. Wing closures varied in rate from 10 to 250/sec. Four species had unpredicted complexities in their stridulatory movements: one silently snapped its wings shut after each acoustically effective stroke; two alternated long and short wing closures; and one made repeated groups of 4 to 9 progressively changing closures.

### INTRODUCTION

THE ADVENT of tape recording prompted many studies concerning the physical characteristics of the acoustic signals of insects (BUSNEL, 1963; ALEXANDER, 1967). However, the stridulatory movements responsible for these sounds were largely neglected, perhaps because such movements were presumed to be simple and nearly sinusoidal. Recent reports by WALKER and DEW (1972) and ELSNER (1974) have demonstrated that insect sounds are sometimes generated by surprisingly elaborate motor patterns, and that the details of stridulatory movements cannot be deduced from the nature of the sounds.

Unlike many other tettigoniids, the 8 species of *Neoconocephalus* discussed in this paper produce calling songs that are simple and quickly repetitious in their amplitude modulation patterns, and one would expect minimal complexity and variety in their stridulatory movements. I am reporting on these species rather than others that were originally of more interest because (1) they (unlike most of the others) occasionally continued to stridulate under the scrutiny of the high-speed camera, and (2) their stridulatory movements proved unexpectedly complex and varied.

### MATERIALS AND METHODS

Stridulatory movements and associated sounds were recorded by a high-speed camera on 16 mm film at speeds up to 3500 frames/sec. The camera simultaneously photographed the stridulating insect and the face of a dual-beam oscilloscope displaying the insect's sound and a time standard (5 kHz square wave). Equipment

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and techniques were those described by WALKER *et al.* (1970) except the top was removed from the insect's cage prior to filming and the output from the microphone (12.7 mm diameter, condenser type) was fed not only to the oscilloscope but also to a Nagra IV D sound recorder operating at a tape speed of 15 in/sec.

All individuals photographed were collected as adults and kept in a chamber having reversed photoperiod to encourage daytime singing. When an individual was heard stridulating, its cage was taken from the dark chamber and the lid removed. The insect was then positioned under the camera and exposed to the intense light required for filming. By this time, it had usually stopped stridulating and was returned to the dark. If it had not stopped, it often did so as the camera was started—resulting in 100 ft of film of a silent insect.

An undetected fragment of film that lodged inside the camera blocked its view of the oscilloscope for several days with the result that the films for two species, *melanorhinus* and *bivocatus*, had no sound or timing traces.

The successful reels were analysed by the first and sometimes the second of these two methods: (1) Viewing at 1 to 24 frames/sec and observing the wing movements and their relation to the oscillographic trace of the sound. (The sound trace was 5 frames behind the movement because of the design of the camera.) (2) Frame-by-frame measuring of wing separation and of the maximum displacement of the oscillographic trace. Many films were difficult to analyse by the second method because the wings were in poor focus or because there were no reference points on the wings that could be used for measurements throughout a cycle of wing movement. Applying dots of white paint to the wings prior to filming might have alleviated the latter difficulty.

Preparing objective illustrations of the wing movements and their relation to the sound was complicated by several circumstances. For example, the film speed varied continuously during each 'take' (i.e. one 100-ft reel): the camera required about 2500 frames to reach the set speed and decelerated for the remaining 1500 frames. By reference to the filmed trace of the 5 kHz square wave, film speed for each reel was plotted as a function of frame number, and this graph was used to convert the frame-by-frame measurements to a linear time scale. The dots plotted in Figs. 2 to 13 gradually spread or close in keeping with slowing or accelerating of the film. The oscillograms (made with a Honeywell Model 2106 Visicorder) in Figs. 2 to 13 have a linear time scale because they were made from the Nagra IV D tapes. These tapes were made as the stridulating insect was filmed, but except with *exiliscanorus* and in some instances with *triops* I found no way to match a specific phonatome with its actual cycle of wing movement. (Phonatome is the acoustical unit corresponding to a cycle of wing movement. Some katydids produce two or more types of phonatomes (WALKER and DEW, 1972), but except for *triops*, each species discussed here produces sequences of a single type of phonatome.) However, which part of a phonatome corresponded with which part of a cycle of wing movement was evident from both visual and frame-by-frame analysis. The phase relationships of the oscillograms and the wing movement plots were adjusted accordingly. Since the films for *melanorhinus* and *bivocatus* had no sound traces, the

phase relations within Figs. 2, 3, and 7 had to be based on comparisons with other species.

### RESULTS

Eight species were photographed. Individuals of two other species, *N. palustris* and *N. velox*, stridulated in the laboratory but always stopped during the preliminaries of filming.

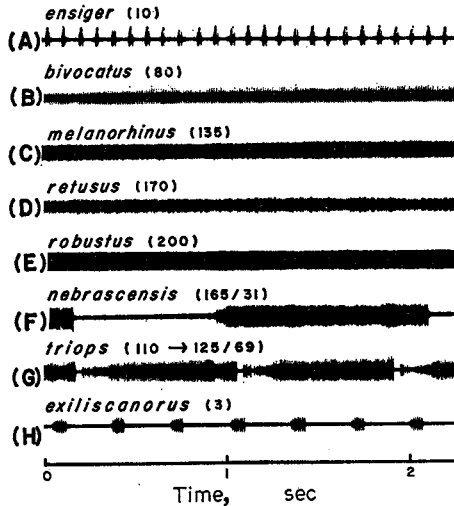
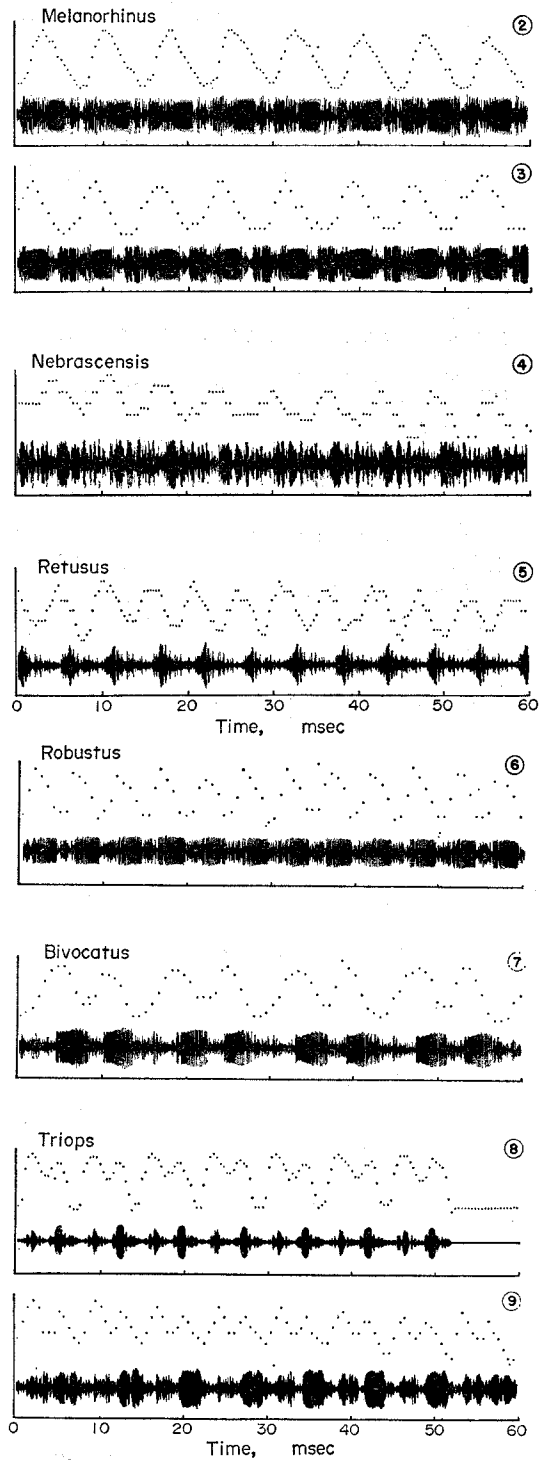
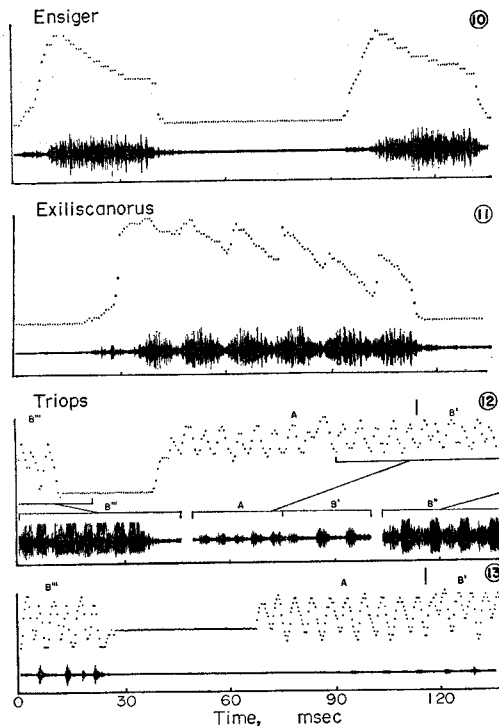


FIG. 1. Oscillograms showing song patterns of 8 species of *Neoconocephalus*. (A to E) Species that generally produce their phonatomes without pause for minutes at a time. (F to H) Species that pause regularly many times per minute. Numbers in parentheses after species names indicate phonatomes per sec and phonatome sequences per min. Species (B) and (G) have two acoustically effective wing closures per phonatome. Species (G) starts each sequence with one type phonatome and then shifts to a second, faster type. Species (H) makes 6 to 7 acoustically effective wing closures per phonatome at a rate of 80/sec. Temperatures 21 to 27°C.

Fig. 1 illustrates the overall amplitude modulation patterns of the calling songs of the 8 species. *N. ensiger*, *bivocatus*, *melanorhinus*, *retusus*, and *robustus* (Fig. 1A-E) produce songs that the human ear hears as continuous rattles, buzzes, or whines; in each case the wing-movement cycles are repeated for 1 min or more without interruption. The cycles, and the phonatomes they generate, are at nearly constant, though temperature-dependent, rates ranging between 10 and 200/sec. *N. nebrascensis* (Fig. 1F, 21°C) produces phonatomes at a rate of 165/sec but stops (and starts) production in a stereotyped fashion 31/min. *N. triops* (Fig. 1G, 27°C) interrupts its song with brief pauses 69/min. During the first 50 to 100 msec of each phrase it shifts from one type phonatome with a rate of 110/sec to another type phonatome with a rate of 125/sec. *N. exiliscanorus* (Fig. 1H, 25°C) produces





FIGS. 2 to 13. Stridulatory movements (dots) and oscillograms of calling songs of *Neoconocephalus*. (The higher the dots the more the wings are apart; and the lower the dots the more nearly closed are the wings. The oscillograms were prepared from tape recordings made during filming. Phase relationships between stridulatory movements and oscillograms have been adjusted to agree with frame-by-frame analysis of the film, including its sound trace. In most instances the particular phonotomes illustrated were not produced by the particular wingstrokes illustrated. For further details, see text.) Figs. 2 and 3. Two individuals of *N. melanorhinus*. Figs. 9 and 12. Portions of a single film of one *N. triops*. (Figs. 8 and 13 are of two other individuals.) Figs. 12 and 13. The B phonotomes are further classified as initial (B'), medial (B''), and terminal (B''').

rhythmic buzzy chirps at a rate of 185/min. Major modulations within each chirp, at first thought to be phonotomes, occur at 80/sec.

Although all rates are highly temperature dependent (WALKER, 1974), the amplitude modulation patterns do not change. The rate at a given temperature and amplitude modulation pattern are species specific. Intraspecific variation in the characteristics of the calling song is slight.

The wing movements during calling are described below.

*N. melanorhinus* (Figs. 2 and 3) moves its wings in nearly sinusoidal fashion and is acoustically effective in both opening and closing movements. The closing movements are noticeably slower than the opening ones, but the sounds made by closing

and opening are of approximate equal amplitude (at least below 20 kHz, the upper limit of flat response of the Nagra IV D). The terminology proposed by MORRIS and PIPHER (1972) is useful here. They note the existence of two pulse types in katydid songs. One is a *rapid-decay pulse*, a brief complex wave train of rapidly decreasing amplitude, and the other is a *prolonged pulse*, a wave train of relatively longer duration and uniform or smoothly changing frequency that approximates a pure tone. Closure in *N. melanorhinus* is essentially a single prolonged pulse.

*N. nebrascensis* (Fig. 4) and *N. retusus* (Fig. 5) apparently have stridulatory movements and related sounds comparable to *melanorhinus*. Cinematographic projection of the films showed regularly repeated wing movements with closure sounds including prolonged pulses. However, none of the films of these two species were of sufficient quality to give repeatable frame-by-frame measurements.

*N. robustus* (Fig. 6) is yet another species having simple wing movements. It differs from the others in having a higher phonatome rate (200/sec) and in the fact that the prolonged pulses (one per closure) generally dominate the calling song to such an extent that the aural impression is that of a penetrating whine.

*N. bivocatus* (Fig. 7) is morphologically so similar to *robustus* that the two were considered a single species until recently (WALKER *et al.*, 1973). Its wing movements are distinctive: long and short closures alternate and single prolonged pulses are produced during closures of both types. In spite of the different closure distances, successive prolonged pulses are similar in duration. The adjacent opening movements are more dissimilar than the adjacent closing movements—a longer (of greater amplitude) and slower (less distance moved per unit time) opening stroke is followed by a shorter and quicker one. The result is that the closure sounds occur in pairs. Since a cycle of wing movements is completed only after a long opening, a short closing, a short opening, and a long closing, the phonatome of *bivocatus* includes the sounds associated with all four movements.

*N. triops* (Figs. 8, 9, 12, 13) produces two types of phonatomes during each of its rhythmically repeated 1-sec bursts of singing. Each burst begins with a brief series of apparently unpaired trains of rapid-decay pulses produced on closing at a rate of approximately 220 trains/sec. These are labelled as 'A' phonatomes in Figs. 12 and 13. The remainder of each burst consists of 'B' phonatomes (Figs. 8, 9, 12, 13) in which closure pulse trains of two intensities alternate and the total rate is approximately 250/sec (i.e. 125 pairs/sec). The more intense closure pulse trains are dominated by single prolonged pulses while the less intense ones generally resemble those of the A phonatomes—i.e. trains of rapid-decay pulses. The cycles of wing movements responsible for A phonatomes resemble those of *robustus*, but careful scrutiny reveals that alternate cycles are more closely similar than consecutive cycles (Figs. 12, 13). Therefore, a complete cycle of A-type wing movement involves two closures, and A phonatomes have two closure pulse trains (*cf.* *bivocatus*). The sequence of A phonatomes is sometimes preceded by silent wing movements, and the intensity of the closure pulse trains increases during the sequence. The cycles of wing movement responsible for B phonatomes resemble those of *bivocatus* except that the long opening is at approximately the same speed

as the short one with the result that the two closure pulse trains of a phonatome are only slightly closer together than the adjacent closure pulse trains of consecutive phonatomes. Furthermore, the pulse train of the shorter closing stroke is conspicuously less intense than that of the longer closing stroke and is occasionally lacking (Figs. 12B', 13B', B''). The relative lengths of short and long closures vary in a single sequence (cf. Fig. 12B' and Fig. 9 of the same sequence) and from individual to individual (cf. phonatomes near the end of a sequence for the three individuals of Figs. 8, 13, and 9 and 12).

*N. ensiger* (Fig. 10) produces pulse trains at the slowest rate of any of the 8 species. After a nearly silent opening movement an acoustically effective closure generates a train of rapid decay pulses and returns the wings slightly more than half way to the original position. Then the wings snap quickly and nearly silently shut. Almost half of the distance moved by the wings during a phonatome has no obvious function.

*N. exiliscanorus* (Fig. 11) produces buzzy chirps that consist of 4 to 9 evenly spaced trains of rapid-decay pulses. Originally I supposed that each pulse train was produced by a similar cycle of wing movement, but the films showed otherwise: Each chirp is made by a series of progressively changing opening and closing movements, and a complete cycle of wing movement includes the entire series rather than a single opening and closing. Consequently, a phonatome in *exiliscanorus* is an entire chirp rather than the sound produced by a single open-close movement. Wing movements of *exiliscanorus* show some resemblance to those of *ensiger* (cf. Figs. 10, 11). Each species makes its acoustically effective closures slowly and then quietly snaps its wings shut prior to brief rests.

#### DISCUSSION

Stridulatory movements have been described in detail for only 6 species of Tettigoniidae, other than the 8 species just treated. PIERCE (1948) used cinematography at 16 to 64 frames/sec to study movements of 5 species representing 4 subfamilies. Four of the species have simple cycles of wing movement (comparable to Figs. 2-6): *Scudderia curvicauda*, *S. texensis* (Phaneropterinae), *Pterophylla camellifolia* (Pseudophyllinae), *Orchelimum vulgare* ('click' type phonatome) (Conocephalinae). The remaining species, *Atlanticus testaceous* (Decticinae), has wing-movement cycles with two closures (comparable to Figs. 7-9). WALKER and DEW (1972), using the same techniques as the present ones for *Neoconocephalus*, showed that *Amblycorypha uhleri* (Phaneropterinae) has a different wing-movement cycle for each of its four types of phonatomes. The most complex cycle includes a two-step closure and a nearly silent close-open movement.

Less detailed descriptions of stridulatory movements have been published for 6 additional species. PASQUINELLI and BUSNEL (1955) photographed a stridulating *Ephippiger bitterensis* (Ephippigerinae) at 65 frames/sec. SUGA (1966) removed teeth from the stridulatory file to determine in what direction the wings were moving during acoustically effective strokes of 4 species: *Drepanoxiphus modestus* (Pseudophyllinae), 2 species of *Phlugis* (Listroscellinae), and *Conocephalus saltator*

(Conocephalinae). MORRIS and PIPHER (1972) studied *Metrioptera sphagnorum* (Decticinae) by repeatedly photographing stridulating individuals and synchronized oscilloscopic traces of the sounds emitted. They demonstrated that the two types of phonatomes of this species are produced by cycles of movement at opposite ends of the file. One of the types is apparently made by 5 to 8 stops and starts of the apparatus during a single closure—resembling *N. exiliscanorus* (Fig. 11) but with stops rather than partial returns separating the stages of closure.

The strongest generalization that emerges from the sample of 20 species, 11 genera, and 7 subfamilies is that a diversity of stereotyped wing-movement patterns produce tettigoniid phonatomes. At least 6 qualitatively different patterns occur, and 4 of these are represented among the 8 species of *Neoconocephalus*. Single species may have two or more patterns (e.g. *M. sphagnorum*, *A. uhleri*), and the same complex pattern may occur in phylogenetically distant species (e.g. *N. bivocatus* and *A. testaceus*). The variety of wing movements known contrasts with the fact that a single pattern of wing movement is sufficient to produce hundreds of species-specific calling songs. For instance, the simplest pattern—an uninterrupted opening movement followed by an uninterrupted closing movement—can produce prolonged or decay pulses or both, can be made acoustically effective to varying degrees on opening, closing, or both, and can have opening and closing movements of varying durations and speeds. Furthermore, with any particular cycle of wing movement and its associated phonatome, distinctive calling songs can be made with different phonatome rates, different phonatome groupings, and different intervals between phonatome groupings. A variety of wing-movement patterns is not prerequisite to a variety of calling songs. Nevertheless, wing-movement patterns have been subject to frequent evolutionary change. The raw material for such a change is intraspecific variation, as illustrated in this paper with *N. melanorhinus* and *N. triops*. JOSEPHSON and HALVERSON (1971) and WALKER *et al.* (1973) provide myophysiological and behavioural evidence of such variation in *N. robustus*.

A second generalization, previously proposed by MORRIS and PIPHER (1972), is that the most prolonged song components are produced on closure. In the species studied thus far the ratio of the durations of closing and opening varies from more than 4 : 1 (*A. uhleri*, Type I phonatome) to nearly 1 : 1 (*N. melanorhinus*).

MORRIS and PIPHER (1972) also suggested that the most intense song components are produced on closure. This is usually the case but sounds made on opening vary in intensity from near zero (e.g. *Phlugis* spp.; *N. ensiger*) to moderate (e.g. *C. saltator*, *M. sphagnorum*), to approximately the same intensity as closing sounds (e.g. *A. uhleri*, Type I phonatome; *N. melanorhinus*).

The carrier frequencies of tettigoniid calling songs are apparently determined more by the physical characteristics of the stridulatory apparatus than by wing-movement patterns; however, during prolonged pulses tooth contact rate and dominant frequency coincide and speed of wing movement becomes a function of tooth spacing and tegminal resonance (BAILEY, 1970; BAILEY and BROUGHTON, 1970; MORRIS and PIPHER, 1972).



Too little is known to allow reconstructing the phylogeny of the diverse movement patterns of stridulating tettigoniids, but knowing the movements can prevent false homologies of amplitude modulation patterns and provide clues to evolutionary relationships. If the neurophysiological bases of the wing movements were known, another layer of false homology might be revealed. However, neurophysiologists have thus far studied only species with simple movements (eg. BENTLEY, 1969; KUTSCH and HUBER, 1970; JOSEPHSON and HALVERSON, 1971).

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#### REFERENCES

- ALEXANDER R. D. (1967) Acoustical communication in arthropods. *A. Rev. Ent.* **12**, 495–526.
- BAILEY W. J. (1970) The mechanics of stridulation in bush crickets (Tettigoniidae, Orthoptera)—I. The tegminal generator. *J. exp. Biol.* **52**, 495–505.
- BAILEY W. J. and BROUGHTON W. B. (1970) The mechanics of stridulation in bush crickets (Tettigoniidae, Orthoptera)—II. Conditions for resonance in the tegminal generator. *J. exp. Biol.* **52**, 507–517.
- BENTLEY D. R. (1969) Intracellular activity in cricket neurons during generation of song patterns. *Z. vergl. Physiol.* **62**, 267–283.
- BUSNEL R.-G. (Ed.) (1963) *Acoustic Behaviour of Animals*. Elsevier, New York.
- ELSNER N. (1974) Neuroethology of sound production in gomphocerine grasshoppers (Orthoptera: Acrididae)—I. Song patterns and stridulatory movements. *J. comp. Physiol.* **88**, 67–102.
- JOSEPHSON R. K. and HALVERSON R. C. (1971) High frequency muscles used in sound production by a katydid—I. Organization of the motor system. *Biol. Bull., Woods Hole* **141**, 411–433.
- KUTSCH W. and HUBER E. (1970) Zentrale versus periphere Kontrolle des Gesanges von Grillen (*Gryllus campestris*). *Z. vergl. Physiol.* **67**, 140–159.
- MORRIS G. K. and PIPHER R. E. (1972) The relation of song structure to tegminal movement in *Metrioptera sphagnorum* (Orthoptera: Tettigoniidae). *Can. Ent.* **104**, 977–985.
- PASQUINELLI F. and BUSNEL M.-C. (1954) Études préliminaires sur les mécanismes de la production des sons par les Orthoptères. In *Colloque sur l'Acoustique des Orthoptères* (Ed. by BUSNEL R.-G.), pp. 145–152. Inst. Rech. Agron., Paris.
- PIERCE G. W. (1948) *The Songs of Insects*. Harvard University Press, Cambridge, Mass.
- SUGA N. (1966) Ultrasonic production and its reception in some neotropical Tettigoniidae. *J. Insect Physiol.* **12**, 1039–1050.
- WALKER T. J. (1974) Effects of temperature on rates in poikilotherm nervous systems: evidence from the songs of meadow katydids (Orthoptera: Tettigoniidae: *Orchelimum*) and reanalysis of published data. *J. comp. Physiol.* In press.
- WALKER T. J., BRANDT J. F., and DEW D. (1970) Sound-synchronized, ultra-high-speed photography: a method for studying stridulation in crickets and katydids (Orthoptera). *Ann. ent. Soc. Am.* **63**, 910–912.
- WALKER T. J. and DEW D. (1972) Wing movements of calling katydids: fiddling finesse. *Science, Wash.* **178**, 174–176.
- WALKER T. J., WHITESELL J. J., and ALEXANDER R. D. (1973) The robust conehead: two widespread sibling species (Orthoptera: Tettigoniidae: *Neoconocephalus 'robustus'*). *Ohio J. Sci.* **73**, 321–330.