THE SONGFLIGHT OF THE LAPWING ON LUNDY

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ABSTRACT

The population of Lapwings *Vanellus vanellus* on Lundy Island was observed to determine the sequences of flight components in a typical songflight display. The sequence is found to be closely similar to that described by Dabelsteen (1977).

In addition, the units of song used in the display are shown to be closely linked to particular components of the flight, and an additional flight pattern thought to be associated with mate selection is described.

INTRODUCTION

The Lapwing *Vanellus vanellus* is one of the few birds that has been studied for its songflight. A plover, it, like most other waders, performs flight displays with both visual and acoustic elements during its breeding season (late March to early May).

Lind (1966) has hypothesised that songflight in waders has developed through a process of ritualisation from aggressive conflict behaviour, and is 'internally controlled' — one part of the flight leading on directly to the next.

Dabelsteen (1977), working in Tipperne, Denmark, analysed the flight patterns of a local Lapwing colony, and found that a typical flight would consist of several distinguishable components:

Butterfly flight (BF): Immediately after Take-off (possibly part of it), the bird flies slowly, close to the ground, with large wing beats, the wings being almost vertical at the extremes of the up and down-strokes. This form of flight is brief, lasting no more than five or six wing-beats.

Alternating Flight (AF): Four to five metres above the ground, the bird regularly twists its body to produce a zig-zag path, with short two or three metres ascent and rescent.

Low Flight (LF): Occurs at maximum one metre above the ground, with shallow, slow wing beats over varying distances, but sometimes for as far as fifty metres.

Ascent (AS): A rapid climb of about ten metres, with the body almost vertical.

High Flight (HF): Resembles alternating flight, with small dives and climbs, and some zig-zagging.

Vertical Dive (VD): The bird ascends slightly, revolves until one wing is pointing down, then, turning on its back, dives more or less vertically, revolving until the other wing points down, when it recovers and partly flies, partly glides for a few more metres.

These units usually formed a typical sequence of:

Take-off — BF — AF — LF — AS — HF — VD — AF — LF — etc., repeating the middle part until landing after the vertical dive or the subsequent alternating flight. In addition, during the AS — HF — VD section of flight the birds would sing, and Dabelsteen (1977) divided their song into three parts, or motifs.

The first motif consists of a shallow falling note, a rapid "ee-ee" and then a rising tone, separated by hoarse, wheezing sounds. The second motif is a loud "weet-weet", and the third is a two part, rising note "cheehweet".

Over a two year period the Lapwing population on Lundy was studied by students from Exeter University to verify Dabelsteen's analysis, and also to examine the links between the three song motifs and the flight units, to see if they were in fact tied to particular parts of the flight as he suggested, or whether they were just associated with the display as a whole. If each motif was reliably used in conjunction with a specific flight unit, then his conclusions concerning the ritualisation of the display could be supported, since the behaviour would be taking on the stereotyped appearance normally associated with such displays, or Fixed Action Patterns.

METHOD

Observations were made in two parts, firstly by P. Comyn and M. Parkinson, from 6th to 15th April, 1981 (under conditions of high wind and driving rain), and then by

Jon May and Sarah-Jane Hall, from the 1st to 5th April, 1982 (with rather fairer weather). Using 10 x 50 binoculars the behaviours of the birds in the Pondsbury area of the island (between Quarter Wall and Halfway Wall) were studied. The vocalisations made during flight were recorded, using a cardioid field directional microphone and a Marantz cassette recorder.

Pondsbury is largely moorland, about 100m above sea level, with fresh water marshes and run-off streams. The southern end is used by ponies and cattle for grazing towards evening, but otherwise the area is largely undisturbed except for the occasional rambler. The majority of Lapwing nests on the island are found there.

RESULTS

The flight of the Lapwings could be readily broken down into the units described by Dabelsteen, and tables 1a and 1b set out the combinations in which the units were observed.

TABLE ONE

Tables giving frequencies of binary sequences of flight units:

a) from Comyn & Parkinson, 1981:

	Second flight Unit:						
	BF	AF	AS	HF	VD	LF	Landing
First unit: Take off	12	0	5	x	x	2	0
BF	—	2	10	0	0	1	4
AF	2	—	1	0	8	0	4
AS	1	8	—	0	10	x	x
HF	0	0	x	—	0	x	x
VD	1	4	3	x	—	2	8
LF	1	1	1	x	x	—	2

b) from May & Hall, 1982:

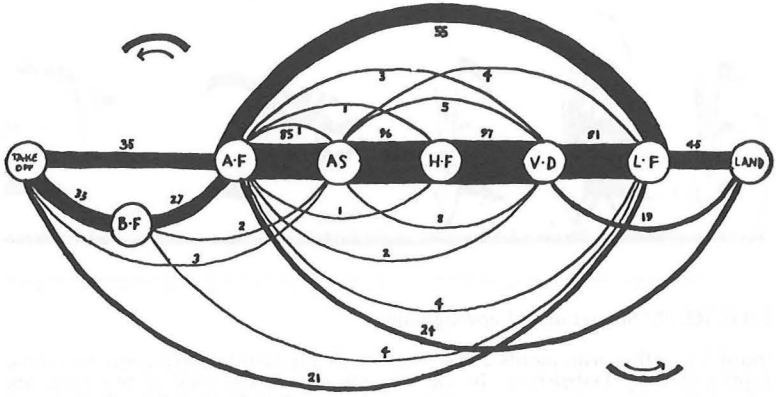
	Second flight Unit:						
	BF	AF	AS	HF	VD	LF	Landing
First unit: Take off	33	35	3	x	x	21	0
BF	—	27	2	0	0	4	0
AF	0	—	85	1	2	4	24
AS	0	1	—	96	8	x	x
HF	0	1	x	—	97	x	x
VD	0	3	5	x	—	81	19
LF	0	55	4	x	x	—	45

'x' represents a combination which is impossible by definition of the units, i.e. VD after LF

The flight sequences observed during 1982 corresponded quite closely to those described by Dabelsteen, the typical display being:

Take Off — BF — AF — AS — HF — VD — LF — etc., followed either by a landing or a repetition from AF onwards. The only differences are the omission of an LF before the ascent, and the substitution of LF for an AF after the dive. Figure 1 represents these combinations in a graphical form that makes the nature of this sequence clear.

FIGURE 1: Graphical represention of binary flight sequences



figures indicate frequencies of each binary sequence.

During the spring of 1981, when high winds persisted, a markedly different sequence was observed:

Take Off — BF — AS — AV — VD — landing frequently without the BF unit.

The song motifs described by Dabelsteen were also easily identified, and table 2 shows where in the flight display these motifs occurred. Motif 1 was usually emitted in the ascent, but sometime in alternating flight and occasionally in high flight. It

TABLE TWO **Associations of song motifs with flight units (May and Hall, 1982)**

	Flight Unit:					
	BF	AF	AS	HF	VD	LF
Song Motif: 1	0	18	43	8	0	1
2	0	0	1	46	1	0
3	0	0	0	0	48	0

could also occur singularly, without the second and third motifs. However, when the latter were emitted they always appeared together. Motif 2 was invariably sung in high flight, while motif 3 only occurred during the dive, the rising tone reaching a climax just before the bird entered low flight. The song of the Lapwing is therefore clearly associated with the most spectacular part of the flight display, the AS — HF — VD segment.

The tape recordings made of the song motifs were analysed using a Kay Elemetrics B/65 Sonogram, and two examples are shown in figures 2a and 2b. In 2a, the end of

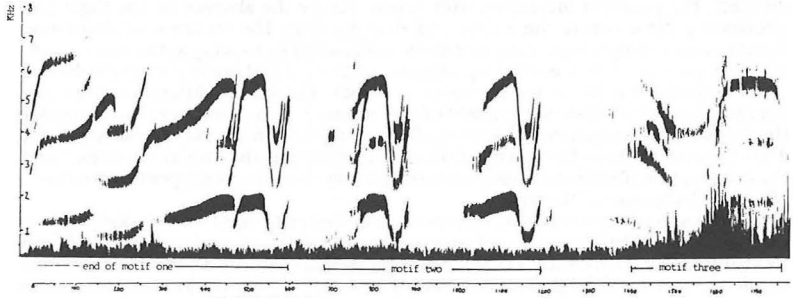


FIGURE 2a: Sonogram of Lapwing song

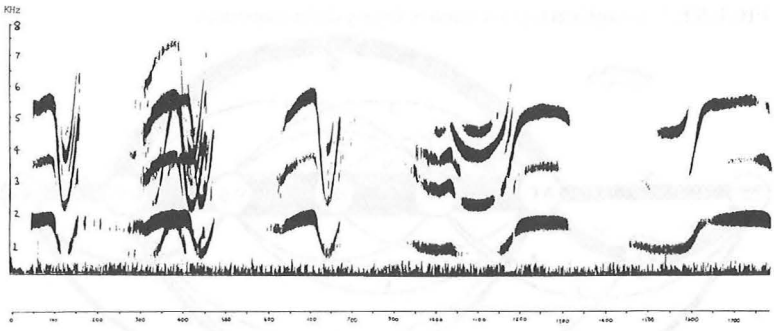


FIGURE 2b: Sonogram of Lapwing song

motif 1 together with motifs 2 and 3 can be clearly seen to correspond with those represented by Dabelsteen. In the example shown, the song of two birds are superimposed, and it was not possible to get an unadulterated sample of all of motif 1. Nevertheless, it can be seen that the final part of this motif, showing two plateaus and a rounded peak (between 150ms and 450ms), together with the appropriate harmonics, is similar to that described by Dabelsteen. Interestingly, just after this motif there appears a sound very much like the first part of motif 2 — however, close examination of the sound together with the other extraneous sounds early in the recording (which look like the end of another motif 1), forces the suggestion that these particular sounds were emitted by the other bird.

Figure 2b also shows two birds singing simultaneously, but motifs 2 and 3 are clearly visible.

DISCUSSION

In the second observation period, at least, the birds on Lundy were behaving in the same way as there counterparts in Denmark. A typical display would consist of the bird taking off into alternating flight (often via butterfly flight), zig-zagging and diving before a sharp ascent, towards the end of which it would sing motif 1, before levelling off into high flight. It would then sing motif 2, rise slightly then dive, twisting and singing motif 3, before finaly going into low flight, and then even landing or repeating the sequence from alternating flight onwards. Sometimes, though, the birds on Lundy would miss out various units of the flight, for instance omitting the high flight and ascending and diving, without singing.

The observations made during 1981, however, seem to be of a truncated version of the full sequence of behaviour. The most obvious explanation of this abbreviation is that the behaviour is modified by the strength of the wind on Lundy. In the conditions under which these observations were made, flight into the wind would be difficult, the problem increasing with height. Hence the absence of low flight and alternating flight before the ascent and after the dive. The presence of alternating flight instead of high flight can perhaps be understood by looking at the descriptions of these units — both contain a zig-zagging component and involve short climbs and dives (alternating flight to a greater amount), the major difference from the observer's point of view being height of performance. If the wind were too strong for the birds to fly to sufficient heights high flight would look much like alternating flight. That the birds were in fact having difficulty in performing the display is evident from the observation that birds usually landed after only one dive, not repeating the AS — HF — VD segment of the flight.

In both sets of observations, the omission of Butterfly flight on occasions may be due simply to its brief nature and occurrence close to the ground, which would limit its visibility from a distance. Dabelsteen suggests that it is more a part of take-off than a unit on its own, the large wing beats being necessary to provide the initial lift, and so it may have been of less consequence on Lundy, where there is usually a ground wind

to aid the birds. Dabelsteen also found that birds ascended from low flight and descended into alternating flight, whereas these observations suggest the opposite. This could be due merely to misinterpretation, low and alternating flight being similar, except for the revolving of the body that gives alternating flight its characteristic zig-zagging appearance. If the extent of revolving can vary, the zig-zagging effect could be reduced, and it is possible that small amounts of alternating flight could resemble low flight.

In addition to this songflight, another spectacular display was occasionally seen during the 1982 observations. Two birds would fly closely together, rarely more than a metre apart, in low flight, then simultaneously ascend to about twenty or thirty metres (higher than normal in songflight). There they would hover for a few seconds before diving apart in large semicircular swoops, meeting again to repeat the sequence (figure 3). Song motifs 1, 2 and 3 could be heard during the ascent, hovering and circling dives respectively, although motif 1 could also be heard during the hovering.

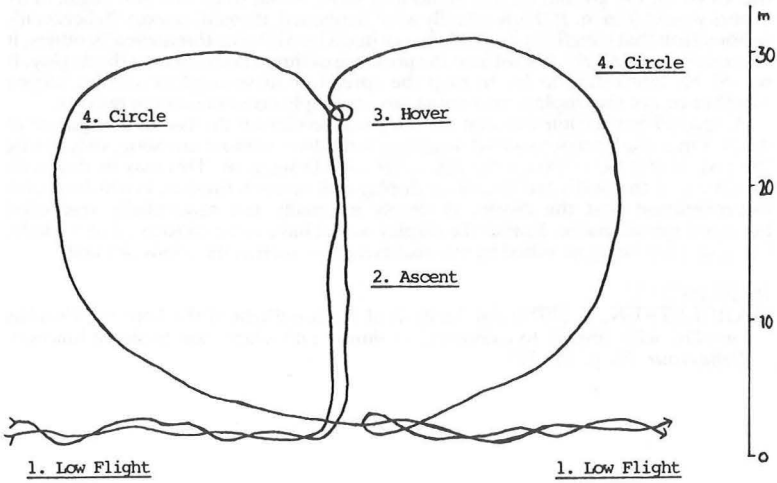


FIGURE 3: A courtship display?

Because of the distance at which these displays were observed, it was impossible to determine whether just one or both of the birds were singing. There remains, then, some doubt as to whether this was a courtship or perhaps a territorial display: Dabelsteen says that only male birds sing. If both birds were singing, then either the display would have to be territorial, or Dabelsteen wrong. However, if the display were territorial, it could be expected to occur primarily at the boundaries of territories, and to be enacted in a fairly constant area — but the display could last several minutes, and because of the wide circling and low flight, take place over a large area, much larger than the supposed extent of territories (a mean of 23.5m, according to the distances between nests found during 1981). Further, the birds had not, at the time of the 1982 observations, begun to lay eggs, and were still in the process of pairing, which would seem to make a courtship display the more likely interpretation. This hypothesis may be tested quite easily by examining the frequency of songflight throughout the breeding season in relation to the strength of the pair bond and subsequent breeding success. The former may be assessed by an examination of courtship behaviour up to egg-laying, while the latter may be quantified by calculating the ratio of eggs laid to chicks fledged.

There are not references to or descriptions of this flight pattern in other works on Lapwings, so it is possible that the display may be peculiar to Lundy.

The occurrence of motifs 1 and 2 with the hovering part of this display could be damaging to Dabelsteen's conclusions (which the observations otherwise support), namely that the songflight is self-regulatory, one unit leading onto the next in a fixed sequence, with the song more a part of the units themselves, rather than something extra the bird can do at the same time. That the units of flight are being used in a display which appears to be different to the song flight does not count against this view, since agonistic displays are frequently found to be associated with sexual behaviour, sometimes in modified forms, especially if the display is ritualised in the first place. The hovering itself may not be a new unit, however, but merely high flight directed into the wind — further observations, examining the orientation of the birds bodies with respect to the wind direction, could establish this.

There were two other tentative impressions that arose from the observations. One was that there would be long periods of inactivity, with no birds visible or audible in the air or on the ground for half an hour or more — but when one bird began to fly others would join in. If this is actually what happened, it could support Dabelsteen's supposition that songflight is agonistic — when a bird is being threatened by others, it responds aggressively, but without the presence of threat does not emit the display. It would be interesting to try to map the spread of these displays and investigate whether or not the displays are contagious, or simply occur in random fashion.

A second impression was that the song was louder on the last of a sequence of dives. On some occasions a bird would perform dives without any song, only to sing the last time it flew through the AS — HF — VD segment. This may be due to an intention on the bird's part to end the display well before it finishes, in which case the interpretation that the display is simply internally and sequentially controlled becomes questionable. Rather the display would have to be considered as a whole, the sequence being modified by external factors — such as the winds of Lundy.

REFERENCE

DABELSTEEN, T. (1978) An Analysis of the songflight of the Lapwing *Vanellus vanellus* with respect to causation, evolution and adaptation to signal function. *Behaviour, 66,* p. 136-178.