

## SHORT COMMUNICATIONS

LOCAL DIALECTS IN THE WINGFLAPS OF  
FLAPPET LARKS *MIRAFRA RUFOCINNAMOMEA*

Geographical variation in the song of birds has been known since the last century. Newton (1896: 893) commented, 'A curious question, which has as yet attracted but little attention, is whether the notes of the same species of Bird are in all countries alike. From my own observation I am inclined to think that they are not, and there exist "dialects", so to speak, of the song.' More recently it has been suggested that dialects, now known to be much more local in some species, are the result of habitat specializations (Nottebohm 1969, 1975), of cultural drift in non-dispersive populations (Thielcke 1970, Baker 1975) or of adaptive preferences among genetic races in mate choice (Nottebohm 1969, Baptista 1975, Baker 1975). Nottebohm (1975) found differences in vegetation structure that were related to song differences in a South American emberizid and suggested that each song dialect may best be heard by conspecifics in its local habitat. Dialects also may involve behavioural adaptation to the social organization of a local population (Verner 1976, Payne & Payne 1977). Here I provide a limited test of these hypotheses of the ecological significance of display dialects among Flappet Larks *Mirafra rufocinnamomea*.

Observations were made at Lochinvar National Park, Zambia, within 10 km of 15° 50' S, 27° 15' E, from February to April in 1973 and 1974, mainly in 1974, the driest year of five years of observation. The southern half of the park is open woodland, described by Douthwaite & van Lavieren (1973), and is surrounded by settled and intensively farmed land. Larks were almost entirely restricted to the park, where tall grass with scattered trees and shrubs were abundant. Recordings were made at 9.5 cm s<sup>-1</sup> with a Uher 4000-L tape recorder and M-516 microphone with a parabolic reflector, and were audiospectrographed with a Kay 3090-A Vibralyzer using the wide-band filter.

Flappet Larks display with a series of two to four bursts of flapping sounds in flight (Wickler 1967, Payne 1973, Seibt 1975). Larks apparently flap over their territories; the displaying birds circled repeatedly above areas no more than 200 m across (Payne 1973). Displays recorded at least 0.5 km apart were assumed to be made by different individuals, and displays within 0.5 km were counted as distinct only if more than one bird was heard and recorded at the same time. An attempt was made to tape all birds, but only about half of the displays heard were recorded successfully.

Examination of the spectrograms showed some variation among neighbouring birds at Lochinvar, in contrast to earlier reports based on smaller local samples (Payne 1973, Seibt 1975). All birds flapped at a rate of 24–25 notes per second within a phrase. Birds varied in the number of phrases, the number of flapping sounds per phrase, and in the time interval between phrases. Spectrograms showed no difference between displays, except in the number of notes in the terminal phrase of two birds. When displays varied, the longest was used for comparison.

Local dialects were readily apparent, larks in the eastern half of the park having three phrases of flapping notes in a display and birds in the west having two (compare Plate 9 and Fig. 1). Within each dialect area, neighbouring birds sometimes though not always were more similar to each other than to more remote birds. Birds most similar to each other included one twosome (*F* and *G*) that were within 200 m of each other in the field. In contrast, birds *A* and *B* and also birds *C* and *D* were not as similar as were each of these to another bird. A subdialect is apparent with the displays of *F*, *G* and *H*

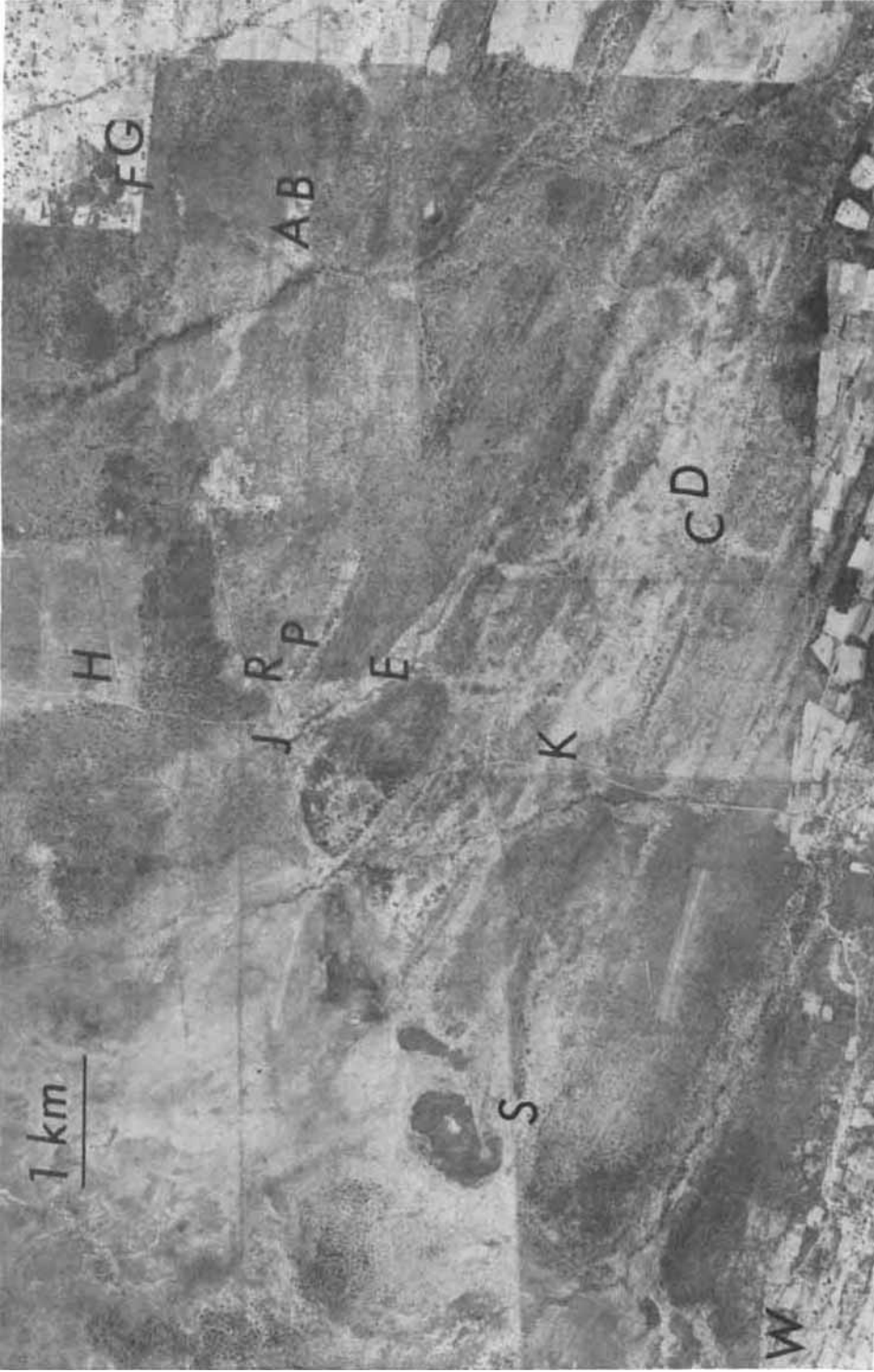


PLATE 9. Aerial photograph of the southern portion of Lochinvar National Park, Zambia, taken in 1969 or 1970. The areas of different shading represent different types of woodland and grassland vegetation and each shade corresponds closely to a vegetation type described by Douthwaite & van Laviercn (1973). Locations of 14 Flappet Larks are indicated by the letters.



more similar to each other than to the other eastern birds. These three were in the north-eastern woodland but were not all closer to each other than to all other birds.

Differences between the two display populations of Flappet Larks do not appear to be related to any barrier to dispersal. As shown by the aerial photograph (Plate 9) and the vegetation map of Lochinvar Park (Douthwaite & van Lavieren 1973), the land is flat, and the same open woodland types exist on both sides of the park in similar representation. In the eastern area, birds *A*, *B*, *C*, *D*, *E* and *Ƴ* all were within woodland type W8a, an open woodland with abundant scrubby *Acacia nilotica* and short annual grasses.

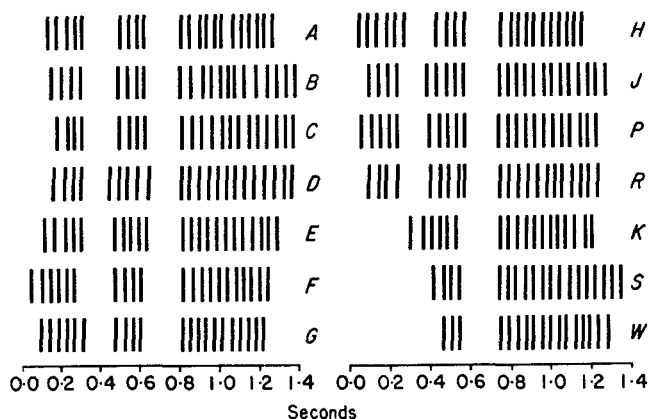


FIGURE 1. Wingflap displays of 14 Flappet Larks at Lochinvar National Park, Zambia. Temporal patterns of displays were traced from audiospectrograms.

*F* and *G* were in W4, *Acacia polycantha*; *R* was in W2, a mixed *Combretum-Pericopsis-Xeroderis* woodland; *P* in W3, a mixed *Combretum-Acacia* area; and *H* in W10, abandoned cultivation with invading scrubby *Acacia sieberana*. In the west, *K* was in W8a, *W* in W3, and *S* in W5, a woodland with much *Albizia harveyi*, mixed clumped perennial grasses, and dispersed annual grasses. Since the observers spent much time in the eastern W8a, the higher apparent frequentation of this vegetation type by the larks may reflect a sampling bias. Although the sample is too small for statistical comparison, the vegetation types where each bird was recorded clearly show overlap of habitats frequented in the two dialect areas and also a diversity of habitats frequented within a dialect area.

The eastern dialect is restricted to 10 km<sup>2</sup>. The terrain to the north is treeless floodplain with no larks; to the east and south of the park the heavily grazed and farmed land has no larks. The geographic limits of the western dialect were not determined; Flappet Larks probably occur west and southwest beyond the study area. The population in the eastern dialect area may be larger than observations indicate. It is known that Flappet Larks display less actively in the rains in February to April than during the drier months, when the birds breed (Benson *et al.* 1971).

Folse (1975) reported three male Flappet Larks (or pairs) per km<sup>2</sup> in open habitats in the Serengeti National Park, Tanzania; locally he found (pers. comm.) about 12/km<sup>2</sup> in the partly wooded areas near the Serengeti Research Institute (SRI) east of Seronera, and none in the treeless plains where most of his censuses were made. W. J. Maher (pers. comm.) censused two areas of Ruwenzori National Park, Uganda, and found 10 and 36/km<sup>2</sup>. At Lochinvar Park we tape-recorded fewer than 2/km<sup>2</sup>, but we heard larks at other locations, including three birds 1.2–1.6 km SW of *Ƴ* (all three had three-phrase displays). A rough estimate of Flappet Lark density at Lochinvar is 4/km<sup>2</sup>, suggesting about 40 pairs in the 10 km<sup>2</sup> area of the eastern dialect. This population seems rather small to be a genetically differentiated isolate (Lewontin 1974).

Character traits of flapping display are shared on a local level in other populations of Flappet Larks, and the results of other studies are consistent with those of Lochinvar. Bertram (1977) found similarities in the displays of neighbouring birds in Ruwenzori National Park, Uganda. Seibt (1975) described display differences in five localities in northern Tanzania and southern Kenya. Seibt's populations 4 and 5 were more than 40 km apart, population 3 was only 15 km from 2, but the latter was ecologically isolated as the intervening habitat was generally treeless and unsuitable for the larks (Herlocker 1974, my observations). Her populations 1 and 2 were as close as 10 km, with suitable open woodland extending between the areas (Herlocker 1974), but no birds were sampled in the intervening habitat. The difference in behaviour between Seibt's populations 1 and 2 suggests a population structure similar to that at Lochinvar Park, with very local dialects occurring even when nearby areas are not isolated by unsuitable habitat and where the habitats are similar.

The results allow some discussion of the hypotheses listed initially, in relation to the display dialects in this species. First, no one vegetation type is used within a dialect area and no obvious differences in vegetation occur between dialect areas. Thus habitat-specialization of birds for each dialect pattern seems unlikely. Second, the small population size argues against the existence of unique genetic adaptations of each population (Lewontin 1974). Third, non-directed drift among isolated populations, as proposed by Thielcke (1970) for other species, seems unlikely as no geographic barriers to dispersal exist between dialects. The observed social context of flap display together with the apparent lack of habitat differences and of presumed genetic differences between birds with different dialects do not support a racial model based on mate choice. The observations are however consistent with the idea that social interactions may maintain the display similarities among individuals living in the same area. The context of display is in agonistic male-male advertisement of a territory, with counterflapping among neighbouring males; when a male approaches a female he switches to a vocal song (Payne 1973). Perhaps there is an advantage in territorial establishment and maintenance gained by birds that copy the territorial advertisement pattern of established males, with a dialect restricted to the area that a few individuals could use economically. Rigorous testing of this hypothesis of social adaptation of dialects would involve repeated observations of known individuals.

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Museum of Zoology,  
University of Michigan,  
Ann Arbor, Michigan 48109,  
U.S.A.

R. B. PAYNE

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**DEPENDENCE OF FLEDGING SUCCESS ON EGG-SIZE,  
PARENTAL PERFORMANCE AND EGG-COMPOSITION AMONG  
COMMON AND ROSEATE TERNS, *STERNA HIRUNDO* AND  
*S. DOUGALLII***

In several species of birds, chicks hatching from large eggs have a higher probability of survival to fledging than those hatching from small eggs (Parsons 1970, 1975, Nisbet 1973, Schifferli 1973, Davis 1975). It has been debated whether this phenomenon is attributable to characteristics of the eggs, such as the larger lipid reserves in larger eggs (Parsons 1970), or to characteristics of the parents, such as the tendency for younger and less experienced parents to lay smaller eggs (Davis 1975). This paper reports egg-exchange experiments designed to investigate the relative roles of egg-size and parental performance in determining the survival and growth of chicks of Common and Roseate Terns, *Sterna hirundo* and *S. dougallii*.

FIELD STUDIES AND METHODS

The experiments were part of a series of studies conducted at Bird Island (41° 40' N, 70° 43' W) and Monomoy (41° 38' N, 69° 58' W), Massachusetts, U.S.A., between 1971 and 1976 (Table 1). Each study was conducted in a sample plot of 30-60 nests, fenced for ease of locating chicks (Nisbet & Drury 1972). Nests and eggs were marked when first seen and checked daily or almost daily until hatching. Eggs were weighed to the nearest 0.1 g soon after laying. For those not weighed on the day of laying, fresh weights were estimated using the measured rate of weight-loss (Rahn *et al.* 1976). Chicks were marked on the day of hatching and weighed daily or almost daily until they fledged or died. Predation was absent or negligible in each colony and most deaths were attributable to starvation.

The first, second, and third eggs in each clutch are denoted *A*, *B*, and *C* respectively. Common Terns usually lay two or three eggs, and Roseate Terns usually one or two. In each species the eggs hatch asynchronously and the older chicks survive much better